Introduction

**Historical Antecedents**
- Historical Developments in the Study of the Mind
- Historical Developments in the Study of Reflexes

**The Dawn of the Modern Era**
- Comparative Cognition and the Evolution of Intelligence
- Functional Neurology
- Animal Models of Human Behavior
- Animal Models and Drug Development
- Animal Models and Machine Learning

**The Definition of Learning**
- The Learning-Performance Distinction
- Learning and Other Sources of Behavior Change
- Learning and Levels of Analysis

**Methodological Aspects of the Study of Learning**
- Learning as an Experimental Science
- The General-Process Approach to the Study of Learning

**Use of Nonhuman Animals in Research on Learning**
- Rationale for the Use of Nonhuman Animals in Research on Learning
- Laboratory Animals and Normal Behavior
- Public Debate About Research with Nonhuman Animals

**SAMPLE QUESTIONS**

**KEY TERMS**
The goal of Chapter 1 is to introduce the reader to behavioral studies of learning. I begin by characterizing behavioral studies of learning and describing how these are related to cognition and the conscious control of behavior. I then describe the historical antecedents of key concepts in modern learning theory. This is followed by a discussion of the origins of contemporary experimental research in studies of the evolution of intelligence, functional neurology, and animal models of human behavior. I also discuss the implications of contemporary research for the development of memory-enhancing drugs and the construction of artificial intelligent systems or robots. I then provide a detailed definition of learning and discuss how learning can be examined at different levels of analysis. Methodological features of studies of learning are described in the next section. Because numerous experiments on learning have been performed with nonhuman animals, I conclude the chapter by discussing the rationale for the use of nonhuman animals in research, with comments about the public debate about animal research.

People have always been interested in understanding behavior, be it their own or the behavior of others. This interest is more than idle curiosity. Our quality of life depends on our actions and the actions of others. Any systematic effort to understand behavior must include consideration of what we learn and how we learn it. Numerous aspects of the behavior of both human and nonhuman animals are the results of learning. We learn to read, to write, and to count. We learn to walk down stairs without falling, to open doors, to ride a bicycle, and to swim. We also learn when to relax and when to become anxious. We learn what foods we are likely to enjoy and what foods will make us sick. We also learn the numerous subtle gestures that are involved in effective social interactions. Life is filled with activities and experiences that are shaped by what we have learned.

Learning is one of the biological processes that facilitate adaptation to one’s environment. The integrity of life depends on successfully accomplishing a number of biological functions such as respiration, digestion, and resisting disease. Physiological systems have evolved to accomplish these tasks. However, for many species, finely tuned physiological processes do not take care of all of the adaptive functions that are required, and even those that are fairly efficient are improved by learning (Domjan, 2005). For example, reproduction, which is central to the survival of a species, is significantly improved by learning.

Animals, including people, have to learn to find new food sources when old ones become unavailable or when they move to a new area. They also
have to find new shelter when storms destroy their old ones, as happened during Hurricane Katrina. Accomplishing these tasks obviously requires motor behavior, such as walking and manipulating objects. These tasks also require the ability to predict important events in the environment, such as when and where food will be available. All these things involve learning. Animals learn to go to a new water hole when their old one dries up and they learn to anticipate new sources of danger. These learned adjustments to the environment are as important as physiological processes such as respiration and digestion.

It is common to think about learning as involving the acquisition of new behavior. Indeed, learning is required before someone can read, ride a bicycle, or play a musical instrument. However, learning can just as well consist of the decrease or loss of a previously common response. A child, for example, may learn to not cross the street when the traffic light is red, to not grab food from someone else’s plate, and to not yell and shout when someone is trying to take a nap. Learning to withhold responses is just as important as learning to make responses.

When considering learning, we are likely to think about forms of learning that require special training, such as the learning that takes place in schools and colleges. Solving calculus problems or completing a triple somersault when diving requires special instruction. However, we also learn all kinds of things without an expert teacher or coach during the course of routine interactions with our social and physical environment. Children learn how to open doors and windows, what to do when the phone rings, when to avoid a hot stove, and when to duck so as not to get hit by a flying ball. College students learn how to find their way around campus, how to avoid heartburn from cafeteria food, and how to predict when a roommate will stay out late at night, all without special instruction.

In the coming chapters, I will describe research on the basic principles of learning and behavior. We will focus on basic types of learning and behavior that are fundamental to life but, like breathing, are often ignored. These pervasive and basic forms of learning are a normal (and often essential) part of daily life, even though they rarely command our attention. I will describe the learning of relationships between events in the environment, the learning of motor movements, and the learning of emotional reactions to stimuli. These forms of learning are investigated in experiments that involve conditioning or “training” procedures of various sorts. However, these forms of learning occur in the lives of human and nonhuman animals without explicit or organized instruction or schooling.

Much of the research that I will describe is in the behaviorist tradition of psychology that emphasizes analyzing behavior in terms of its antecedent stimuli and consequences. Conscious reflection and reasoning are deliberately left out of this analysis. I will describe automatic procedural learning that does not require awareness (e.g., Lieberman, Sumucks, & Kirk, 1998; Smith et al., 2005) rather than declarative or episodic learning that is more accessible to conscious report. One might argue that this restriction leaves out many interesting aspects of human behavior. However, social psychologists who have been examining these issues empirically have concluded that many important aspects of human behavior occur without awareness. Gosling, John, Craik, and Robins (1998), for example, found that people are relatively inaccurate in
reporting about their own behavior (see also Stone et al., 2000). Wegner (2002) summarized his research on the experience of conscious intent in a book whose title, *The illusion of conscious will*, says it all. Bargh and Chartrand (1999) similarly concluded that “most of a person’s everyday life is determined not by their conscious intentions and deliberate choices but by mental processes that are put into motion by features of the environment and that operate outside of conscious awareness and guidance (p. 462)” (See also Bargh & Morsella, 2008.)

The following chapters will describe how features of the environment gain the capacity to trigger our behavior whether we like it or not. This line of research has its origins in what has been called behavioral psychology. During the last quarter of the twentieth century, behavioral psychology was overshadowed by “the cognitive revolution.” However, the cognitive revolution did not eliminate the taste aversions that children learn when they get chemotherapy, it did not reduce the cravings that drug addicts experience when they see their friends getting high, and it did not stop the proverbial Pavlovian dog from salivating when it encountered a signal for food. Cognitive science did not grow by taking over the basic learning phenomena that are the focus of this book. Rather, it grew by extending psychology into new areas of research, such as attention, problem solving, and knowledge representation. For example, in one prominent contemporary textbook on cognition (Anderson, 2005), classical and instrumental conditioning are not even mentioned. However, as important as are the new topics of cognitive psychology, they do not tell us how good and bad habits and emotions are acquired or how they may be effectively modified.

Basic behavioral processes remain important in the lives of organisms even as we learn more about other aspects of psychology. In fact, there is a major resurgence of interest in the basic behavioral mechanisms. This resurgence of interest is fueled by the growing appreciation of the limited role of consciousness in behavior (e.g., Pockett, Banks, & Gallagher, 2006) and the recognition that much of what takes us through the day involves habitual responses that we spend little time thinking about (Wood, & Neal, 2007). We don’t think about how we brush our teeth, dry ourselves after a shower, put on our clothes, or chew our food. All of these are learned responses. Contemporary interest in behavior theory is also fueled by the tremendous growth of interest in the neural mechanisms of learning (Fanselow & Poulos, 2005). Animals interact with their environment through their actions. Therefore, behavioral phenomena provide the gold standard for assessing the functional significance of neural mechanisms. Behavioral models of conditioning and learning are also fundamental to the understanding of recalcitrant clinical problems such as pathological fears and phobias (Craske, Hermans, & Vansteenevagen, 2006), and drug addiction (Hyman, 2005; Hyman, Malenka, & Nestler, 2006; Olmstead, 2006). As Wiers and Stacy (2006) pointed out, “The problem, often, is not that substance abusers do not understand that the disadvantages of continued use outweigh the advantages; rather, they have difficulty resisting their automatically triggered impulses to use their substance of abuse” (p. 292). This book deals with how such behavioral impulses are learned.
HISTORICAL ANTECEDENTS

Theoretical approaches to the study of learning have their roots in the philosophy of René Descartes (see Figure 1.1). Before Descartes, most people thought of human behavior as entirely determined by conscious intent and free will. People’s actions were not considered to be controlled by external stimuli or mechanistic natural laws. What someone did was presumed to be the result of his or her will or deliberate intent. Descartes took exception to this view of human nature because he recognized that many things people do are automatic reactions to external stimuli. However, he was not prepared to entirely abandon the idea of free will and conscious control. He therefore formulated a dualistic view of human behavior known as Cartesian dualism.

According to Cartesian dualism, there are two classes of human behavior: involuntary and voluntary. Descartes proposed that involuntary behavior consists of automatic reactions to external stimuli and is mediated by a special mechanism called a reflex. Voluntary behavior, by contrast, does not have to be triggered by external stimuli and occurs because of the person’s conscious intent to act in that particular manner.

The details of Descartes’ dualistic view of human behavior are diagrammed in Figure 1.2. Let us first consider the mechanisms of involuntary, or reflexive,
behavior. Stimuli in the environment are detected by the person’s sense organs. The sensory information is then relayed to the brain through nerves. From the brain, the impetus for action is sent through nerves to the muscles that create the involuntary response. Thus, sensory input is reflected in response output. Hence, Descartes called involuntary behavior reflexive.

Several aspects of this system are noteworthy. Stimuli in the external environment are assumed to be the cause of all involuntary behavior. These stimuli produce involuntary responses by way of a neural circuit that includes the brain. However, Descartes assumed that only one set of nerves was involved. According to Descartes the same nerves transmitted information from the sense organs to the brain and from the brain down to the muscles. He believed this circuit permitted rapid reactions to external stimuli; for example, quick withdrawal of one’s finger from a hot stove.

Descartes assumed that the involuntary mechanism of behavior was the only one available to animals other than humans. According to this view, all of nonhuman animal behavior occurs as reflex responses to external stimuli. Thus, Descartes believed that nonhuman animals lacked free will and were incapable of voluntary, conscious action. He considered free will and voluntary behavior to be uniquely human attributes. This superiority of humans over other animals existed because only human beings were thought to have a mind, or soul.

The mind was assumed to be a nonphysical entity. Descartes believed that the mind was connected to the physical body by way of the pineal gland, near the brain. Because of this connection, the mind could be aware of and keep track of involuntary behavior. Through this mechanism, the mind could also initiate voluntary actions. Because voluntary behavior was initiated in the mind, it could occur independently of external stimulation.

The mind-body dualism introduced by Descartes stimulated two intellectual traditions. One, mentalism, was concerned with the contents and workings of the mind, while the other, reflexology, was concerned with the mechanisms of

**FIGURE 1.2**

Diagram of Cartesian dualism. Events in the physical world are detected by sense organs. From here the information is transmitted to the brain. The brain is connected to the mind by way of the pineal gland. Involuntary action is produced by a reflex arc that involves messages sent first from the sense organs to the brain and then from the brain to the muscles. Voluntary action is initiated by the mind, with messages sent to the brain and then the muscles.
reflexive behavior. These two intellectual traditions form the foundations of the modern study of learning.

**Historical Developments in the Study of the Mind**

Philosophers concerned with the mind were interested in what was in the mind and how the mind works. These questions are similar to those that preoccupy present day cognitive psychologists. Because Descartes thought the mind was connected to the brain by way of the pineal gland, he believed that some of the contents of the mind came from sense experiences. However, he also believed that the mind contained ideas that were innate and existed in all human beings independent of personal experience. For example, he believed that all humans were born with the concept of God, the concept of self, and certain fundamental axioms of geometry, such as the fact that the shortest distance between two points is a straight line. The philosophical approach that assumes we are born with innate ideas about certain things is called **nativism**.

Some philosophers after Descartes took issue with the nativist position. In particular, the British philosopher John Locke (1632–1704) believed that all the ideas people had were acquired directly or indirectly through experiences after birth. He believed that human beings were born without any preconceptions about the world. According to Locke, the mind started out as a clean slate (*tabula rasa*, in Latin), to be gradually filled with ideas and information as the person had various sense experiences. This philosophical approach to the contents of the mind is called **empiricism**. Empiricism was accepted by a group of British philosophers who lived from the seventeenth to the nineteenth centuries and who came to be known as the **British empiricists**.

The nativist and empiricist philosophers disagreed not only about what the mind was assumed to contain, but also on how the mind was assumed to operate. Descartes believed that the mind did not function in a predictable and orderly manner, according to strict rules or laws that one could identify. One of the first to propose an alternative to this position was the British philosopher Thomas Hobbes (1588–1679). Hobbes accepted the distinction between voluntary and involuntary behavior stated by Descartes and also accepted the notion that voluntary behavior was controlled by the mind. However, unlike Descartes, he believed that the mind operated just as predictably and lawfully as a reflex. More specifically, he proposed that voluntary behavior was governed by the principle of **hedonism**. According to this principle, people do things in the pursuit of pleasure and the avoidance of pain. Hobbes was not concerned with whether the pursuit of pleasure and the avoidance of pain were laudable or desirable. For Hobbes, hedonism was simply a fact of life. As we will see, the notion that behavior is controlled by positive and negative consequences has remained with us in one form or another to the present day.

According to the British empiricists, another important aspect of how the mind works involved the concept of **association**. Recall that empiricism assumes that all ideas originate from sense experiences. But how do our experiences of various colors, shapes, odors, and sounds allow us to arrive at more complex ideas? Consider, for example, the concept of a car. If someone says the word *car*, you have an idea of what the thing looks like, what it is used for, and how you might feel if you sat in it. Where do all these ideas come from given just the sound of the letters *c*, *a*, and *r*? The British empiricists
proposed that simple sensations were combined into more complex ideas by associations. Because you have heard the word *car* when you saw a car, considered using one to get to work, or sat in one, connections or associations became established between the word *car* and these other attributes of cars. Once the associations are established, the word *car* will activate memories of the other aspects of cars that you have experienced. The British empiricists considered such associations to be the building blocks of mental activity. Therefore, they devoted considerable effort to characterizing the rules of associations.

**Rules of Associations**

The British empiricists accepted two sets of rules for the establishment of associations: one primary and the other secondary. The primary rules were originally set forth by the ancient Greek philosopher Aristotle. He proposed three principles for the establishment of associations: 1) contiguity, 2) similarity, and 3) contrast. Of these, the contiguity principle has been the most prominent in studies of associations and continues to play an important role in contemporary work. It states that if two events repeatedly occur together in space or time, they will become associated. For example, if you encounter the smell of tomato sauce with spaghetti often enough, your memory of spaghetti will be activated by the smell of tomato sauce by itself. The similarity and contrast principles state that two things will become associated if they are similar in some respect (i.e., both are red) or have some contrasting characteristics (i.e., one might be strikingly tall and the other strikingly short). Similarity as a basis for the formation of associations has been confirmed by modern studies of learning (e.g., Rescorla & Furrow, 1977). However, there is no contemporary evidence that making one stimulus strikingly different from another (contrast) facilitates the formation of an association between them.

Various secondary laws of associations were set forth by a number of empiricist philosophers, among them, Thomas Brown (1778–1820). Brown proposed that a number of factors influence the formation of associations between two sensations. These include the intensity of the sensations, and how frequently or recently the sensations occurred together. In addition, the formation of an association between two events was considered to depend on the number of other associations in which each event was already involved, and the similarity of these past associations to the current one being formed.

The British empiricists discussed rules of association as a part of their philosophical discourse. They did not perform experiments to determine whether or not the rules were valid, nor did they attempt to determine the circumstances in which one rule was more important than another. Empirical investigation of the mechanisms of associations did not begin until the pioneering work of the nineteenth-century German psychologist Hermann Ebbinghaus (1850–1909).

To study how associations are formed, Ebbinghaus invented **nonsense syllables**. Nonsense syllables are three-letter combinations (*bap*, for example), devoid of any meaning that might influence how someone might react to them. Ebbinghaus used himself as the experimental subject. He studied lists of nonsense syllables and measured his ability to remember them under various...
experimental conditions. This general method enabled him to answer such questions as how the strength of an association improved with increased training, whether nonsense syllables that appeared close together in a list were associated more strongly with one another than syllables that were farther apart, and whether a syllable became more strongly associated with the next one on the list than with the preceding one. Many of the issues that were addressed by the British empiricists and Ebbinghaus have their counterparts in modern studies of learning and memory.

**Historical Developments in the Study of Reflexes**

Descartes made a very significant contribution to the understanding of behavior when he formulated the concept of the reflex. The basic idea that behavior can reflect a triggering stimulus remains an important building block of behavior theory. However, Descartes was mistaken in his beliefs about the details of reflex action. He believed that sensory messages going from sense organs to the brain and motor messages going from the brain to the muscles traveled along the same nerves. He thought that nerves were hollow tubes, and neural transmission involved gases called *animal spirits*. The animal spirits, released by the pineal gland, were assumed to flow through the neural tubes and enter the muscles, causing them to swell and create movement. Finally, Descartes considered all reflexive movements to be innate and to be fixed by the anatomy of the nervous system. Over the course of several hundred years, all of these ideas about reflexes were demonstrated to be incorrect.

Charles Bell (1774–1842) in England and Francois Magendie (1783–1855) in France showed that separate nerves are involved in the transmission of sensory information from sense organs to the central nervous system and motor information from the central nervous system to muscles. If a sensory nerve is cut, the animal remains capable of muscle movements; if a motor nerve is cut, the animal remains capable of registering sensory information.

The idea that animal spirits are involved in neural transmission was also disproved after the death of Descartes. In 1669, John Swammerdam (1637–1680) showed that mechanical irritation of a nerve was sufficient to produce a muscle contraction. Thus, infusion of animal spirits from the pineal gland was not necessary. In other studies, Francis Glisson (1597–1677) demonstrated that muscle contractions were not produced by swelling due to the infusion of a gas, as Descartes had postulated.

Descartes and most philosophers after him assumed that reflexes were responsible only for simple reactions to stimuli. The energy in a stimulus was thought to be translated directly into the energy of the elicited response by the neural connections. The more intense the stimulus was, the more vigorous the resulting response would be. This simple view of reflexes is consistent with many causal observations. If you touch a stove, for example, the hotter the stove, the more quickly you withdraw your finger. However, some reflexes are much more complicated.

The physiological processes responsible for reflex behavior became better understood in the nineteenth century, and that understanding stimulated broader conceptions of reflex action. Two Russian physiologists, I. M. Sechenov (1829–1905) and Ivan Pavlov (1849–1936), were primarily responsible for these
developments. Sechenov proposed that stimuli did not always elicit reflex responses directly. Rather, in some cases a stimulus could release a response from inhibition. Where a stimulus released a response from inhibition, the vigor of the response would not depend on the intensity of the stimulus. This simple idea opened up all sorts of new possibilities.

If the vigor of an elicited response does not invariably depend on the intensity of its triggering stimulus, it would be possible for a very faint stimulus to produce a large response. Small pieces of dust in the nose, for example, can cause a vigorous sneeze. Sechenov took advantage of this type of mechanism to provide a reflex model of voluntary behavior. He suggested that complex forms of behavior (actions or thoughts) that occurred in the absence of an obvious eliciting stimulus were in fact reflexive responses. It is just that, in these cases, the eliciting stimuli are so faint that we do not notice them. Thus, according to Sechenov, voluntary behavior and thoughts are actually elicited by inconspicuous, faint stimuli.

Sechenov’s ideas about voluntary behavior greatly extended the use of reflex mechanisms to explain a variety of aspects of behavior. However, his ideas were philosophical extrapolations from the actual research results he
obtained. In addition, Sechenov did not address the question of how reflex mechanisms can account for the fact that behavior is not fixed and invariant throughout an organism’s lifetime, but can be altered by experience. From the time of Descartes, reflex responses were considered to be innate and fixed by the connections of the nervous system. Reflexes were thought to depend on a prewired neural circuit connecting the sense organs to the relevant muscles. According to this view, a given stimulus could be expected to elicit the same response throughout an organism’s life. Although this is true in some cases, there are also many examples in which responses to stimuli change as a result of experience. Explanation of such cases by reflex processes had to await the experimental and theoretical work of Ivan Pavlov.

Pavlov showed experimentally that not all reflexes are innate. New reflexes to stimuli can be established through mechanisms of association. Thus, Pavlov’s role in the history of the study of reflexes is comparable to the role of Ebbinghaus in the study of the mind. Both were concerned with establishing the laws of associations through empirical research. However, Pavlov did this in the physiological tradition of reflexology rather than in the mentalistic tradition.

Much of modern behavior theory has been built on the reflex concept of stimulus-response, or S-R unit, and the concept associations. S-R units and associations continue to play prominent roles in contemporary behavior theory. However, these basic concepts have been elaborated and challenged over the years. As I will describe in later chapters, in addition to S-R units or connections, modern studies of learning have also demonstrated the existence of stimulus-stimulus (S-S) connection and modulatory, or hierarchical, associative structures (Schmajuk & Holland, 1998). Quantitative descriptions of learned behavior that do not employ associations have gained favor in some quarters (e.g., Gallistel & Gibbon, 2000, 2001; Leslie, 2001) and have been emphasized by contemporary scientists working in the Skinnerian tradition of behavioral analysis (e.g., Staddon, 2001). However, associative analyses continue to dominate behavior theory and provide the conceptual cornerstone for much of the research on the neural mechanisms of learning.

THE DAWN OF THE MODERN ERA

Experimental studies of basic principles of learning often are conducted with nonhuman animals and in the tradition of reflexology. Research in animal learning came to be pursued with great vigor starting a little more than a hundred years ago. Impetus for the research came from three primary sources (see Domjan, 1987). The first of these was interest in comparative cognition and the evolution of the mind. The second was interest in how the nervous system works (functional neurology), and the third was interest in developing animal models to study certain aspects of human behavior. As we will see in the ensuing chapters, comparative cognition, functional neurology, and animal models of human behavior continue to dominate contemporary research in learning.
Comparative Cognition and the Evolution of Intelligence

Interest in comparative cognition and the evolution of the mind was sparked by the writings of Charles Darwin (see Figure 1.4) who took Descartes’ ideas about human nature one step further. Descartes started chipping away at the age-old notion that human beings have a unique and privileged position in the animal kingdom by proposing that at least some aspects of human behavior (their reflexes) were animal-like. However, Descartes preserved some privilege for human beings by assuming that humans (and only humans) have a mind.

Darwin attacked this last vestige of privilege. In his second major work, *The Descent of Man and Selection in Relation to Sex*, Darwin argued that “man is descended from some lower form, notwithstanding that connecting-links have not hitherto been discovered” (Darwin, 1897, p. 146). In claiming continuity from nonhuman to human animals, Darwin attempted to characterize not only the evolution of physical traits, but also the evolution of psychological or mental abilities. He argued that the human mind is a product of evolution. In making this claim, Darwin did not deny that human beings had such mental abilities such as the capacity for wonder, curiosity, imitation,
attention, memory, reasoning, and aesthetic sensibility. Rather, he suggested that nonhuman animals also had these abilities. For example, he maintained that nonhuman animals were capable even of belief in spiritual agencies (Darwin, 1897, p. 95).

Darwin collected anecdotal evidence of various forms of intelligent behavior in animals in an effort to support his claims. Although the evidence was not compelling by modern standards, the research question was. Ever since, investigators have been captivated by the possibility of tracing the evolution of intelligence by studying the abilities of various species of animals.

Before one can investigate the evolution of intelligence in a systematic fashion, one must have a criterion for identifying intelligent behavior in animals. A highly influential proposal for a criterion was offered by George Romanes, in his book *Animal Intelligence* (Romanes, 1882). Romanes suggested that intelligence be identified by determining whether an animal learns “to make new adjustments, or to modify old ones, in accordance with the results of its own individual experience” (p. 4). Thus, Romanes defined intelligence in terms of the ability to learn. This definition was widely accepted by comparative psychologists at the end of the nineteenth and the start of the twentieth century and served to make the study of animal learning the key to obtaining information about the evolution of intelligence.

Only a subset of research on the mechanisms of animal learning has been concerned with the evolution of intelligence. Nevertheless, the cognitive abilities of nonhuman animals continue to fascinate both the lay public and the scientific community. In contemporary science, these issues are covered under the topic of “comparative cognition” or “comparative psychology” (e.g., Papini, 2008; Shettleworth, 1998). However, the connection to historical concerns is still evident, as in the title of a recent major text, *Comparative cognition: Experimental explorations of animal intelligence* (Wasserman & Zentall, 2006). We will discuss the results of contemporary research on comparative cognition in many chapters of this text, but especially in Chapters 11 and 12.

**Functional Neurology**

The modern era in the study of learning processes was also greatly stimulated by efforts to use studies of learning in nonhuman animals to gain insights into how the nervous system works. This line of research was initiated by the Russian physiologist Pavlov, quite independently of the work of Darwin, Romanes, and others interested in comparative cognition.

While still a medical student, Pavlov became committed to the principle of *nervism*. According to nervism, all key physiological functions are governed by the nervous system. Armed with this principle, Pavlov devoted his life to documenting how the nervous system controlled various aspects of physiology. Much of his work was devoted to identifying the neural mechanisms of digestion.

For many years, Pavlov’s research progressed according to plan. But, in 1902, two British investigators, Bayliss and Starling, published results showing that the pancreas, an important digestive organ, was partially under hormonal rather than neural control. Some time later, Pavlov’s friend and
The biographer noted that these novel findings produced a crisis in the laboratory because they “shook the very foundation of the teachings of the exclusive nervous regulation of the secretory activity of the digestive glands” (Babkin, 1949, p. 228).

The evidence of hormonal control of the pancreas presented Pavlov with a dilemma. If he continued his investigations of digestion, he would have to abandon his interest in the nervous system. On the other hand, if he maintained his commitment to nervism, he would have to stop studying digestive physiology. Nervism won out. In an effort to continue studying the nervous system, Pavlov changed from studying digestive physiology to studying the conditioning of reflexes. Thus, Pavlov regarded his studies of conditioning (which is a form of learning) as a way to obtain information about the functions of the nervous system: how the nervous system works. Pavlov’s claim that studies of learning tell us about the functions of the nervous system is well accepted by contemporary neuroscientists. Kandel, for example, has commented that “the central tenet of modern neural science is that all behavior is a reflection of brain function” (Kandel, Schwartz, & Jessell, 1991, p. 3).

The behavioral psychologist is like a driver who tries to find out about an experimental car by taking it out for a test drive instead of first looking under the hood. By driving the car, a driver can learn a great deal about how it functions. He or she can discover its acceleration, its top speed, the quality of its ride, its turning radius, and how quickly it comes to a stop. Driving the car will not reveal how these various functions are accomplished, but it will reveal the major functional characteristics of the internal machinery of the car.

Knowledge of the functional characteristics of a car can, in turn, provide clues about its internal machinery. For example, if the car accelerates sluggishly and never reaches high speeds, chances are it is not powered by a rocket engine. If the car only goes forward when facing downhill, it is probably propelled by gravity rather than by an engine. On the other hand, if the car cannot be made to come to a stop quickly, it may not have brakes.

In a similar manner, behavioral studies of learning can provide clues about the machinery of the nervous system. Such studies tell us about the kinds of plasticity the nervous system can exhibit, the conditions under which learning can take place, how long learned responses persist, and the circumstances under which learned information is accessible or inaccessible. By detailing the functions of the nervous system, behavioral studies of learning define the features or functions that have to be explained by neurophysiological investigations.

**Animal Models of Human Behavior**

The third major impetus for the modern era in the study of animal learning was the belief that research with nonhuman animals can provide information that may help us better understand human behavior. Animal models of human behavior are of more recent origin than comparative cognition or functional neurology. The approach was systematized by Dollard and Miller and their collaborators (Dollard, Miller, Doob, Mowrer, & Sears, 1939; Miller & Dollard, 1941), and developed further by B. F. Skinner (1953).

Drawing inferences about human behavior on the basis of research with other animal species can be hazardous and controversial. The inferences are
hazardous if they are unwarranted; they are controversial if the rationale for the model system approach is poorly understood. Model systems have been developed based on research with a variety of species, including several species of primates, pigeons, rats, and mice.

In generalizing from research with rats and pigeons to human behavior, one does not make the assumption that rats and pigeons are just like people. Animal models are used as we use other types of models. Architects, pharmacologists, medical scientists, and designers of automobiles all rely on models, which are often strikingly different from the real thing. Architects, for example, make small-scale models of buildings they are designing. Obviously, such models are not the same as a real building. The models are much smaller, made of cardboard and small pieces of wood instead of bricks and mortar, and they support little weight.

As Overmier (1999) pointed out, "Models are basic and powerful tools in science." Models are commonly used because they permit investigation of certain aspects of what they represent under conditions that are simpler, more easily controlled, and less expensive. With the use of a model, an architect can study the design of the exterior of a planned building without the expense of actual construction. The model can be used to determine what the building will look like from various vantage points and how it will appear relative to other nearby buildings. Studying a model in a design studio is much simpler than studying an actual building on a busy street corner. Factors that may get in the way of getting a good view, such as other buildings, traffic, and power lines, can be controlled and minimized in a model.

In a comparable fashion, a car designer can study the wind resistance of various design features of a new automobile with the use of a model in the form of a computer program. The program can be used to determine how the addition of spoilers or changes in the shape of the car will change its wind resistance. The computer model bears little resemblance to a real car. It has no tires or engine and cannot be driven. However, the model permits testing the wind resistance of a car design under conditions that are much simpler, better controlled, and less expensive than if the actual car were built and driven down the highway under various conditions.

Considering all the differences between a model and the real thing, what makes models valid for studying something? For a model to be valid, it must be comparable to its target referent in terms of the feature or function under study. This is called the relevant feature or relevant function. If the model of a building is used to study the building's exterior appearance, then all the exterior dimensions of the model must be proportional to the corresponding dimensions of the planned building. Other features of the model, such as its structural elements, are irrelevant. In contrast, if the model is used to study how well the building would withstand an earthquake, then its structural elements (beams and how they are connected) would be critical.

In a similar manner, the only thing relevant in a computer model of car wind resistance is that the computer program provides calculations for wind resistance that match the results obtained with real cars that are driven through real air. No other feature is relevant; therefore, the fact that the computer program lacks an engine or rubber tires is of no consequence.

The rationale and strategies associated with using nonhuman animals as models for human behavior are similar to those pertaining to models in other
areas of inquiry. Animal models permit investigating problems that are difficult, if not impossible, to study directly with people. A model permits the research to be carried out under circumstances that are simpler, better controlled, and less expensive. Furthermore, the validity of animal models is based on the same criterion as the validity of other types of models. The important thing is similarity between the animal model and human behavior in relevant features for the problem at hand. As Schuster pointed out, “The demonstration that animals would self-administer many drugs of abuse led to a major reformulation of the conceptual framework of the problem of drug addiction” (Schuster, 1999, p. xiii). The fact that the animals had long tails and walked on four legs instead of two was entirely irrelevant to the issue.

The critical task in constructing a successful animal model is to identify the relevant similarity between the animal model and the human behavior of interest. The relevant similarity concerns the causal factors that are responsible for particular forms of behavior (Overmier, 1999). We can gain insights into human behavior based on the study of nonhuman animals if the causal relations in the two species are similar. Because animal models are often used to push back the frontiers of knowledge, the correspondence between the animal findings and human behavior always must be carefully verified by empirical data. This interaction between animal and human research continues to make important contributions to our understanding of human behavior (e.g., Branch & Hackenberg, 1998; Delgado, Olsson, & Phelps, 2006; Gosling, 2001), and has also informed our understanding of the behavior of nonhuman animals (e.g., Escobar, Matute, & Miller, 2001; Miller & Matute, 1996).

Applications of learning principles got a special boost in the 1960s with the accelerated development of behavior therapy. As O’Donohue commented, “the model of moving from the learning laboratory to the clinic proved to be an extraordinarily rich paradigm. In the 1960s, numerous learning principles were shown to be relevant to clinical practice. Learning research quickly proved to be a productive source of ideas for developing treatments or etiological accounts of many problems” (1998, p. 4). This fervor was tempered during subsequent developments of cognitive behavior therapy. However, recent advances in learning theory have encouraged a return to learning explanations of important human problems such as panic disorder (Bouton, Mineka, & Barlow, 2001).

In the upcoming chapters, I will describe animal models of love and attachment, drug tolerance and addiction, food-aversion learning, learning of fears and phobias, and stress and coping, among others. Animal models have also led to the development of numerous procedures now commonly employed with people, such as biofeedback, programmed instruction, exposure therapy, token economies, and other techniques of behavior modification. I will provide examples of such applications at relevant points in the text. (For additional examples, see Carroll & Overmier, 2001; Haug & Whalen, 1999; Higgins, Heil, & Lussier, 2004; and Higgins, Silverman, & Heil, 2008.)

**Animal Models and Drug Development**

Whether we visit a doctor because we have a physical or psychiatric illness, we are likely to leave with a prescription to alleviate our symptoms. Pharma-
ceutical companies are eager to bring new drugs to the market and to develop drugs for symptoms that were previously handled in other ways (e.g., erectile dysfunction). Drug development is not possible without animal models. The animal learning paradigms described in this text are especially important for developing new drugs to enhance learning and cognition. As people live longer, cognitive decline with aging is becoming more prevalent, as is the demand for drugs to slow that decline. Animal models of learning and memory are playing a central role in the development of these new drugs. Animal models are also important for the development of antianxiety medications and drugs that facilitate the progress of behavior and cognitive therapy (e.g., Davis et al., 2005; Gold, 2008; Richardson, Ledgerwood, & Cranney, 2004). Another important area of research is evaluation of the potential for drug abuse associated with new medications for pain relief and other medical problems (e.g., Ator & Griffiths, 2003). Experiments with animals that evaluate drug abuse potential are advisable before these drugs are distributed for human use. Many of these experiments employ methods described in this book.

**Animal Models and Machine Learning**

Animal models of learning and behavior are also of considerable relevance to robotics and intelligent artificial systems (machine learning). Robots are machines that are able to perform particular functions or tasks. The goal in robotics is to make the machines as “smart” as possible. Just as Romanes defined “intelligence” in terms of the ability to learn, contemporary roboticists view the ability to remember and learn from experience an important feature of smart, artificial systems. Information about the characteristics and mechanisms of such learning may be gleaned from studies of learning in nonhuman animals (e.g., Gnadt & Grossberg, 2007; Schaal, et al., 2004). Associative mechanisms are frequently used in artificial intelligent systems to enable the response of those systems to be altered by experience. One prominent approach called “reinforcement learning” (Sutton & Barto, 1998; Prescott, Bryson, & Seth, 2007) tackles many of the same issues that arise in studies of instrumental conditioning, which we will discuss starting in Chapter 5.

**THE DEFINITION OF LEARNING**

Learning is such a common human experience that people rarely reflect on exactly what it means to say that something has been learned. A universally accepted definition of learning does not exist. However, many important aspects of learning are captured in the statement:

*Learning is an enduring change in the mechanisms of behavior involving specific stimuli and/or responses that results from prior experience with those or similar stimuli and responses.*

This definition has many important consequences for the study of learning. These implications are spelled out in the following sections.
The Learning-Performance Distinction
Whenever we see evidence of learning, we see the emergence of a change in behavior: the performance of a new response or the suppression of a response that occurred previously. A child becomes skilled in snapping the buckles of her sandals or becomes more patient in waiting for the popcorn to cook in the microwave oven. Such changes in behavior are the only way we can tell whether or not learning has occurred. However, notice that the preceding definition attributes learning to a change in the mechanisms of behavior, not to a change in behavior directly.

Why should we define learning in terms of a change in the mechanisms of behavior? The main reason is that behavior is determined by many factors in addition to learning. Consider, for example, eating. Whether you eat something depends on how hungry you are, how much effort is required to obtain the food, how much you like the food, and whether you know where to find food. Of all these factors, only the last one necessarily involves learning.

Performance refers to all of the actions of an organism at a particular time. Whether an animal does something or not (its performance) depends on many things. Even the occurrence of a simple response such as jumping into a swimming pool is multiply determined. Whether you jump depends on the availability, depth, temperature of the water, physical ability to spring away from the side of the pool, and so forth. Therefore, a change in performance cannot be automatically considered to reflect learning.

Learning is defined in terms of a change in the mechanisms of behavior to emphasize the distinction between learning and performance. The behavior of an organism (its performance) is used to provide evidence of learning. However, because performance is determined by many factors in addition to learning, one must be very careful in deciding whether a particular aspect of performance does or does not reflect learning. Sometimes evidence of learning cannot be obtained until special test procedures are introduced. Children, for example, learn a great deal about driving a car just by watching others drive, but this learning is not apparent until they are permitted behind the steering wheel. In other cases, a change in behavior is readily observed but cannot be attributed to learning because it does not last long enough or result from experience with specific environmental events.

Learning and Other Sources of Behavior Change
Several mechanisms produce changes in behavior that are too short–lasting to be considered instances of learning. One such process is fatigue. Physical exertion may result in a gradual reduction in the vigor of a response because the individual becomes tired. This type of change is produced by experience. However, it is not considered an instance of learning, because the decline in responding disappears if the individual is allowed to rest for a while.

Behavior also may be temporarily altered by a change in stimulus conditions. If the house lights in a movie theater suddenly come on in the middle of the show, the behavior of the audience is likely to change dramatically. However, this is not an instance of learning, because the audience is likely to return to watching the movie when the house lights are turned off again.

Other short-term changes in behavior that are not considered learning involve alterations in the physiological or motivational state of the organism.
Hunger and thirst induce responses that are not observed at other times. Changes in the level of sex hormones cause changes in responsiveness to sexual stimuli. Short-lasting behavioral effects may also accompany the administration of psychoactive drugs.

In some cases persistent changes in behavior occur, but without the type of experience with environmental events that satisfies the definition of learning. The most obvious example of this is maturation. A child cannot get something from a high shelf until he grows tall enough. However, the change in behavior in this case is not an instance of learning because it occurs with the mere passage of time. The child does not have to be trained to reach high places as he becomes taller. Maturation can also result in the disappearance of certain responses. For example, shortly after birth, touching an infant’s feet results in foot movements that resemble walking, and stroking the bottom of the foot causes the toes to fan out. Both of these reflexes disappear as the infant gets older.

Generally, the distinction between learning and maturation is based on the importance of special experiences in producing the behavior change of interest. However, the distinction is blurred in cases where environmental stimulation is necessary for maturational development. Experiments with cats, for example, have shown that the visual system will not develop sufficiently to permit perception of horizontal lines unless the cats were exposed to such stimuli early in life (e.g., Blakemore & Cooper, 1970). The appearance of sexual behavior at puberty also depends on developmental experience. In particular, successful sexual behavior requires experience with playmates before puberty (e.g., Harlow, 1969).

**Learning and Levels of Analysis**

Because of its critical importance in everyday life, learning is being studied at many different levels of analysis (Byrne, 2008). Some of these are illustrated in Figure 1.5. Our emphasis will be on analyses of learning at the level

[Figure 1.5]

Levels of analysis of learning. Learning mechanisms may be investigated at the organism level, at the level of neural circuits and transmitter systems, and at the level of nerve cells or neurons.
of behavior. The behavioral level of analysis is rooted in the conviction that the function of learning is to facilitate an organism’s interactions with its environment. We interact with our environment primarily through our actions. Therefore, the behavioral level of analysis occupies a cardinal position.

Much research on learning these days is also being conducted at the level of neural mechanisms. This interest has been stimulated by tremendous methodological and technical advances that permit scientists to directly examine biological processes that previously were only hypothetical possibilities. The neural mechanisms involved in learning may be examined at the systems level that is concerned with how neural circuits and neurotransmitter systems are organized to produce learned responses. Neural mechanisms may also be examined at the level of individual neurons and synapses, with an emphasis on molecular and cellular mechanisms, including genetic mechanisms. Advances in the neural mechanisms of learning at several levels of analysis are described in boxes that appear throughout the text.

Periodically, we will also describe changes in learning that occur as a function of age. These are referred to as developmental changes. It is also useful to consider the adaptive significance of learning. Conceptually, adaptive significance refers to the contribution of a process to evolution. Practically, the basic measure of adaptive significance is how successful an organism is in reproducing and leaving healthy offspring behind. Most scientists would agree that learning mechanisms evolved because they increase reproductive fitness. The contribution of learning to reproductive fitness is often indirect. By learning to find food more efficiently, for example, an organism may live longer and have more offspring. However, studies of sexual conditioning have shown that learning can also facilitate the physiological and behavioral processes involved in reproduction and directly increase fertility (Matthews et al., 2007; Hollis et al., 1997).

METHODOLOGICAL ASPECTS OF THE STUDY OF LEARNING

There are two prominent methodological features of studies of learning. The first of these is a direct consequence of the definition of learning and involves the exclusive use of experimental—as contrasted with observational—research methods. The phenomena of learning simply cannot be investigated without the use of an experimental methodology. The second methodological feature is reliance on a general-process approach. Reliance on a general-process approach is more a matter of intellectual style than a matter of necessity.

Learning as an Experimental Science

Studies of learning focus on identifying how prior experience causes long-term changes in behavior. At the behavioral level, this boils down to identifying the critical components of training or conditioning protocols. The emphasis on identifying causal variables necessitates an experimental approach.

Consider the following example. Mary goes into a dark room. She quickly turns on a switch near the door and the lights in the room go on.
Can you conclude that turning on the switch “caused” the lights to go on? Not from the information provided. Perhaps the lights were on an automatic timer and would have come on without Mary’s actions. Alternatively, the door may have had a built-in switch that turned on the lights after a slight delay. Or, there may have been a motion detector in the room that activated the lights.

How could you determine that manipulation of the wall switch caused the lights to go on? You would have to test various scenarios to prove the causal model. For example, you might ask Mary to enter the room again, but ask her not to turn on the wall switch. If the lights did not go on under these circumstances, certain causal hypotheses could be rejected. You could conclude that the lights were not turned on by a motion detector or by a switch built into the door. As this simple example illustrates, an experiment has to be conducted in which the presumed cause is removed in order to identify a cause. The results obtained with and without the presumed cause can then be compared.

In the study of learning, the behavior of living organisms is of interest, not the behavior of lights. But, scientists have to proceed in a similar fashion. They have to conduct experiments in which behavior is observed with and without the presumed cause. The most basic question is to identify whether a training procedure produces a particular type of learning effect. To answer this question, individuals who previously received the training procedure have to be compared to individuals who did not receive that training. This requires experimentally varying the presence and absence of the training experience. Because of this, learning can be investigated only with experimental techniques. This makes the study of learning primarily a laboratory science.

The necessity of using experimental techniques to investigate learning is not adequately appreciated by allied scientists. Many aspects of behavior can be studied with observational procedures that do not involve experimental manipulations of the presumed causes of the behavior. For example, observational studies can provide a great deal of information about whether and how animals set up territories, the manner in which they defend those territories, the activities involved in the courtship and sexual behavior of a species, the ways in which animals raise their offspring, and the changes in the activities of the offspring as they mature.

Fascinating information has been obtained with observational techniques that involve minimal intrusion into the ongoing activities of the animals. Unfortunately, learning cannot be studied that way. To be sure that the changes in behavior are not due to changes in motivation, sensory development, hormonal fluctuations, or other possible non-learning mechanisms, it is necessary to conduct experiments in which the presumed training experiences are systematically manipulated. The basic learning experiment compares two groups of subjects (see Figure 1.6). The experimental group receives the training procedure of interest, and how this procedure changes behavior is measured. The performance of the experimental group is compared to a control group that does not receive the training procedure but is otherwise treated in a similar fashion. Learning is presumed to have taken place if the experimental group responds differently from the control group. A similar rationale can be used to study learning in a single individual provided that one can be certain that the behavior is stable in the absence of a training intervention.
The General-Process Approach to the Study of Learning

The second prominent methodological feature of studies of learning is the use of a general-process approach. In adopting a general-process approach, investigators of animal learning are following a long-standing tradition in science.

Elements of the General-Process Approach

The most obvious feature of nature is its diversity. Consider, for example, the splendid variety of minerals that exist in the world. Some are soft, some are hard, some are brilliant in appearance, others are dull, and so on. Plants and animals also exist in many different shapes and sizes. Dynamic properties of objects are diverse. Some things float up, whereas others rapidly drop to the ground; some remain still; others remain in motion.

In studying nature, one can either focus on differences or try to ignore the differences and search for commonalities. Scientists ranging from physicists to chemists, from biologists to psychologists, have all elected to search for commonalities. Rather than being overwhelmed by the tremendous diversity in nature, scientists have opted to look for uniformities. They have attempted to formulate general laws with which to organize and explain the diversity of events in the universe. Investigators of animal learning have followed this well-established tradition.

Whether or not general laws are discovered often depends on the level of analysis that is pursued. The diversity of the phenomena scientists try to understand and organize makes it difficult to formulate general laws at the level of the observed phenomena. It is difficult, for example, to discover the general laws that govern chemical reactions by simply documenting the nature of the chemicals involved in various reactions. Similarly, it is difficult to explain the diversity of species in the world by cataloging the features of various animals. Major progress in science comes from analyzing phenomena at a more elemental or molecular level. For example, by the nineteenth century, chemists knew many specific facts about what would happen when various chemicals were combined. However, a general account of chemical reactions had to
await the development of the periodic table of the elements, which organized chemical elements in terms of their constituent atomic components.

Investigators of conditioning and learning have been committed to the general-process approach from the inception of this field of psychology. They have focused on the commonalities of various instances of learning and have assumed that learning phenomena are products of elemental processes that operate in much the same way in different learning situations.

The commitment to a general-process approach guided Pavlov's work on functional neurology and conditioning. Commitment to a general-process approach to the study of learning is also evident in the writings of early comparative psychologists. For example, Darwin (1897) emphasized commonalities among species in cognitive functions: “My object...is to show that there is no fundamental difference between man and the higher mammals in their mental faculties” (p. 66). At the start of the twentieth century, Jacques Loeb (1900) pointed out that commonalities occur at the level of elemental processes: “Psychic phenomena...appear, invariably, as a function of an elemental process, namely the activity of associative memory” (p. 213). Another prominent comparative psychologist of the time, C. Lloyd Morgan, stated that elementary laws of association “are, we believe, universal laws” (Morgan, 1903, p. 219).

The assumption that “universal” elemental laws of association are responsible for learning phenomena does not deny the diversity of stimuli that different animals may learn about, the diversity of responses they may learn to perform, and species differences in rates of learning. The generality is assumed to exist in the rules or processes of learning, not in the contents or speed of learning. This idea was clearly expressed nearly a century ago by Edward Thorndike, one of the first prominent American psychologists who studied learning:

Formally, the crab, fish, turtle, dog, cat, monkey, and baby have very similar intellects and characters. All are systems of connections subject to change by the laws of exercise and effect. The differences are: first, in the concrete particular connections, in what stimulates the animal to response, what responses it makes, which stimulus connects with what response, and second, in the degree of ability to learn. (Thorndike, 1911, p. 280)

What an animal can learn (the stimuli, responses, and stimulus-response connections it learns about) varies from one species to another. Animals also differ in how fast they learn—in the degree of ability to learn. However, Thorndike assumed that the rules of learning were universal. We no longer share Thorndike’s view that these universal rules of learning are the “laws of exercise and effect.” However, contemporary scientists continue to adhere to the idea that universal rules of learning exist. The job of the learning psychologist is to discover those universal laws. (More about the work of Thorndike will follow in Chapter 5.)

**Methodological Implications of the General-Process Approach**

If we assume that universal rules of learning exist, then we should be able to discover those rules in any situation in which learning occurs. Thus, an important methodological implication of the general-process approach is that general rules of learning may be discovered by studying any species or
response system that exhibits learning. This implication has encouraged scientists to study learning in a small number of experimental situations. Investigators have converged on a few standard, or conventional, experimental paradigms. Most studies of learning are conducted in one of these paradigms. Figure 1.7, for example, shows an example of a pigeon in a standard Skinner box. I will describe other examples of standard experimental paradigms as I introduce various learning phenomena in future chapters.

Conventional experimental paradigms have been fine tuned over the years to fit well with the behavioral predispositions of the research animals. Because of these improvements, conventional experimental preparations permit laboratory study of reasonably naturalistic responses (Timberlake, 1990).

**Proof of the Generality of Learning Phenomena**

The generality of learning processes is not proven by adopting a general-process approach. Assuming the existence of common elemental learning processes is not the same as empirically demonstrating those commonalities. Direct empirical verification of the existence of common learning processes in a variety of situations remains necessary in effort to build a truly general account of how learning occurs.

The available evidence suggests that elementary principles of learning of the sort that will be described in this text have considerable generality (Papini, 2008). Most research on animal learning has been performed with pigeons, rats, and (to a much lesser extent) rabbits and monkeys. Similar forms of learning have been found with fish, hamsters, cats, dogs, human beings,
dolphins, and sea lions. In addition, some of the principles of learning observed with these vertebrate species also have been demonstrated in newts (Ellins, Cramer, & Martin, 1982); fruit flies (Cadieu, Ghadraoui, & Cadieu, 2000; Davis, 1996; Holliday & Hirsch, 1986); honeybees (Bitterman, 1988, 1996); terrestrial mollusks (Sahley, Rudy, & Gelperin, 1981; Ungless, 1998); wasps (Kaiser & De Jong, 1995), and various marine mollusks (Carew, Hawkins, & Kandel, 1983; Colwill, Goodrum, & Martin, 1997; Farley & Alkon, 1980; Rogers, Schiller, & Matzel, 1996; Susswein & Schwarz, 1983).

Examples of learning in diverse species provide support for the general-process approach. However, the evidence should be interpreted cautiously. With the exception of the extensive program of research on learning in honeybees conducted by Bitterman and his associates, the various invertebrate species in the studies I cited have been tested on a limited range of learning phenomena, and we do not know whether their learning was mediated by the same mechanisms that are responsible for analogous instances of learning in vertebrate species.

USE OF NONHUMAN ANIMALS IN RESEARCH ON LEARNING

Although the principles described in this book apply to people, many of the experiments we will be considering have been conducted with nonhuman animals. Numerous types of animals have been used. Many of the studies have been conducted with pigeons and laboratory rats and mice for both theoretical and methodological reasons.

Rationale for the Use of Nonhuman Animals in Research on Learning

As I have argued, experimental methods are needed to investigate learning phenomena. Experimental methods make it possible to attribute the acquisition of new behaviors to particular previous experiences. Such experimental control of past experience cannot always be achieved with the same degree of precision in studies with human participants as in studies with laboratory animals. With laboratory animals, scientists can study how strong emotional reactions are learned and how learning is involved in acquiring food, avoiding pain or distress, or finding potential sexual partners. With people, investigators are limited to trying to modify maladaptive emotional responses after such responses have been already acquired. However, even the development of successful therapeutic procedures for the treatment of maladaptive emotional responses has required knowledge of how such emotional responses are learned in the first place—knowledge that required studies with laboratory animals.

Knowledge of the evolution and biological bases of learning also cannot be obtained without the use of nonhuman animals in research. How cognition and intelligence evolved is one of the fundamental questions about human nature. The answer to this question will shape our view of human nature, just as knowledge of the solar system has shaped our view of the place of mother Earth in the universe. As I have discussed, investigation of the evolution of cognition and intelligence rests heavily on studies of learning in nonhuman animals.
Knowledge of the neurobiological bases of learning may not change our views of human nature, but it is apt to yield important dividends in the treatment of learning and memory disorders. Such knowledge also rests heavily on research with laboratory animals. The kind of detailed investigations that are necessary to unravel how the nervous system learns and remembers simply cannot be conducted with people. Studying the neurobiological bases of learning first requires documenting the nature of learning processes at the behavioral level. Therefore, behavioral studies of learning in animals are a necessary prerequisite to any animal research on the biological bases of learning.

Laboratory animals also provide important conceptual advantages over people for studying learning processes. The processes of learning may be simpler in animals reared under controlled laboratory conditions than in people, whose backgrounds are more varied and often poorly documented. The behavior of nonhuman animals is not complicated by linguistic processes that have a prominent role in certain kinds of human behavior. Another important advantage is that demand characteristics are not involved in research with laboratory animals. In research with people, one has to make sure that the actions of the participants are not governed by their efforts to please, or displease, the experimenter. Such factors are not likely to determine what rats and pigeons do in an experiment.

Laboratory Animals and Normal Behavior

Some have suggested that domesticated strains of laboratory animals may not provide useful information because such animals have degenerated as a result of many generations of inbreeding and long periods of captivity (e.g., Lockard, 1968). However, this notion is probably mistaken. In an interesting test, Boice (1977) took five male and five female albino rats of a highly inbred laboratory stock and housed them in an outdoor pen in Missouri without artificial shelter. All ten rats survived the first winter with temperatures as low as −22°F. The animals reproduced normally and reached a stable population of about 50 members. Only three of the rats died before showing signs of old age during the two-year study period. Given the extreme climatic conditions, this level of survival is remarkable. Furthermore, the behavior of these domesticated rats in the outdoors was very similar to the behavior of wild rats observed in similar circumstances.

The results I will describe in this text should not be discounted simply because many of the experiments were conducted with domesticated animals. In fact, it may be suggested that laboratory animals are preferable in research to their wild counterparts. After all, most human beings live in what are largely “artificial” environments. Therefore, research may prove most relevant to human behavior if the research is carried out with domesticated animals that live in artificial laboratory situations. As Boice (1973) commented, “The domesticated rat may be a good model for domestic man” (p. 227).

Public Debate About Research with Nonhuman Animals

There has been much public debate about the pros and cons of research with nonhuman animals. Part of the debate has centered on the humane treatment of animals. Other aspects of the debate have centered on what constitutes
ethical treatment of animals, whether human beings have the right to benefit at the expense of animals, and possible alternatives to research with nonhuman animals.

**The Humane Treatment of Laboratory Animals**

Concern for the welfare of laboratory animals has resulted in the adoption of strict federal standards for animal housing and for the supervision of animal research. Some argue that these rules are needed because without them, scientists would disregard the welfare of the animals in their zeal to obtain research data. However, this argument ignores the fact that good science requires good animal care. Scientists, especially those studying behavior, must be concerned about the welfare of their research subjects. Information about normal learning and behavior cannot be obtained from diseased or disturbed animals. Investigators of animal learning must ensure the welfare of their subjects if they are to obtain useful scientific data.

Learning experiments sometimes involve discomfort. However, every effort is made to minimize the degree of discomfort. In studies of food reinforcement, for example, animals are food deprived before each experimental session to ensure their interest in food. However, the hunger imposed is no more severe than the hunger animals are likely to encounter in the wild, and often it is less severe (Poling, Nickel, & Alling, 1990).

The investigation of certain forms of learning and behavior require the administration of aversive stimulation. Important topics, such as punishment or the learning of fear and anxiety, cannot be studied without some discomfort to the participants. However, even in such cases, efforts are made to keep the discomfort to a minimum.

**What Constitutes the Ethical Treatment of Animals?**

Although making sure that animals serving in experiments are comfortable is in the best interests of the animals as well as the research, formulating general ethical principles is difficult. Animal rights cannot be identified in the way we identify human rights (Lansdell, 1988), and animals seem to have different rights under different circumstances.

Currently, substantial efforts are made to house laboratory animals in conditions that promote their health and comfort. However, a laboratory mouse or rat loses the protection afforded by federal standards when it escapes from the laboratory and takes up residence in the walls of the building (Herzog, 1988). The trapping and extermination of rodents in buildings is a common practice that has not been the subject of either public debate or restrictive federal regulation. Mites, fleas, and ticks are also animals, but we do not tolerate them in our hair or on our pets. Which species have the right to life, and under what circumstances do they have that right? Such questions defy simple answers.

Assuming that a species deserves treatment that meets government mandated standards, what should those standards be? Appropriate treatment of laboratory animals is sometimes described as being “humane treatment.” However, we have to be careful not to take this term literally. “Humane treatment” means treating someone as we would treat a human being. It is important to keep in mind that rats and other laboratory animals are not human beings. Rats prefer to live in dark burrows made of dirt that they never
clean. People, in contrast, prefer to live in well illuminated and frequently cleaned rooms. Laboratories typically have rats in well-lit rooms that are frequently cleaned. One cannot help but wonder whether these housing standards were dictated more by considering human rather than rat comfort.

**Should Human Beings Benefit From the Use of Animals?**

Part of the public debate about animal rights has been fueled by the argument that human beings have no right to benefit at the expense of animals; humans have no right to *exploit* animals. This argument goes far beyond issues concerning the use of animals in research. Therefore, I will not discuss the argument in detail here, except to point out that far fewer animals are used in research than are used for food, clothing, and recreation (hunting and fishing). In addition, a comprehensive count of human exploitation of animals has to include disruptions of habitats that occur whenever we build roads, housing developments, and factories. We should also add the millions of animals that are killed by insecticides and other pest-control efforts in agriculture and elsewhere.

**Alternatives to Research with Animals**

Increased awareness of ethical issues involved in the use of nonhuman animals in research has encouraged a search for alternative techniques. Some years ago, Russell and Burch (1959) formulated the “three Rs” for animal research: replacement of animals with other testing techniques, reducing the number of animals used with statistical techniques, and refining the experimental procedures to cause less suffering. Replacement strategies have been successful in the cosmetic industry and in the manufacture of certain vaccines and hormones (Murkerjee, 1997). However, as Gallup and Suarez (1985) pointed out, good research on learning processes cannot be conducted without experiments on live organisms, be they animal or human. Some alternatives that have been proposed have been the following.

1. *Observational techniques.* As I discussed earlier, learning processes cannot be investigated with unobtrusive observational techniques. Experimental manipulation of past experience is necessary in studies of learning. Therefore, field observations of undisturbed animals cannot yield information about the mechanisms of learning.

2. *Plants.* Learning cannot be investigated in plants because plants lack a nervous system, which is required for learning.

3. *Tissue cultures.* Although tissue cultures may reveal the operation of cellular processes, how these cellular processes operate in an intact organism can be discovered only by studying the intact organism. Furthermore, a search for cellular mechanisms of learning first requires characterizing learning at the behavioral level.

4. *Computer simulations.* Writing a computer program to simulate a natural phenomenon requires a great deal of knowledge about the phenomenon. In the case of learning, programmers would have to have precise and detailed information about the nature of learning phenomena and the mechanisms and factors that determine learning before they could create a successful computer simulation. The absence of such knowledge necessitates experimental research with live organisms. Thus, experimen-
tal research with live organisms is a prerequisite for effective computer simulations. For that reason, computer simulations cannot be used in place of experimental research.

Computer simulations serve many useful functions in science. Simulations are effective in showing us the implications of the experimental observations that have been already obtained, or showing the implications of various theoretical assumptions. They can help identify gaps in knowledge and can suggest important future lines of research. However, they cannot be used to generate new, previously unknown facts about behavior. That can only be done by studying live organisms.

Earlier in this chapter, we described a computer simulation to measure the wind resistance of various automobile designs. Why is it possible to construct a computer program to study wind resistance, but it is not possible to construct one to study learning processes? The critical difference is that we know a lot more about wind resistance than we know about learning. Wind resistance is determined by the laws of mechanics: laws that have been thoroughly explored since the days of Sir Isaac Newton. Application of those laws to wind resistance has received special attention in recent years, as aerodynamics has become an important factor in the design of cars.

Designing automobiles with low wind resistance is an engineering task. It involves the application of existing knowledge, rather than the discovery of new knowledge and new principles. Research on animal learning involves the discovery of new facts and new principles. It is science, not engineering. As Conn and Parker (1998) pointed out, “Scientists depend on computers for processing data that we already possess, but can’t use them to explore the unknown in the quest for new information.”

SAMPLE QUESTIONS

1. Describe how historical developments in the study of the mind contributed to the contemporary study of learning.
2. Describe Descartes’ conception of the reflex and how the concept of the reflex has changed since his time.
3. Describe the rationale for using animal models to study human behavior.
4. Describe the definition of learning and how learning is distinguished from other forms of behavior change.
5. Describe why learning can only be studied by using experimental methods.
6. Describe several alternatives to the use of animals in research and describe their advantages and disadvantages.

KEY TERMS

**association** A connection or linkage between the representations of two events (two stimuli or a stimulus and a response) so that the occurrence of one of the events activates the representation of the other.

**declarative or episodic learning** Learning about a specific event or fact, usually accessible to consciousness.
dualism  The view of behavior according to which actions can be separated into two categories: voluntary behavior controlled by the mind, and involuntary behavior controlled by reflex mechanisms.

empiricism  A philosophy according to which all ideas in the mind arise from experience.

fatigue  A temporary decrease in behavior caused by repeated or excessive use of the muscles involved in the behavior.

hedonism  The philosophy proposed by Hobbes according to which the actions of organisms are determined entirely by the pursuit of pleasure and the avoidance of pain.

learning  An enduring change in the mechanisms of behavior involving specific stimuli and/or responses that results from prior experience with similar stimuli and responses.

maturation  A change in behavior caused by physical or physiological development of the organism in the absence of experience with particular environmental events.

nativism  A philosophy according to which human beings are born with innate ideas.

nervism  The philosophical position adopted by Pavlov that all behavioral and physiological processes are regulated by the nervous system.

nonsense syllable  A three-letter combination (two consonants separated by a vowel) that has no meaning.

performance  An organism’s activities at a particular time.

procedural learning  Learning ways of doing things rather than learning about specific events. Procedural learning is typically not governed by conscious controlled processes.

reflex  A mechanism that enables a specific environmental event to elicit a specific response.
Elicited Behavior, Habituation, and Sensitization

The Nature of Elicited Behavior
- The Concept of the Reflex
- Modal Action Patterns
- Eliciting Stimuli for Modal Action Patterns
- The Sequential Organization of Behavior

Effects of Repeated Stimulation
- Salivation and Hedonic Ratings of Taste in People
- Visual Attention in Human Infants
- The Startle Response
- Sensitization and the Modulation of Elicited Behavior
- Adaptiveness and Pervasiveness of Habituation and Sensitization
- Habituation versus Sensory Adaptation and Response Fatigue

The Dual-Process Theory of Habituation and Sensitization
- Applications of the Dual-Process Theory
- Implications of the Dual-Process Theory
- Extensions to Emotions and Motivated Behavior
- Emotional Reactions and Their Aftereffects
- The Opponent Process Theory of Motivation

Concluding Comments

SAMPLE QUESTIONS
KEY TERMS
CHAPTER 2 • Elicited Behavior, Habituation, and Sensitization

CHAPTER PREVIEW

Chapter 2 begins the discussion of contemporary principles of learning and behavior with a description of modern research on elicited behavior—behavior that occurs in reaction to specific environmental stimuli. Many of the things we do are elicited by discrete stimuli, including some of the most extensively investigated forms of behavior. Elicited responses range from simple reflexes to more complex behavior sequences and complex emotional responses and goal-directed behavior. Interestingly, simple reflexive responses can be involved in the coordination of elaborate social interactions. Elicited responses are also involved in two of the most basic and common forms of behavioral change: habituation and sensitization. Habituation and sensitization are important to understand because they are potentially involved in all learning procedures. They modulate simple elicited responses like the eyeblink response and are also involved in the regulation of complex emotions and motivated behavior like drug addiction.

Is behavior totally flexible or is it subject to constraints set by the organism’s genetic history? This is an age-old question that has taken different forms during the course of intellectual history. One form of this question was the debate between the nativist position of René Descartes and the empiricist position of John Locke that was described in Chapter 1. Locke favored the view that experience and learning can shape behavior in virtually any direction. Descartes believed in innate contents of the mind, which in modern parlance suggests that the impact of learning is constrained by pre-existing behavior tendencies. The nativist/empiricist debate continues to this date (Pinker, 2002). The consensus emerging from modern behavioral neuroscience is that the nativists were closer to the truth than the empiricists. Behavior is not infinitely flexible, to move in any direction that a trainer may push it. Rather, organisms are born with pre-existing behavior systems and tendencies that set limits on how learning occurs and what the impact of learning can be.

The nativist position on learning was described elegantly by an analogy offered by Rachlin (1976), who compared learning to sculpting a wooden statue. The sculptor begins with a piece of wood that has little resemblance to a statue. As the carving proceeds, the piece of wood comes to look more and more like the final product. But, the process is not without limitation since the sculptor has to take into account the direction and density of the wood grain and any knots the wood may have. Wood carving is most successful if it is in harmony with the pre-existing structure of the wood. In a similar fashion, learning is most successful if it takes into account the pre-existing behavior structures of the organism. This chapter describes the most prominent of these pre-existing behavior structures.
THE NATURE OF ELICITED BEHAVIOR

All animals, whether they are single-celled paramecia or complex human beings, react to events in their environment. If something moves in the periphery of your vision, you are likely to turn your head in that direction. A particle of food in the mouth elicits salivation. Exposure to a bright light causes the pupils of the eyes to constrict. Touching a hot surface elicits a quick withdrawal response. Irritation of the respiratory passages causes sneezing and coughing. These and similar examples illustrate that much behavior occurs in response to stimuli. It is elicited.

Elicited behavior has been the subject of extensive investigation. Many of the chapters of this text deal, in one way or another, with responses to stimuli. We begin our discussion of elicited behavior by describing its simplest form: reflexive behavior.

The Concept of the Reflex

A light puff of air directed at the cornea makes the eye blink. A tap just below the knee causes the leg to kick. A loud noise causes a startle reaction. These are all examples of reflexes. A reflex involves two closely related events: an eliciting stimulus and a corresponding response. Furthermore, the stimulus and response are linked. Presentation of the stimulus is followed by the response, and the response rarely occurs in the absence of the stimulus. For example, dust in the nasal passages elicits sneezing, which does not occur in the absence of nasal irritation.

The specificity of the relation between a stimulus and its accompanying reflex response is a consequence of the organization of the nervous system. In vertebrates (including humans), simple reflexes are typically mediated by three neurons, as illustrated in Figure 2.1. The environmental stimulus for a

![Figure 2.1](image-url)

**Figure 2.1**

Neural organization of simple reflexes. The environmental stimulus for a reflex activates a sensory neuron, which transmits the sensory message to the spinal cord. Here, the neural impulses are relayed to an interneuron, which in turn relays the impulses to the motor neuron. The motor neuron activates muscles involved in movement.
reflex activates a sensory neuron (also called afferent neuron), which transmits the sensory message to the spinal cord. Here, the neural impulses are relayed to the motor neuron (also called efferent neuron), which activates the muscles involved in the reflex response. However, sensory and motor neurons rarely communicate directly. Rather, the impulses from one to the other are relayed through at least one interneuron. The neural circuitry ensures that particular sensory neurons are connected to a corresponding set of motor neurons. Because of this restricted “wiring,” a particular reflex response is elicited only by a restricted set of stimuli. The afferent neuron, interneuron, and efferent neuron together constitute the reflex arc.

The reflex arc in vertebrates represents the fewest neural connections necessary for reflex action. However, additional neural structures also may be involved in the elicitation of reflexes. For example, the sensory messages may be relayed to the brain, which in turn may modify the reflex reaction in various ways. I will discuss such effects later in the chapter. For now, it is sufficient to keep in mind that the occurrence of even simple reflexes can be influenced by higher nervous system activity.

Most reflexes contribute to the well-being of the organism in obvious ways. For example, in many animals, painful stimulation of one limb causes withdrawal, or flexion, of that limb and extension of the opposite limb (Hart, 1973). If a dog, for example, stubs a toe while walking, it will automatically withdraw that leg and simultaneously extend the opposite leg. This combination of responses removes the first leg from the source of pain and at the same time allows the animal to maintain balance.

Reflexes constitute much of the behavioral repertoire of newborn infants. If you touch an infant’s cheek with your finger, the baby will reflexively turn her head in that direction, with the result that your finger will fall in the baby’s mouth. This head-turning reflex probably evolved to facilitate finding the nipple. The sensation of an object in the mouth causes

**FIGURE 2.2**

reflexive sucking. The more closely the object resembles a nipple, the more vigorously the baby will suck.

Another important reflex, the *respiratory occlusion reflex*, is stimulated by a reduction of air flow to the baby, which can be caused by a cloth covering the baby’s face, or by the accumulation of mucus in the nasal passages. In response to the reduced air flow, the baby’s first reaction is to pull her head back. If this does not remove the eliciting stimulus, the baby will move her hands in a face-wiping motion. If this also fails to remove the eliciting stimulus, the baby will begin to cry. Crying involves vigorous expulsion of air, which may be sufficient to remove whatever was obstructing the air passages.

The respiratory occlusion reflex is obviously essential for survival. If the baby does not get enough air, he or she may suffocate. A problem arises, however, when the respiratory occlusion reflex is triggered during nursing. While nursing, the baby can get air only through the nose. If the mother presses the baby too close to the breast during feeding so that the baby’s nostrils are covered by the breast, the respiratory occlusion reflex will be triggered. The baby will attempt to pull her head back from the nipple, may move her hands in a face-wiping motion that pushes away the nipple, and may begin to cry. Successful nursing requires a bit of experience. The mother and child have to adjust their positions so that nursing can progress without stimulation of the respiratory occlusion reflex (Gunther, 1961). (See Figure 2.3.)

Interestingly, successful nursing involves reflex responses not only on the part of the infant, but also on the part of the mother. The availability of milk in the breast is determined by the milk-letdown reflex. During early stages of nursing, the milk-letdown reflex is triggered by the infant’s suckling behavior. However, after extensive nursing experience, the milk-letdown reflex can be
also stimulated by cues that reliably predict the infant’s suckling, such as the
time of day or the infant’s crying when he or she is hungry. Thus, successful
nursing involves an exquisite coordination of reflex activity on the part of
both the infant and the mother.

**Modal Action Patterns**

Simple reflex responses, such as pupillary constriction to a bright light and
startle reactions to a brief loud noise, are evident in many species. By con-
trast, other forms of elicited behavior occur in just one species or in a small
group of related species. For example, sucking in response to an object placed
in the mouth is a characteristic of mammalian infants. Herring-gull chicks are
just as dependent on parental feeding, but their feeding behavior is very dif-
ferent. When a parent gull returns to the nest from a foraging trip, the chicks
peck at the tip of the parent’s bill (see Figure 2.4). This causes the parent to
regurgitate. As the chicks continue to peck, they manage to get the parent’s
regurgitated food, and this provides their nourishment.

Response sequences, such as those involved in infant feeding, that are typi-
cal of a particular species are referred to as **modal action patterns** (MAPs)
(Baerends, 1988). Species-typical modal action patterns have been identified in
many aspects of animal behavior, including sexual behavior, territorial defense,
aggression, and prey capture. Ring doves, for example, begin their sexual be-
havior with a courtship interaction that culminates in the selection of a nest
site and the cooperative construction of the nest by the male and female. By
contrast, in the three-spined stickleback, a species of small fish, the male first
establishes a territory and constructs a nest. Females that enter the territory af-
after the nest has been built are then courted and induced to lay their eggs in the
nest. Once a female has deposited her eggs, she is chased away, leaving the
male stickleback to care for and defend the eggs until the offspring hatch.

![G. P. Baerends](image)

**FIGURE 2.4**

Feeding of herring-gull chicks. The chicks peck a red patch near the tip of the parent’s
bill, causing the parent to regurgitate food for them.
An important feature of modal action patterns is that the threshold for eliciting such activities varies (Cambi, 1984; Baerends, 1988). The same stimulus can have widely different effects depending on the physiological state of the animal and its recent actions. A male stickleback, for example, will not court a female who is ready to lay eggs until he has completed building his nest. And, after the female has deposited her eggs, the male will chase her away rather than court her as he did earlier. Furthermore, these sexual and territorial responses will only occur when environmental cues induce physiological changes that are characteristic of the breeding season in both males and females.

Modal action patterns were initially identified by ethologists, scientists interested in the study of the evolution of behavior. Early ethologists, such as Lorenz and Tinbergen, referred to species-specific action patterns as fixed action patterns to emphasize that the activities occurred pretty much the same way in all members of a species. However, subsequent detailed observations indicated that action patterns are not performed in exactly the same fashion each time. They are not strictly “fixed.” Because of this variability, the term modal action pattern is preferred now (Baerends, 1988).

Eliciting Stimuli for Modal Action Patterns

The eliciting stimulus is fairly easy to identify in the case of simple reflexes, such as the startle response to a brief loud noise. The stimulus responsible for a modal action pattern can be more difficult to isolate if the response occurs in the course of complex social interactions. For example, let us consider again the feeding of a herring-gull chick. To get fed, the chick has to peck the parent’s beak to stimulate the parent to regurgitate. But, exactly what stimulates the chick’s pecking response?

Pecking by the chicks may be elicited by the color, shape, or length of the parent’s bill, the noises the parent makes, the head movements of the parent, or some other stimulus. To isolate which of these stimuli elicits pecking, Tinbergen and Perdeck (1950) tested chicks with various artificial models instead of live adult gulls. From this research, they concluded that a model had to have several characteristics to strongly elicit pecking. It had to be a long, thin, moving object that was pointed downward and had a contrasting red patch near the tip. These experiments suggest that the yellow color of the adult’s bill, the shape and coloration of its head, and the noises it makes are all not required for eliciting pecking in the gull chicks. The specific features that were found to be required to elicit the pecking behavior are called, collectively, the sign stimulus, or releasing stimulus, for this behavior. Once a sign stimulus has been identified, it can be exaggerated to elicit an especially vigorous response. Such an exaggerated sign stimulus is called a supernormal stimulus.

Although sign stimuli were originally identified in studies with nonhuman subjects, sign stimuli also play a major role in the control of human behavior. Following a major disaster, post-traumatic stress disorder (PTSD) and fear and anxiety attendant to trauma are frequently in the news. Better understanding of PTSD requires knowledge about how people react to danger and how they learn from those experiences (Kirmayer, Lemelson, & Barad, 2007).

Responding effectively to danger has been critical in the evolutionary history of all animals, including human beings. Individuals who did not respond effectively to danger succumbed to the assault and did not pass their genes on
to future generations. Therefore, traumatic events have come to elicit strong
defensive modal action patterns. Vestiges of this evolutionary history are evi-
dent in laboratory studies showing that both children and adults detect
snakes faster than flowers, frogs, or other nonthreatening stimuli (e.g., LoBue
& DeLoache, 2008). Early components of the defensive action pattern include
the eyeblink reflex and the startle response. Because of their importance in de-
fensive behavior, we will discuss these reflexes later in this chapter as well as
in subsequent chapters.

Sign stimuli and supernormal stimuli also have a major role in social and
sexual behavior. Copulatory behavior involves a complex sequence of motor
responses that have to be elaborately coordinated with the behavior of one’s
sexual partner. The modal action patterns involved in sexual arousal and copu-
latory behavior are elicited by visual, olfactory, tactile, and other types of sign
stimuli that vary among different species. Visual, tactile, and olfactory stimuli
are all important in human social and sexual interactions. The cosmetic and
perfume industries are in business because they take advantage of the sign sti-
muli that elicit human social attraction and affiliation, and enhance these sti-
muli. Women put rouge on their lips rather than on their ears because only
rouge on the lips enhances the natural sign stimulus for human social attraction.
Plastic surgery to enhance the breasts and lips are also effective because
they enhance naturally occurring sign stimuli for human social behavior.

The studies of learning that we will be describing in this book are based
primarily on modal action patterns involved in eating, drinking, sexual be-
behavior, and defensive behavior.

**The Sequential Organization of Behavior**

Responses do not occur in isolation of one another. Rather, individual actions
are organized into functionally effective behavior sequences. To obtain food,
for example, a squirrel first has to look around for potential food sources,
such as a pecan tree with nuts. It then has to climb the tree and reach one of
the nuts. After obtaining the nut, it has to crack the shell, extract the meat,
and chew and swallow it. All motivated behavior, whether it is foraging for

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**BOX 2.1**

**The Learning of Instinct**

Because modal action patterns oc-
cur in a similar fashion among
members of a given species, they
include activities that are informally
categorized as *instinctive*. Instruc-
tive behavior is considered primarily
to reflect an individual’s genetic
history, leading to the impression
that modal action patterns are not
the product of learning and experi-
ence. However, the fact that all
members of a species exhibit similar
forms of behavior does not neces-
sarily mean that the behavior was
not learned through experience. As
Tinbergen (1951) recognized many
years ago, similar behavior on the
part of all members of a species may
reflect similar learning experiences.
In a more recent expression of this
sentiment, Baerends (1988) wrote
that “learning processes in many
variations are tools, so to speak,
that can be used in the building of
some segments in the species-
specific behavior organization” (p. 801). Thus, learning can be in-
volved in what we commonly refer
to as *instinctive* behaviors (Domjan,
food, finding a potential mate, defending a territory, or feeding one’s young, involves systematically organized sequences of actions. Ethologists called early components of a behavior sequence appetitive behavior and the end components consummatory behavior (Craig, 1918). The term consummatory was meant to convey the idea of consummation or completion of a species’ typical response sequence. In contrast, appetitive responses occur early in a behavior sequence and serve to bring the organism into contact with the stimuli that will release the consummatory behavior.

Chewing and swallowing are responses that complete activities involved in foraging for food. Hitting and biting an opponent are actions that consummate defensive behavior. Copulatory responses serve to complete the sexual behavior sequence. In general, consummatory responses are highly stereotyped species’ typical behaviors that have specific eliciting or releasing stimuli. In contrast, appetitive behaviors are less stereotyped and can take a variety of different forms depending on the situation (Tinbergen, 1951). In getting to a pecan tree, for example, a squirrel can run up one side or the other or jump from a neighboring tree. These are all possible appetitive responses leading up to actually eating the pecan nut. However, once the squirrel is ready to put the pecan meat in its mouth, the chewing and swallowing responses that it makes are fairly stereotyped.

As is evident from the varieties of ethnic cuisine, people of different cultures have many different ways of preparing food (appetitive behavior), but they all pretty much chew and swallow the same way (consummatory behavior). Actions that are considered to be rude and threatening (appetitive defensive responses) also differ from one culture to another. But, people hit and hurt one another (consummatory defensive behavior) in much the same way regardless of culture. Consummatory responses tend to be species-typical modal action patterns. In contrast, appetitive behaviors are more variable and more apt to be shaped by learning.

The sequential organization of naturally occurring behavior is of considerable importance to scientists interested in understanding how behavior is altered by learning because learning effects often depend on which component of the behavior sequence is being modified. As I will describe in later chapters, the outcomes of Pavlovian and instrumental conditioning depend on how these learning procedures modify the natural sequence of an organism’s behavior. Learning theorists are becoming increasingly aware of the importance of considering natural behavior sequences, and have expanded on the appetitive and consummatory distinction made by early ethologists (Domjan, 1997; Fanselow, 1997; Timberlake, 1994, 2001).

In considering how animals obtain food, for example, it is now common to characterize the foraging response sequence as starting with a general search mode, followed by a focal search mode, and ending with a food handling and ingestion mode. Thus, in modern learning theory, the appetitive response category has been subdivided into general search and focal search categories (e.g., Timberlake, 2001). General search responses occur when the subject does not yet know where to look for food. Before a squirrel has identified a pecan tree, it will move around looking for potential sources of food. General search responses are not spatially localized. Once the squirrel has found a pecan tree, however, it will switch to the focal search mode and begin to search for pecans only in that tree. Thus, focal search behavior is
characterized by considerable spatial specificity. Focal search behavior yields to food handling and ingestion (consummatory behavior) once a pecan nut has been obtained.

**EFFECTS OF REPEATED STIMULATION**

A common assumption is that an elicited response, particularly a simple reflex response, will automatically occur the same way every time the eliciting stimulus is presented. This is exactly what Descartes thought. In his view, reflexive behavior was unintelligent in the sense that it was automatic and invariant. According to the reflex mechanism Descartes proposed, each occurrence of the eliciting stimulus would produce the same reflex reaction because the energy of the eliciting stimulus was transferred to the motor response through a direct physical connection. If elicited behavior occurred the same way every time, it would be of limited interest, particularly for investigators of learning.

Contrary to Descartes, elicited behavior is not invariant. In fact, one of the most impressive features of elicited behavior is its plasticity. Even simple elicited responses do not occur the same way each time. Alterations in the nature of elicited behavior often occur simply as a result of repeated presentations of the eliciting stimulus. The following examples illustrate such results.

**Salivation and Hedonic Ratings of Taste in People**

The taste of food elicits salivation as a reflex response. This occurs as easily in people as in Pavlov’s dogs. In one study, salivation was measured in eight women in response to the taste of either lemon juice or lime juice (Epstein, Rodefer, Wisniewski, & Caggiula, 1992). A small amount of one of the flavors (.03 ml) was placed on the participant’s tongue on each of 10 trials. The participant was asked to rate how much she liked the taste on each trial, and salivation to each taste presentation was also measured. The results are summarized in Figure 2.5.

Salivation in response to the taste increased slightly from Trial 1 to Trial 2, but from Trial 2 to Trial 10, responding systematically decreased. A similar decrease was observed in hedonic ratings of the taste. Thus, as the taste stimulus was repeated 10 times, it became less effective in eliciting both salivation and hedonic responses. On Trial 11, the flavor of the taste was changed (to lime for participants that had been exposed to lemon, and to lemon for participants that had been previously exposed to lime). This produced a dramatic recovery in both the salivary reflex and the hedonic rating. (For similar results in a study with children, see Epstein et al., 2003.)

The results presented in Figure 2.5 are relatively simple but tell us a number of important things about the plasticity of elicited behavior. First, and most obviously, they tell us that elicited behavior is not invariant across repetitions of the eliciting stimulus. Both salivation and hedonic ratings decreased with repeated trials. In the case of salivation, the ultimate decline in responding was preceded by a brief increase from Trial 1 to Trial 2. The decline in responding that occurs with repeated presentation of a stimulus is called a **habituation effect**. Habituation is a prominent feature of elicited behavior that is evident in virtually all species and situations (Beck & Rankin, 1997).
Another prominent feature of the results presented in Figure 2.5 is that the decrease in responding was specific to the habituated stimulus. Individuals habituated to the taste of lemon showed invigorated responding when tested with the taste of lime at the end of the experiment (and vice versa). Thus, habituation was stimulus specific.

The stimulus specificity of habituation tells us that the subjects in this experiment could tell the difference between lemon and lime. That might not be an impressive finding, since we could have just as well asked the participants to tell us whether they could tell the difference between the two flavors. However, the stimulus specificity of habituation provides a powerful behavioral assay with individuals, such as infants, who cannot talk.

Although this was a rather simple experiment, it has interesting implications for how to present and prepare food. Chefs who expect to charge hefty prices for a gourmet dinner cannot afford to have people get bored with what they are eating within 10 bites, as occurred in this experiment. How, then, can such a habituation effect be avoided? The solution is to prepare and present food so that each bite provides a different flavor. The ingredients in a meal should not be mixed together into a homogeneous mass. Different ingredients should be kept separate to avoid having successive bites all taste the

**FIGURE 2.5**

Salivation and ratings of pleasantness in response to a taste stimulus (lime or lemon) repeatedly presented to women on Trials 1–10. The alternate taste was presented on Trial 11, causing a substantial recovery in responding. (After Epstein, Rodefer, Wisniewski & Caggiula, 1992).
same. On the other hand, if the goal is to reduce eating (as in a weight loss program), then variation in flavors should be discouraged. It is hard to resist going back to a buffet table given the variety of flavors that are offered, but rejecting a second helping of mashed potatoes is easy if the second helping tastes the same as the first. (For a study of the relation between habituation to taste and obesity, see Epstein et al., 2008.)

Another major variable that influences the rate of taste habituation is attention to the taste stimulus. In a fascinating study, children were tested for habituation to a taste stimulus while they were working on a problem that required their close attention. In another condition, either no distracting task was given or the task was so easy that it did not require much attention. Interestingly, if the children’s attention was diverted from the taste presentations, they showed much less habituation to the flavor (Epstein et al., 2005). This is a very important finding because it helps us understand why food tastes better and why people eat more if they are having dinner with friends or while watching TV. Having attention directed to non-food cues keeps the food from losing its flavor through habituation.

**Visual Attention in Human Infants**

Human infants have a lot to learn about the world. One way they obtain information is by looking at things. Visual cues elicit a looking response, which can be measured by how long the infant keeps his or her eyes on one object before shifting gaze elsewhere (see Figure 2.6).

In one study of visual attention (Bashinski, Werner, & Rudy, 1985; see also Kaplan, Werner, & Rudy, 1990), four-month-old infants were assigned to one of two groups, and each group was tested with a different visual stimulus. The stimuli are shown in the right panel of Figure 2.7. Both were check-
erboard patterns, but one had four squares on each side (the 4 x 4 stimulus) whereas the other had 12 squares on each side (the 12 x 12 stimulus). Each stimulus presentation lasted 10 seconds, and the stimuli were presented eight times at 10 second intervals.

Both stimuli elicited visual attention initially, with the babies spending an average of about 5.5 seconds looking at the stimuli. With repeated presentations of the 4 x 4 stimulus, visual attention progressively decreased, showing a habituation effect. By contrast, the 12 x 12 stimulus produced an initial sensitization effect, evident in increased looking during the second trial as compared to the first. But, after that, visual attention to the 12 x 12 stimulus also habituated.

This relatively simple experiment tells us a great deal about both visual attention, and habituation and sensitization. The results show that visual attention elicited by a novel stimulus changes as babies gain familiarity with the stimulus. The nature of the change is determined by the nature of the

---

**FIGURE 2.7**

Time infants spent looking at a visual stimulus during successive trials. For one group, the stimulus consisted of a 4 x 4 checkerboard pattern. For a second group, the stimulus consisted of a 12 x 12 checkerboard pattern. The stimuli are illustrated to the right of the results. (From “Determinants of Infant Visual Attention: Evidence for a Two-Process Theory,” by H. Bashinski, J. Werner, and J. Rudy, *Journal of Experimental Child Psychology*, 39, pp. 580–598. Copyright © 1985 by Academic Press. Reprinted by permission of Elsevier.)
stimulus. With a relatively simple 4 x 4 pattern, only a progressive habituation effect occurs. With a more complex 12 x 12 pattern, a transient sensitization occurs, followed by habituation. Thus, whether or not sensitization is observed depends on the complexity of the stimulus. With both stimuli, the infants eventually showed less interest as they became more familiar with the stimulus. It may be too harsh to say that familiarity bred contempt, but familiarity certainly did not elicit much interest. Interest in what appeared on the screen would have recovered if a new or different stimulus had been presented after familiarization with the first one.

Infants cannot tell us in words how they view or think about things. Scientists are therefore forced to use behavioral techniques to study infant perception and cognition. The visual attention task can provide information about visual acuity. For example, from the data in Figure 2.7, we may conclude that these infants were able to distinguish the two different checkerboard patterns. This type of habituation procedure has also been used to study a wide range of other, more complicated questions about infant cognition and perception. One recent study, for example, examined the way 3.5 month old infants perceive human faces.

Faces provide a great deal of information that is critical in interpersonal interactions. People are experts at recognizing and remembering faces, but they show better discrimination if the faces are of their own race than if the faces are from individuals of a different race. This effect is known as the other race effect. Hayden et al. (2007) sought to determine whether the other-race effect occurs in 3.5 month old infants. Two groups of Caucasian infants were tested using the visual habituation task. One group was shown a Caucasian face on successive trials until their attentional response decreased at least 50% of its initial level. The second group of infants received the same kind of procedure, but for them an Asian face was shown on each trial. Thus, during this phase, one group became familiar with a face of their own race (Caucasian), while the second group became familiar with a face of the alternate race (Asian).

The investigators then asked whether a small change in the familiar face would be detectable for the infants. To answer this question, a special test was conducted. The test involved presenting two faces. One of the two faces was the same as what the infants had seen before, and therefore was not expected to elicit much looking behavior. In contrast, the second face was created by morphing a familiar face with a face of the alternate race. The resultant image was 70% like the familiar face and 30% like the alternate race. If the infants could detect this small change in features, they were expected to show more looking behavior to the new face.

The results are shown in Figure 2.8. Infants who were familiarized with Caucasian faces showed the expected results. They increased their looking time when the new face was presented that had some features from the alternate race. This result did not occur with the infants who were familiarized with Asian faces. They did not increase their looking when a new face was introduced. The authors interpreted this result as showing that the infants were more skilled at detecting small changes in facial features when those changes were variations in their own race (Caucasian) than when those variations were in the features of another race (Asian). Thus, these findings suggest that the other-race effect occurs in infants as young as 3.5 months of age.
The visual attention paradigm has become a prominent tool in the study of infant perception as well as more complex forms of cognition. For example, it has been used to study whether infants are capable of rudimentary mathematical operations, reasoning about the laws of the physical world, and discrimination between drawings of objects that are physically possible vs. ones that are physically not possible (Baillargeon, 2008; McCrink & Wynn, 2007; Shuwairi, Albert, & Johnson, 2007). Some of this type of research has been called into serious question by those who emphasize that habituation of visual attention in infants and recovery from habituation reflect perceptual properties of the stimuli rather than their meaning within the knowledge structure of the infant (Schöner & Thelen, 2006). Regardless of how this controversy is resolved, there is no doubt that the visual attention paradigm has provided a wealth of information about infant cognition at ages that long precede the acquisition of language. This is just one example of how the behavioral techniques described in this book can be used to examine cognition in nonverbal organisms.

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<th>Familiarized with Caucasian faces</th>
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**FIGURE 2.8**
The other-race effect in Caucasian infants. After having been habituated to either a Caucasian or an Asian face, infants were tested with a familiar face and a novel one that had 30% features from the alternate race. (Based on Hayden et al., 2007.)
The Startle Response

As I mentioned earlier, the startle response is part of an organism’s defensive reaction to potential or actual attack. If someone unexpectedly blows a fog horn behind your back, you are likely to jump. This is the startle response. It consists of a sudden jump and tensing of the muscles of the upper part of the body, usually involving the raising of the shoulders. It also includes blinking of the eyes. The startle reaction can be measured by placing the subject on a surface that measures sudden movements. The startle response has been investigated extensively because of its role in fear and defensive behavior. Scientists interested in the neurobiology of fear, and the development of drugs that help alleviate fear, have often used the startle response as their behavioral anchor. Some of these studies have been conducted with primates, but in most of the studies, laboratory rats have been used as subjects.

Figure 2.9 shows a diagram of a stabilimeter chamber used to measure the startle response in rats. The chamber rests on pressure sensors. When startled, the rat jumps and thereby jiggles the chamber. These movements are measured by the pressure sensors under the chamber and are used as indicators of the vigor of the startle reaction.

The startle reaction can be elicited in rats by a variety of stimuli, including brief loud tones and bright lights. In one experiment (Leaton, 1976), the startle stimulus was a high pitched, loud tone presented for two seconds. The animals were first allowed to get used to the experimental chamber without any tone presentations. Each rat then received a single tone presentation once a day for 11 days. In the next phase of the experiment the tones were presented much more frequently (every three seconds) for a total of 300 trials.

Stabilimeter apparatus to measure the startle response of rats. A small chamber rests on pressure sensors. Sudden movements of the rat are detected by the pressure sensors and recorded on a computer.
Finally, the animals were given a single tone presentation on each of the next three days as in the beginning of the experiment.

Figure 2.10 shows the results. The most intense startle reaction was observed the first time the tone was presented. Progressively less intense reactions occurred during the next 10 days. Because the animals received only one tone presentation every 24 hours in this phase, the progressive decrements in responding indicated that the habituating effects of the stimulus presentations persisted throughout the 11-day period. It is worth noting, though, that this long-term habituation did not result in complete loss of the startle reflex. Even on the 11th day, the animals still reacted a little.

By contrast, startle reactions quickly ceased when the tone presentations occurred every three seconds in Phase 2 of the experiment. However, this dramatic loss of responsiveness was only temporary. In Phase 3 of the experiment, when trials were again administered just once each day, the startle response recovered to the level of the 11th day of the experiment. This recovery, known as spontaneous recovery, occurred simply because the tone had not been presented for a long time (24 hours).

FIGURE 2.10
This experiment illustrates that two different forms of habituation occur depending on the frequency of the stimulus presentations. If the stimuli are presented widely spaced in time, a long-term habituation effect occurs, which persists for 24 hours or longer. In contrast, if the stimuli are presented very closely in time (every three seconds in this experiment), a short-term habituation effect occurs. The short-term habituation effect is identified by spontaneous recovery of responding if a period without stimulation is introduced.

Repeated presentations of a stimulus do not always result in both long-term and short-term habituation effects. With the spinal leg-flexion reflex in cats, for example, only the short-term habituation effect is observed (Thompson & Spencer, 1966). In such cases, spontaneous recovery completely restores the animal’s reaction to the eliciting stimulus if a long enough period of rest is permitted after habituation. By contrast, spontaneous recovery is never complete in situations that also involve long-term habituation, as in Leaton’s experiment (see also Beck & Rankin, 1997; Pedreira et al., 1998; Staddon & Higa, 1996). As Figure 2.10 indicates, the startle response was restored to some extent in the last phase of the experiment, but the animals did not react as vigorously to the tone as they had the first time it was presented.

**Sensitization and the Modulation of Elicited Behavior**

Consider your reaction when someone walks up behind you and taps you on the shoulder. If you are in a supermarket, you will be mildly startled and will turn toward the side where you were tapped. Orienting toward a tactile stimulus is a common elicited response. In our evolutionary past, being touched could mean that we were about to be attacked by a predator, which is something that you wouldn’t want to ignore. Being tapped on the shoulder is not a big deal if you are in a supermarket. However, if you are walking in a dark alley at night in a dangerous part of town, being tapped on the shoulder could be a very scary experience and will no doubt elicit a much more vigorous reaction. Generally speaking, if you are already aroused, the same eliciting stimulus will trigger a much stronger reaction. This is called a sensitization effect.

It is easier to study sensitization of the startle response in the laboratory than in a dark alley. In a classic study, Davis (1974), examined sensitization of the startle response of rats to a brief (90-millisecond) loud tone (110 decibels [dB], 4,000 cycles per second [cps]). Two groups of subjects were tested. Each group received 100 trials presented at 30 second intervals. In addition, a noise generator provided background noise that sounded something like water running from a faucet. For one group, the background noise was relatively quiet (60 dB); for the other, the background noise was rather loud (80 dB), but of lower intensity than the brief startle-eliciting tone.

The results of the experiment are shown in Figure 2.11. As in the other examples I described, repeated presentations of the eliciting stimulus (the 4,000 cps tone) did not always produce the same response. For rats tested in the presence of the soft background noise (60 dB), repetitions of the tone resulted in progressively weaker startle reactions. By contrast, when the background noise was loud (80 dB), repetitions of the tone elicited more vigorous startle reactions. This reflects a gradual build-up of sensitization created by the loud noise.

Reflex responses are sensitized when the subject becomes aroused for some reason. Arousal intensifies our experiences, whether those experiences
are pleasant or unpleasant. As is well-known in the live entertainment industry, introducing loud noise is a relatively simple way to create arousal. Live performances of rock bands are so loud that band members suffer hearing loss if they don’t wear earplugs. The music does not have to be so loud for everyone to hear it. The main purpose of the high volume is to create arousal and excitement. Turning a knob on an amplifier is a simple way to increase excitement. Making something loud is a common device for increasing the enjoyment of movies, circus acts, car races, and football games, and is effective because of the phenomenon of sensitization.

Sensitization also plays a major role in sexual behavior. A major component of sexual behavior involves reacting to tactile cues. Consider the tactile cues of a caress or a kiss. The reaction to the same physical caress or kiss is totally different if you are touching your grandmother than if you are touching your boyfriend or girlfriend. The difference reflects sensitization and arousal. In a recent study of this issue, heterosexual males were tested for their sensitivity to a tactile stimulus presented to the right index finger (Jiao, Knight, Weerakoon, & Turman, 2007) before and after watching an erotic movie that was intended to increase their sexual arousal. Tactile sensitivity was significantly increased by the erotic movie. Watching a non-erotic movie did not produce this effect.

Sensitization has been examined most extensively in the defensive behavior system. Numerous studies have shown that fear potentiates the startle

![Figure 2.11](https://example.com/figure211.png)

**FIGURE 2.11**
response (Davis, 1977). Startle can be measured using a stabilimeter like that shown in Figure 2.9, which measures the reaction of the entire body. A simpler procedure, particularly with human participants, is to measure the eyeblink response (Norrholm et al., 2006). The eyeblink is an early component of the startle response and can be elicited in people by directing a brief puff of air towards the eye.

In one study, using the eyeblink startle measure (Bradley, Moulder, & Lang, 2005), college students served as participants and were shown examples of pleasant and unpleasant pictures. To induce fear, one group of students was told that they could get shocked at some point when they saw the pleasant pictures but not when they saw the unpleasant pictures. The second group of participants received shock threat associated with the unpleasant pictures, but not the pleasant pictures. Shock was never delivered to any of the participants, but to make the threat credible, they were fitted with shock electrodes. To measure fear potentiated startle, the magnitude of the eyeblink response to a puff of air was measured during presentation of the pictures.

The results are shown in Figure 2.12. Let us first consider the startle reaction during presentations of the pleasant pictures. If the pleasant pictures were associated with shock threat, the eyeblink response was substantially greater than if the pictures were safe. This represents the fear-potentiated startle effect. The results with the unpleasant pictures were a bit different. With the unpleasant pictures, the startle response was elevated whether or not the pictures were associated with the threat of shock. This suggests that the unpleasant pictures were sufficiently discomforting to sensitize the defensive blink response independent of any shock threat.

**Adaptiveness and Pervasiveness of Habituation and Sensitization**

Organisms are constantly being bombarded by a host of stimuli. Consider the act of sitting at your desk. Even such a simple situation involves a

![Figure 2.12](image)

**FIGURE 2.12**

Magnitude of the eyeblink response of college students to pleasant and unpleasant pictures that signaled shock or were safe. (Based on Bradley, Moulder, & Lang, 2005.)
myriad of sensations. You are exposed to the color, texture, and brightness of the paint on the walls; the sounds of the air-conditioning system; noises from other rooms; odors in the air; the color and texture of the desk; the tactile sensations of the chair against your legs, seat, and back; and so on. If you were to respond to all of these stimuli, your behavior would be disorganized and chaotic. Habituation and sensitization effects help sort out what stimuli to ignore and what to respond to. Habituation and sensitization effects are the end products of processes that help prioritize and focus behavior in the buzzing and booming world of stimuli that organisms live in.

There are numerous instances of habituation and sensitization in common human experience (Simons, 1996). Consider a grandfather clock. Most people who own such a clock do not notice each time it chimes. They have completely habituated to the clock’s sounds. In fact, they are more likely to notice when the clock misses a scheduled chime. In a sense, this is unfortunate because they may have purchased the clock for the reason that they liked its sound. Similarly, people who live on a busy street or near a railroad track may become entirely habituated to the noises that frequently intrude their homes. Visitors who have not become familiarized with such sounds are much more likely to react and be bothered by them.

Driving a car involves exposure to a large array of complex visual and auditory stimuli. In becoming an experienced driver, a person habituates to the numerous stimuli that are irrelevant to driving, such as details of the color and texture of the road, the kind of telephone poles that line the sides of the highway, tactile sensations of the steering wheel, and routine noises from the engine. Habituation to irrelevant cues is particularly prominent during long driving trips. If you are driving continuously for several hours, you are likely to become oblivious to all kinds of stimuli that are irrelevant to keeping the car on the road. If you then come across an accident or arrive in a new town, you are likely to “wake up” and again pay attention to various things that you had been ignoring. Passing a bad accident or coming to a new town is arousing and sensitizes orienting responses that were previously habituated.

Habituation also determines how much we enjoy something. In his book, Stumbling on happiness, Daniel Gilbert noted that “Among life’s cruelest truths is this one: Wonderful things are especially wonderful the first time they happen, but their wonderfulness wanes with repetition” (p. 130). He went on to write, “When we have an experience—hearing a particular sonata, making love with a particular person, watching the sun set from a particular window with a particular person—on successive occasions, we quickly begin to adapt to it, and the experience yields less pleasure each time” (p. 130).

Habituation and sensitization effects can occur in any situation that involves repeated exposures to a stimulus. Therefore, an appreciation of habituation and sensitization effects is critical for studies of learning. As I will describe in Chapter 3, habituation and sensitization are of primary concern in the design of control procedures for Pavlovian conditioning. Habituation and sensitization also play a role in operant conditioning (McSweeney, Hinson, & Cannon, 1996).
Habituation versus Sensory Adaptation and Response Fatigue

The key characteristic of habituation effects is a decline in the response that was initially elicited by a stimulus. However, not all instances in which repetitions of a stimulus result in a response decline represent habituation. To understand alternative sources of response decrement, we need to return to the concept of a reflex. A reflex consists of three components. First, a stimulus activates one of the sense organs, such as the eyes or ears. This generates sensory neural impulses that are relayed to the central nervous system (spinal cord and brain). The second component involves relay of the sensory messages through interneurons to motor nerves. Finally, the neural impulses in motor nerves, in turn, activate the muscles that create the observed response.

Given the three components of a reflex, there are several reasons why an elicited response may fail to occur (see Figure 2.13). The response will not be observed if for some reason the sense organs become temporarily insensitive to stimulation. A person may be temporarily blinded by a bright light, for example, or suffer a temporary hearing loss because of exposure to loud noise. Such decreases in sensitivity are called sensory adaptation and are different from habituation. The response also will not occur if the muscles involved become incapacitated by fatigue. Sensory adaptation and response fatigue are impediments to responding that are produced outside the nervous system in sense organs and muscles. Therefore, they are distinguished from habituation.

Habituation and sensitization are assumed to involve neurophysiological changes that hinder or facilitate the transmission of neural impulses from sensory to motor neurons. In habituation, the organism ceases to respond to a stimulus even though it remains fully capable of sensing the stimulus and making the muscle movements required for the response. The response fails because changes in the nervous system block the relay of sensory neural impulses to the motor neurons.

In studies of habituation, sensory adaptation is ruled out by evidence that habituation is response specific. An organism may stop responding to a stimulus in one aspect of its behavior while continuing to respond to the stimulus in other ways. When a teacher makes an announcement while you are concentrating on taking a test, you may look up from your test at first, but only

![Diagram of a simple reflex](image-url)

**FIGURE 2.13**

Diagram of a simple reflex. Sensory adaptation occurs in the sense organs, and response fatigue occurs in effector muscles. In contrast, habituation and sensitization occur in the nervous system.
briefly. However, you will continue to listen to the announcement until it is over. Thus, your orienting response habituates quickly, but other attentional responses to the stimulus persist.

Response fatigue as a cause of habituation is ruled out by evidence that habituation is stimulus specific. A habituated response will quickly recover when a new stimulus is introduced. This was illustrated in the taste habituation study summarized in Figure 2.5. After the salivary and hedonic responses had habituated during the first 10 trials, presentation of the alternate taste in Trial 11 resulted in a recovery of both response measures. In an analogous fashion, after your orienting response to a teacher’s announcement has habituated, you are likely to look up again if the teacher mentions your name. Thus, a new stimulus will elicit the previously habituated orienting response, indicating that failure of the response was not due to response fatigue.

THE DUAL-PROCESS THEORY OF HABITUATION AND SENSITIZATION

Habituation and sensitization effects are changes in behavior or performance. These are outward behavioral manifestations or results of stimulus presentations. What factors are responsible for such changes? To answer this question we have to shift our level of analysis from behavior to presumed underlying process or theory. Habituation effects can be satisfactorily explained by a single-factor theory that characterizes how repetitions of a stimulus change the efficacy of that stimulus (e.g., Schöner & Thelen, 2006). However, a second factor has to be introduced to explain why responding is enhanced under conditions of arousal. The dominant theory of habituation and sensitization remains the dual-process theory of Groves and Thompson (1970).

The dual-process theory assumes that different types of underlying neural processes are responsible for increases and decreases in responsiveness to stimulation. One neural process produces decreases in responsiveness. This is called the habituation process. Another process produces increases in responsiveness. This is called the sensitization process. The habituation and sensitization processes are not mutually exclusive. Rather, both may be activated at the same time. The behavioral outcome of these underlying processes depends on which process is stronger. Thus, habituation and sensitization processes compete for control of behavior.

It is unfortunate that the underlying processes that suppress and facilitate responding are called habituation and sensitization. One may be tempted to think that decreased responding or a habituation effect is a direct reflection of the habituation process, and that increased responding or a sensitization effect is a direct reflection of the sensitization process. In fact, both habituation and sensitization effects are the sum, or net, result of both habituation and sensitization processes. Whether the net result is an increase or a decrease in behavior depends on which underlying process is stronger in a particular situation. The distinction between effects and processes in habituation and sensitization is analogous to the distinction between performance and learning discussed in Chapter 1. Effects refer to observable behavior and processes refer to underlying mechanisms.

On the basis of neurophysiological research, Groves and Thompson (1970) suggested that habituation and sensitization processes occur in different parts
of the nervous system (see also Thompson et al., 1973). Habituation processes are assumed to occur in what is called the S-R system. This system consists of the shortest neural path that connects the sense organs activated by the eliciting stimulus and the muscles involved in making the elicited response. The S-R system may be viewed as the reflex arc. Each presentation of an eliciting stimulus activates the S-R system and causes some build-up of habituation.

Sensitization processes are assumed to occur in what is called the state system. This system consists of other parts of the nervous system that determine the organism’s general level of responsiveness or readiness to respond. In contrast to the S-R system, which is activated every time an eliciting stimulus is presented, only arousing events activate the state system. The state system is relatively quiescent during sleep, for example. Drugs, such as stimulants or depressants, may alter the functioning of the state system and thereby change responsiveness. The state system is also altered by emotional experiences. For example, the heightened reactivity that accompanies fear is caused by activation of the state system.

In summary, the state system determines the organism’s general readiness to respond, whereas the S-R system enables the animal to make the specific response that is elicited by the stimulus of interest. The level of response a particular stimulus elicits depends on the combined actions of the S-R and state systems.

Applications of the Dual-Process Theory

The examples of habituation and sensitization (illustrated in the experimental evidence I previously reviewed) can be easily interpreted in terms of the dual-process theory. Repeated exposure to the 4 x 4 checkerboard pattern produced a decrement in visual orientation in infants (Figure 2.7). This presumably occurred because the 4 x 4 stimulus did not create much arousal. Rather, the 4 x 4 stimulus activated primarily the S-R system, and hence activated primarily the habituation process. The more complex 12 x 12 checkerboard pattern produced a greater level of arousal. It presumably activated not only the S-R system but also the state system. The activation of the state system resulted in the increment in visual attention that occurred after the first presentation of the 12 x 12 pattern. However, the arousal or sensitization process was not strong enough to entirely counteract the effects of habituation. As a result, after a few trials visual attention also declined in response to the 12 x 12 stimulus. (For an alternative interpretation of the 12 x 12 data, see Schöner & Thelen, 2006.)

A different type of application of the dual-process theory is required for the habituation and sensitization effects we noted in the startle reaction of rats (Figure 2.11). When the rats were tested with a relatively quiet background noise (60 dB), there was little to arouse them. Therefore, we can assume that the experimental procedures did not produce changes in the state system. Repeated presentations of the startle-eliciting tone merely activated the S-R system, which resulted in habituation of the startle response.

The opposite outcome occurred when the animals were tested in the presence of a loud background noise (80 dB). In this case, stronger startle reactions occurred to successive presentations of the tone. Because the identical tone was used for both groups, the difference in the results cannot be attributed to the tone. Rather, one must assume that the loud background noise increased arousal or readiness to respond in the second group. This sensitization of the
state system was presumably responsible for increasing the startle reaction to the tone in the second group.

Implications of the Dual-Process Theory

The preceding interpretations of habituation and sensitization effects illustrate several important features of the dual-process theory. The S-R system is activated every time a stimulus elicits a response because it is the neural circuit that conducts impulses from sensory input to response output. Activation of the S-R system and its attendant habituating influence are universal features of elicited behavior. By contrast, the state system becomes involved only in special circumstances. Some extraneous event, such as intense background noise, may increase the individual’s alertness and sensitize the state system. Alternatively, the state system may be sensitized by the repeated presentations of the test stimulus itself if that stimulus is sufficiently intense or excitatory (a 12 x 12 checkerboard pattern, as compared with a 4 x 4 pattern). If the arousing stimulus is repeated soon enough so that the second presentation occurs while the organism remains sensitized from the preceding trial, an increase in responding will be observed.

Both the habituation process and the sensitization process are expected to decay with the passage of time without stimulation. Thus, one would expect to see spontaneous recovery from both processes. The loss of the habituation process with time results in recovery, or increase, in the elicited behavior to baseline levels (hence the term spontaneous recovery). In contrast, the temporal decay of the sensitization process results in a decrease of the elicited behavior down to its normal non-aroused level.

Because habituation resides in the S-R circuit, the dual-process theory predicts that habituation will be stimulus specific. If following habituation training the eliciting stimulus is changed, the new stimulus will elicit a nonhabituated response because it activates a different S–R circuit. We saw this outcome in the experiment on habituation of salivation and hedonic ratings to a taste (see Figure 2.5). After the salivary and emotional responses to one taste stimulus (e.g., lime) had substantially habituated (Trials 1-10), the responses showed total recovery when a different taste (lemon) was presented (Trial 11). The stimulus specificity of habituation also forms the basis for all of the studies of infant cognition that employ the visual attention paradigm (see Figure 2.8). Similar effects occur in common experience. For example, after you have become completely habituated to the chimes of your grandfather clock, your attention to the clock is likely to become entirely restored if the clock malfunctions and makes a new sound.

Unlike habituation, sensitization is not highly stimulus-specific. If an animal becomes aroused or sensitized for some reason, its reactivity will increase to a range of cues. For example, pain induced by foot-shock increases the reactivity of laboratory rats to both auditory and visual cues. Similarly, feelings of sickness or malaise increase the reactivity of rats to a wide range of novel tastes. However, shock-induced sensitization appears to be limited to exteroceptive cues and illness-induced sensitization is limited to gustatory stimuli (Miller & Domjan, 1981). Cutaneous pain and internal malaise seem to activate separate sensitization systems.

The dual-process theory of habituation and sensitization has been very influential (e.g., Barry, 2004; Pilz & Schnitzler, 1996), although it has not been successful in explaining all habituation and sensitization effects (e.g., Bee,
One of the important contributions of the theory has been the assumption that elicited behavior can be strongly influenced by neurophysiological events that take place outside the reflex arc that is directly involved in a particular elicited response. The basic idea that certain parts of the nervous system serve to modulate S-R systems that are more directly involved in elicited behavior has been substantiated in numerous studies of habituation and sensitization (e.g., Borszcz, Cranney, & Leaton, 1989; Davis, 1997; Falls & Davis, 1994; Frankland & Yeomans, 1995; Lipp, Sheridan, & Siddle, 1994). (For a detailed discussion of other theories of habituation, see Stephenson & Siddle, 1983; Schöner & Thelen, 2006.)

**BOX 2.2**

**Learning in an Invertebrate**

How does the brain acquire, store, and retrieve information? To answer this question, we need to know how neurons operate and how neural circuits are modified by experience. Studying these issues requires that we delve into the neural machinery to record and manipulate its operations. Naturally, people are not keen on volunteering for such experiments. Therefore, such research has to be conducted on other species.

Much can be learned from the vertebrates (rats, rabbits) that are typically used in behavioral studies of learning. Yet, at a neural level, even a rat poses technical challenge for a neurobiologist. Therefore, neurobiologists have focused on creatures with simpler nervous systems. Invertebrates are attractive because some of their neurons are very large, and they have far simpler nervous systems. Using this approach, Eric Kandel and his colleagues have uncovered the mechanisms that mediate some basic learning processes in the marine snail, *Aplysia*. Here, I provide an overview of the mechanisms that underlie habituation and sensitization (for a recent review, see Hawkins, Kandel, & Bailey, 2006).

*Aplysia* have two wing-like flaps (the parapodium) on their back (dorsal) surface. These flaps cover the gill and other components of the respiratory apparatus (see Figure 2.14A). The gill lies under a mantle shelf and a siphon helps to circulate water across the gill. In the relaxed state, the gill is extended (left side of Figure 2.14A), maximizing chemical exchange across its surface. It is a fragile organ that must be protected. For this reason, nature has given *Aplysia* a protective gill-withdrawal reflex. This reflex can be elicited by a light touch applied to the siphon, or mantle. In the laboratory, the reflex is often elicited by a water jet produced from a Water Pik. While the mechanisms that underlie this reflex can be studied in the intact organism, it is often easier to study the underlying system after the essential components have been removed and placed in a nutrient bath that sustains the tissue.

With this simple preparation, it is an easy matter to demonstrate both habituation and sensitization (see Figure 2.14B). Habituation can be produced by repeatedly applying the tactile stimulus to the siphon. With continued exposure, the magnitude of the gill-withdrawal reflex becomes smaller (habituates). Interestingly, this experience has no effect on the magnitude of the gill-withdrawal elicited by touching the mantle shelf. Conversely, if we repeatedly touch the mantle, the withdrawal response observed habituates without affecting the response elicited by touching the siphon.

A modification in one stimulus-response (S-R) pathway has no effect on the response vigor in the other.

In vertebrates, a painful shock engages a mechanism that generally sensitizes behavior, augmenting a variety of response systems including those that generate a startle response (Davis, 1989). A similar effect can be demonstrated in *Aplysia*. If a shock stimulus is applied to the tail, it sensitizes the gill-withdrawal response elicited by touching the mantle or siphon (Walters, 1994). Notice that this is a general effect that augments behavioral reactivity in both the mantle and siphon circuits.

The essential neural components that underlie gill-withdrawal in response to a siphon touch are illustrated in Figure 2.14C. A similar

(continued)
Touching the siphon skin engages a mechanical receptor that is coupled to a sensory neuron (SN). Just one receptor is illustrated here, but additional receptors and neurons innervate adjoining regions of

(continued)
EXTENSIONS TO EMOTIONS AND MOTIVATED BEHAVIOR

To this point, our discussion of changes produced by repetitions of an eliciting stimulus has been limited to relatively simple responses. However, stimuli may also evoke complex emotions such as love, fear, euphoria, terror, or satisfaction. I have already described habituation of an emotional response to repeated presentations of a taste (Figure 2.5). The concepts of habituation and sensitization also have been extended to changes in more complex emotions (Solomon & Corbit, 1974) and various forms of motivated behavior including feeding, drinking, exploration, aggression, courtship, and sexual behavior (McSweeney & Swindell, 1999). An area of special interest is drug addiction (e.g., Baker et al., 2004; Baker, Brandon,
Emotional Reactions and Their Aftereffects

In their landmark review of examples of emotional responses to various stimuli, including drugs, Solomon and Corbit (1974) noticed a couple of striking features. First, intense emotional reactions are often biphasic. One emotion occurs during the eliciting stimulus, and the opposite emotion is observed when the stimulus is terminated. Consider, for example, the psychoactive effects of alcohol. Someone who is drinking beer or wine becomes mellow and relaxed as they are drinking. These feelings, which are generally pleasant, reflect the primary sedative effects of alcohol. In contrast, something quite different occurs after a night of drinking. Once the sedative effects of alcohol have dissipated, the person is likely to become irritable and may experience headaches and nausea. The pleasant sedative effects of alcohol give way to the unpleasant sensations of a hangover. Both the primary direct effects of the drug and the hangover are dependent on dosage. The more you drink, the more sedated, or drunk, you become, and the more intense the hangover is afterward. Similar bi-phasic responses are observed with other drugs. With amphetamine, for example, the presence of the drug creates feelings of euphoria, a sense of well-being, self-confidence, wakefulness, and a sense of control. After the drug has worn off, the person is likely to feel tired, depressed, and drowsy.

Another common characteristic of emotional reactions is that they change with experience. The primary reaction becomes weaker and the after-reaction becomes stronger. Habitual drinkers are not as debilitated by a few beers as someone drinking for the first time. However, habitual drinkers experience more severe withdrawal symptoms if they quit drinking.

Habituation of a primary drug reaction is called drug tolerance. Drug tolerance refers to a decline in the effectiveness of a drug with repeated exposures. Habitual users of all psychoactive drugs (e.g., alcohol, nicotine, heroin, caffeine, sleeping pills, anti-anxiety drugs) are not as greatly affected by the presence of the drug as first-time users. A strong vodka tonic that would make a casual drinker a bit tipsy is not likely to have any effect on a frequent drinker. (We will revisit the role of opponent processes in drug tolerance in Chapter 4.)

Because of the development of tolerance, habitual drug users sometimes do not enjoy taking the drug as much as naive users. People who smoke frequently, for example, do not derive much enjoyment from doing so. Accompanying this decline in the primary drug reaction is a growth in the opponent after-reaction. Accordingly, habitual drug users experience much more severe hangovers when the drug wears off than naive users. A habitual smoker who has gone a long time without a cigarette will experience headaches, irritability, anxiety, tension, and general dissatisfaction. A heavy drinker who stops consuming alcohol is likely to experience hallucinations, memory loss, psychomotor agitation, delirium tremens, and other physiological disturbances. For a habitual user of amphetamine, the fatigue and depression that characterize the opponent aftereffect may be so severe as to cause suicide.

Solomon and Corbit (1974) noted that similar patterns of emotional reaction occur with other emotion arousing stimuli. Consider, for example, love and attachment. Newlyweds are usually very excited about each other and are
very affectionate whenever they are together. This primary emotional reaction habituates as the years go by. Gradually, the couple settles into a comfortable mode of interaction that lacks the excitement of the honeymoon. However, this habituation of the primary emotional reaction is accompanied by a strengthening of the affective after-reaction. Couples who have been together for many years become more intensely unhappy if they are separated by death or disease. After partners have been together for several decades, the death of one may cause an intense grief reaction in the survivor. This strong affective after-reaction is remarkable, considering that by this stage in their relationship the couple may have entirely ceased to show any overt signs of affection.

The Opponent Process Theory of Motivation

The above examples illustrate three common characteristics of emotional reactions: 1) Emotional reactions are biphasic; a primary reaction is followed by an opposite after-reaction. 2) The primary reaction becomes weaker with repeated stimulations. 3) The weakening of the primary reaction with repeated exposure is accompanied by a strengthening of the after-reaction. These characteristics were identified some time ago and led to the formulation of the opponent process theory of motivation (Solomon & Corbit, 1973, 1974).

The opponent process theory assumes that neurophysiological mechanisms involved in emotional behavior serve to maintain emotional stability. Thus, the opponent process theory is a homeostatic theory. It is built on the premise that an important function of mechanisms that control emotions is to keep us on an even keel and minimize the highs and lows. The concept of homeostasis was originally introduced to explain the stability of our internal physiology, such as body temperature. Since then, the concept has also become important in the analysis of behavior. (I will discuss other types of homeostatic theories in later chapters.)

How might physiological mechanisms maintain emotional stability and keep us from getting too excited? Maintaining any system in a neutral or stable state requires that a disturbance that moves the system in one direction be met by an opposing force that counteracts the disturbance. Consider, for example, trying to keep a seesaw level. If something pushes one end of the seesaw down, the other end will go up. To keep the seesaw level, a force pushing one end down has to be met by an opposing force on the other side.

The idea of opponent forces serving to maintain a stable state is central to the opponent process theory of motivation. The theory assumes that an emotion-arousing stimulus pushes a person’s emotional state away from neutrality. This shift away from emotional neutrality is assumed to trigger an opponent process that counteracts the shift. The patterns of emotional behavior observed initially and after extensive experience with a stimulus are the net results of the direct effects of an emotion arousing stimulus and the opponent process that is activated to counteract this direct effect.

The presentation of an emotion-arousing stimulus initially elicits what is called the primary process, or a process, which is responsible for the quality of the emotional state (e.g., happiness) that occurs in the presence of the stimulus. The primary, or a process, is assumed to elicit, in turn, an opponent process, or b process, that generates the opposite emotional reaction (e.g., irritability and dysphoria). Because the opponent process is activated by the primary reaction, it lags behind the primary emotional disturbance.
Opponent Mechanisms During Initial Stimulus Exposure

Figure 2.15 shows how the primary and opponent processes determine the initial responses of an organism to an emotion arousing stimulus. The observed emotional reactions are represented in the top panel. The underlying opponent processes are represented in the bottom panel. Notice that the $b$ process starts a bit after the onset of the $a$ process. In addition, the $b$ process ends much later than the $a$ process. This last feature allows the opponent emotions to dominate after the end of the stimulus. (From “An Opponent Process Theory of Motivation: I. The Temporal Dynamics of Affect,” by R. L. Solomon and J. D. Corbit, 1974, Psychological Review, 81, pp. 119–145. Copyright © 1974 by the American Psychological Association. Reprinted by permission.)

Opponent Mechanisms After Extensive Stimulus Exposure

Figure 2.16 shows how the primary and opponent processes operate after extensive exposure to a stimulus. As I noted earlier, a highly familiar stimulus...
does not elicit strong emotional reactions, but the affective after-reaction tends to be much stronger. The opponent process theory explains this outcome by assuming that the \( b \) process becomes strengthened with repeated use. It becomes activated sooner after the onset of the \( a \) process and is much stronger than in Figure 2.15. In addition, the \( b \) process ends much later than the \( a \) process. Because of these changes in the \( b \) process, the primary emotional response is nearly invisible during the stimulus, but the affective after-reaction is very strong. (From “An Opponent Process Theory of Motivation: I. The Temporal Dynamics of Affect,” by R. L. Solomon and J. D. Corbit, 1974, Psychological Review, 81, pp. 119–145. Copyright © 1974 by the American Psychological Association. Reprinted by permission.)

Opponent Aftereffects and Motivation

If the primary pleasurable effects of a psychoactive drug are gone for habitual users, why do they continue taking the drug? Why are they addicted? The opponent process theory suggests that drug addiction is mainly an attempt to
reduce the aversiveness of the affective after-reaction to the drugs such as the bad hangovers, the amphetamine “crashes,” and the irritability that comes from not having the usual cigarette. Based on their extensive review of research on emotion and cognition, Baker et al. (2004) proposed an affective processing model of drug addiction that is built on opponent process concepts and concludes that “addicted drug users sustain their drug use largely to manage their misery” (p. 34) (see also Baker, Brandon, & Chassin, 2004; Ettenberg, 2004).

The opponent process interpretation of drug addiction as escape from the misery of withdrawal is also supported by a large body of neuroscience evidence. In their recent review of this evidence, Koob and Le Moal (2008) concluded that extensive drug use results in reduced activity in brain circuits associated with reward and strengthening of opponent neural mechanisms referred to as the anti-reward circuit. Drug seeking behavior is reinforced largely by the fact that drug intake reduces activity in the anti-reward circuit. As they pointed out, “the combination of decreases in reward neurotransmitter function and recruitment of anti-reward systems provides a powerful source of negative reinforcement that contributes to compulsive drug-seeking behavior and addiction” (p. 38). Thus, drug addicts are not “trapped” by the pleasure they derive from the drug (since activity in the reward circuit is reduced by chronic drug intake). Rather, they take the drug to reduce withdrawal pains. (For an alternative perspective, see Robinson & Berridge, 2003.)

CONCLUDING COMMENTS

The quality of life and survival itself depends on an intricate coordination of behavior with the complexities of the environment. Elicited behavior represents one of the fundamental ways in which the behavior of all animals, from single-celled organisms to people, is adjusted to environmental events.

Elicited behavior takes many forms, ranging from simple reflexes mediated by just three neurons to complex emotional reactions. Although elicited behavior occurs as a reaction to a stimulus, it is not rigid and invariant. In fact, one of its hallmark features is that elicited behavior is altered by experience. If an eliciting stimulus does not arouse the organism, repeated presentations of the stimulus will evoke progressively weaker responses (a habituation effect). If the organism is in a state of arousal, the elicited response will be enhanced (a sensitization effect).

Repeated presentations of an eliciting stimulus produce changes in simple responses as well as in more complex emotional reactions. Organisms tend to minimize changes in emotional state caused by external stimuli. According to the opponent process theory of motivation, emotional responses stimulated by an environmental event are counteracted by an opposing process in the organism. If the original elicited emotion is rewarding, the opponent process will activate anti-reward circuits and create an aversive state. The compensatory, or opponent, process is assumed to become stronger each time it is activated. Drug addiction involves efforts to minimize the aversive nature of the opponent or anti-reward processes attendant to repeated drug intake.
Habituation, sensitization, and changes in the strength of opponent processes are the simplest mechanisms, whereby organisms adjust their reactions to environmental events on the basis of past experience.

**SAMPLE QUESTIONS**

1. Describe how elicited behavior can be involved in complex social interactions, like breast feeding.
2. Describe sign stimuli involved in the control of human behavior.
3. Compare and contrast appetitive and consummatory behavior, and describe how these are related to general search, focal search, and food handling.
4. Describe components of the startle response and how the startle response may undergo sensitization.
5. Describe the distinction between habituation, sensory adaptation, and fatigue.
6. Describe the two processes of the dual-process theory of habituation and sensitization and the differences between these processes.
7. Describe how habituation and sensitization are involved in emotion regulation and drug addiction.

**KEY TERMS**

* a process Same as primary process in the opponent process theory of motivation.

* afferent neuron A neuron that transmits messages from sense organs to the central nervous system. Also called sensory neuron.

* appetitive behavior Behavior that occurs early in a natural behavior sequence and serves to bring the organism in contact with a releasing stimulus. (See also general search mode and focal search mode.)

* b process Same as opponent process in the opponent process theory of motivation.

* consummatory behavior Behavior that serves to bring a natural sequence of behavior to consummation or completion. Consummatory responses are usually species-typical modal action patterns. (See also food handling mode.)

* drug tolerance Reduction in the effectiveness of a drug as a result of repeated use of the drug.

* efferent neuron A neuron that transmits impulses to muscles. Also called a motor neuron.

* fatigue A temporary decrease in behavior caused by repeated or excessive use of the muscles involved in the behavior.

* focal search mode The second component of the feeding behavior sequence following general search, in which the organism engages in behavior focused on a particular location or stimulus that is indicative of the presence of food. Focal search is a form of appetitive behavior that is more closely related to food than general search.

* food handling mode The last component of the feeding behavior sequence, in which the organism handles and consumes the food. This is similar to what ethologists referred to as consummatory behavior.
general search mode  The earliest component of the feeding behavior sequence, in which the organism engages in nondirected locomotor behavior. General search is a form of appetitive behavior.

habituation effect  A progressive decrease in the vigor of elicited behavior that may occur with repeated presentations of the eliciting stimulus.

habituation process  A neural mechanism activated by repetitions of a stimulus that reduces the magnitude of responses elicited by that stimulus.

interneuron  A neuron in the spinal cord that transmits impulses from afferent (or sensory) to efferent (or motor) neurons.

modal action pattern (MAP)  A response pattern exhibited by most, if not all, members of a species in much the same way. Modal action patterns are used as basic units of behavior in ethological investigations of behavior.

motor neuron  Same as efferent neuron.

opponent process  A compensatory mechanism that occurs in response to the primary process elicited by biologically significant events. The opponent process causes physiological and behavioral changes that are the opposite of those caused by the primary process. Also called the b process.

primary process  The first process that is elicited by a biologically significant stimulus. Also called the a process.

reflex arc  Neural structures consisting of the afferent (sensory) neuron, interneuron, and efferent (motor) neuron, that enable a stimulus to elicit a reflex response.

releasing stimulus  Same as sign stimulus.

sensitization effect  An increase in the vigor of elicited behavior that may result from repeated presentations of the eliciting stimulus or from exposure to strong extraneous stimulus.

sensitization process  A neural mechanism that increases the magnitude of responses elicited by a stimulus.

sensory adaptation  A temporary reduction in the sensitivity of sense organs caused by repeated or excessive stimulation.

sensory neuron  Same as afferent neuron.

sign stimulus  A specific feature of an object or animal that elicits a modal action pattern in another organism. Also called releasing stimulus.

spontaneous recovery  Recovery of a response produced by a period of rest after habituation or extinction. (Extinction is discussed in Chapter 9.)

S-R system  The shortest neural pathway that connects the sense organs stimulated by an eliciting stimulus and the muscles involved in making the elicited response.

state system  Neural structures that determine the general level of responsiveness, or readiness to respond, of the organism.

supernormal stimulus  An artificially enlarged or exaggerated sign stimulus that elicits an unusually vigorous response.
Classical Conditioning: Foundations

The Early Years of Classical Conditioning
The Discoveries of Vul’fson and Snarskii
The Classical Conditioning Paradigm

Experimental Situations
Fear Conditioning
Eyeblink Conditioning
Sign Tracking
Learning What Tastes Good or Bad

Excitatory Pavlovian Conditioning Procedures
Common Pavlovian Conditioning Procedures
Measuring Conditioned Responses
Control Procedures for Classical Conditioning
Effectiveness of Common Conditioning Procedures

Inhibitory Pavlovian Conditioning Procedures for Inhibitory Conditioning
Measuring Conditioned Inhibition

Prevalence of Classical Conditioning
Concluding Comments

SAMPLE QUESTIONS
KEY TERMS
**CHAPTER PREVIEW**

Chapter 3 provides an introduction to another basic form of learning, namely classical conditioning. Investigations of classical conditioning began with the work of Pavlov, who studied how dogs learn to anticipate food. Since then, the research has been extended to a variety of other organisms and response systems. Some classical conditioning procedures establish an excitatory association between two stimuli and serve to activate behavior. Other procedures promote learning to inhibit the operation of excitatory associations. I will describe both excitatory and inhibitory conditioning procedures, and discuss how these are involved in various important life experiences.

In the preceding chapter, I described how environmental events can elicit behavior and how such elicited behavior can be modified by sensitization and habituation. These relatively simple processes help to bring the behavior of organisms in tune with their environment. However, if human and nonhuman animals only had the behavioral mechanisms described in Chapter 2, they would remain rather limited in the kinds of things they could do. For the most part, habituation and sensitization involve learning about just one stimulus. However, events in the world do not occur in isolation. Rather, much of our experience consists of predictable and organized sequences of stimuli. Every significant event (e.g., a hug from a friend) is preceded by other events (your friend approaching with extended arms) that are part of what leads to the target outcome.

Cause and effect relationships in the world ensure that certain things occur in combination with others. Your car’s engine does not run unless the ignition has been turned on; you cannot walk through a doorway unless the door was first opened; it does not rain unless there are clouds in the sky. Social institutions and customs also ensure that events occur in a predictable order. Classes are scheduled at predictable times; people are predictably better dressed at church than at a picnic; a person who smiles is more likely to act in a friendly manner than one who frowns. Learning to predict events in the environment and learning what stimuli tend to occur together are important for aligning behavior with the environment. Imagine how much trouble you would have if you could not predict how long it takes to make coffee, when stores are likely to be open, or whether your key will work to unlock your apartment.

The simplest mechanism whereby organisms learn about relations between one event and another is classical conditioning. Classical conditioning enables human and nonhuman animals to take advantage of the orderly sequence of events in their environment to then take appropriate action in anticipation of what is about to happen. For example, classical conditioning is the process whereby we learn to predict when and what we might eat, when
we are likely to face danger, and when we are likely to be safe. It is also integrally involved in the learning of new emotional reactions (e.g., fear or pleasure) to stimuli that have become associated with a significant event.

THE EARLY YEARS OF CLASSICAL CONDITIONING

Systematic studies of classical conditioning began with the work of the great Russian physiologist Pavlov (see Box 3.1). Classical conditioning was also independently discovered by Edwin Twitmyer in a PhD dissertation submitted to the University of Pennsylvania in 1902 (see Twitmyer, 1974). Twitmyer repeatedly tested the knee-jerk reflex of college students by sounding a bell 0.5 seconds before hitting the patellar tendon just below the knee cap. After several trials of this sort, the bell was sufficient to elicit the knee-jerk reflex in some of the students. However, Twitmyer did not explore the broader implications of his discoveries, and his findings did not attract much attention.

Pavlov’s studies of classical conditioning were an extension of his research on the processes of digestion. Pavlov made major advances in the study of digestion by developing surgical techniques that enabled dogs to survive for many years with artificial fistulae that permitted the collection of various digestive juices. With the use of a stomach fistula, for example, Pavlov was able to collect stomach secretions in dogs that otherwise lived normally. Technicians in the laboratory soon discovered that the dogs secreted stomach juices in response to the sight of food, or even just upon seeing the person who usually fed them. The laboratory produced considerable quantities of stomach juice in this manner and sold the excess to the general public. The popularity of this juice as a remedy for various stomach ailments helped to supplement the income of the laboratory.

Assistants in the laboratory referred to stomach secretions elicited by food-related stimuli as psychic secretions because they seemed to be a response to the expectation or thought of food. However, the phenomenon of

BOX 3.1

**Ivan P. Pavlov: Biographical Sketch**

Born in 1849 into the family of a priest in Russia, Pavlov dedicated his life to scholarship and discovery. He received his early education in a local theological seminary and planned a career of religious service. However, his interests soon changed, and when he was 21, he entered the University of St. Petersburg, where his studies focused on chemistry and animal physiology. After obtaining the equivalent of a bachelor’s degree, he went to the Imperial Medico-Surgical Academy in 1875 to further his education in physiology. Eight years later, he received his doctoral degree for his research on the efferent nerves of the heart and then began investigating various aspects of digestive physiology. In 1888 he discovered the nerves that stimulate the digestive secretions of the pancreas—a finding that initiated a series of experiments for which Pavlov was awarded the Nobel Prize in Physiology in 1904.

Pavlov did a great deal of original research while a graduate student, as well as after obtaining his doctoral degree. However, he did not have a faculty position or his own laboratory until 1890, when he was appointed professor of pharmacology at the St. Petersburg Military Medical Academy. In 1895 he became professor of physiology at the same institution. Pavlov remained active in the laboratory until close to his death in 1936. In fact, much of the research for which he is famous today was performed after he received the Nobel Prize.
psychic secretions generated little scientific interest until Pavlov recognized that it could be used to study the mechanisms of association learning and could inform us about the functions of the nervous system (Pavlov, 1927). Thus, as many great scientists, Pavlov’s contributions were important not just because he discovered something new, but because he figured out how to place the discovery into a compelling conceptual framework.

The Discoveries of Vul’fson and Snarskii

The first systematic studies of classical conditioning were performed by S. G. Vul’fson and A. T. Snarskii in Pavlov’s laboratory (Boakes, 1984; Todes, 1997). Both of these students focused on the salivary glands, which are the first digestive glands involved in the breakdown of food. Some of the salivary glands are rather large and have ducts that are accessible and can be easily externalized with a fistula (see Figure 3.1). Vul’fson studied salivary responses to various substances placed in the mouth: dry food, wet food, sour water, and sand, for example. After the dogs had these substances placed in the mouth repeatedly, the mere sight of the substances was enough to make them salivate.

Whereas Vul’fson used naturally occurring substances in his studies, Snarskii extended these observations to artificial substances. In one experiment, Snarskii first gave his dogs sour water (such as strong lemon juice) that was artificially colored black. After several encounters with the black sour water, the dogs also salivated to plain black water or to the sight of a bottle containing a black liquid.

The substances tested by Vul’fson and Snarskii could be identified at a distance by sight. The substances also produced distinctive texture and taste sensations in the mouth. Such sensations are called orosensory stimuli. The first time that sand was placed in a dog’s mouth, only the feeling of the sand in the mouth elicited salivation. However, after sand had been placed in the
mouth several times, the sight of sand (its visual features) also came to elicit salivation. Presumably the dog learned to associate the visual features of the sand with its orosensory features. The association of one feature of an object with another is called **object learning**.

To study the mechanisms of associative learning, the stimuli to be associated have to be manipulated independently of one another. This is difficult to do when the two stimuli are properties of the same object. Therefore, in later studies of conditioning, Pavlov used procedures in which the stimuli to be associated came from different sources. This led to the experimental methods that continue to dominate studies of classical conditioning to the present day. However, contemporary studies are no longer conducted with dogs.

### The Classical Conditioning Paradigm

Pavlov’s basic procedure for the study of conditioned salivation is familiar to many. The procedure involves two stimuli. One of these is a tone or a light that does not elicit salivation at the outset of the experiment. The other stimulus is food or the taste of a sour solution placed in the mouth. In contrast to the light or tone, the food or sour taste elicits vigorous salivation even the first time it is presented.

Pavlov referred to the tone or light as the **conditional stimulus** because the effectiveness of this stimulus in eliciting salivation depended on (or was **conditional** on) pairing it several times with the presentation of food. By contrast, the food or sour-taste was called the **unconditional stimulus** because its effectiveness in eliciting salivation did not depend on any prior training. The salivation that eventually came to be elicited by the tone or light was called the **conditional response**, and the salivation that was always elicited by the food or sour taste was called the **unconditional response**. Thus, stimuli and responses whose properties did not depend on prior training were called **unconditional**, and stimuli and responses whose properties emerged only after training were called **conditional**.

In the first English translation of Pavlov’s writings, the term unconditional was erroneously translated as unconditioned, and the term conditional was translated as conditioned. The -ed suffix was used exclusively in English writings for many years. However, the term conditioned does not capture Pavlov’s original meaning of “dependent on” as accurately as the term conditional (Gantt, 1966).

Because the terms conditioned and unconditioned stimulus and conditioned and unconditioned response are used frequently in discussions of classical conditioning, they are often abbreviated. Conditioned stimulus and conditioned response are abbreviated **CS** and **CR**, respectively. Unconditioned stimulus and unconditioned response are abbreviated **US** and **UR**, respectively.

### EXPERIMENTAL SITUATIONS

Classical conditioning has been investigated in a variety of situations and species (e.g., Domjan, 2005; Hollis, 1997; Turkkan, 1989). Pavlov did most of his experiments with dogs using the salivary-fistula technique. Most contemporary experiments on Pavlovian conditioning are carried out with domesticated rats, rabbits, and pigeons using procedures developed by North American scientists during the second half of the twentieth century.
Fear Conditioning

Following the early work of Watson and Rayner (1920/2000), a major focus of investigators of Pavlovian conditioning has been the conditioning of emotional reactions. Watson and Rayner believed that infants are at first limited in their emotional reactivity. They assumed that “there must be some simple method by means of which the range of stimuli which can call out these emotions and their compounds is greatly increased. (p. 313)” That simple method was Pavlovian conditioning. In a famous demonstration, Watson and Rayner conditioned a fear response in a nine-month-old infant, Albert, to the presence of a docile white laboratory rat.

There was hardly anything that Albert was afraid of. However, after testing a variety of stimuli, Watson and Rayner found that little Albert reacted with alarm when he heard the loud noise of a steel bar being hit by a hammer behind his head. Watson and Rayner then used this unconditioned alarming stimulus to condition fear to a white rat. Each conditioning trial consisted of presenting the rat to Albert and then striking the steel bar. At first Albert reached out to the rat when it was presented to him. But, after just two conditioning trials, he became reluctant to touch the rat. After five additional conditioning trials, Albert showed strong fear responses to the rat. He whimpered or cried, leaned as far away from the rat as he could, and sometimes fell over and moved away on all fours. Significantly, these fear responses were not evident when Albert was presented with his toy blocks. However, the conditioned fear did generalize to other furry things (a rabbit, a fur coat, cotton wool, a dog, and a Santa Claus mask).

Fear and anxiety are the sources of considerable human discomfort, and if sufficiently severe, they can lead to serious psychological and behavioral problems. There is considerable interest in how fear and anxiety are acquired, what the neural mechanisms of fear are, and how fear may be attenuated with pharmacological and behavioral treatments (e.g., Craske, Hermans, & Vansteenwegen, 2006; Kirmayer, Lemelson, & Barad, 2007). Many of these questions cannot be addressed experimentally using human subjects (at least not initially). Therefore, most of the research on fear conditioning has been conducted with laboratory rats and mice.

The aversive US in these studies is a brief electric shock delivered through a metal grid floor. Shock is used because it can be regulated with great precision and its intensity can be adjusted so as to cause no physical harm. It is aversive primarily because it is startling, unlike anything the animal has encountered before. The CS may be a discrete stimulus (like a tone or a light), or the contextual cues of the place where the aversive stimulus is encountered.

Unlike little Albert who showed signs of fear by whimpering and crying, rats show their fear by freezing. Freezing is a species typical defense response that occurs in a variety of species in response to the anticipation of aversive stimulation (see Chapter 10). Freezing probably evolved as a defensive behavior because animals that are motionless are not easily seen by their predators. For example, a deer that is standing still in the woods is difficult to see because its coloration blends well with the colors of bark and leaves. However, as soon as the deer starts moving, you can tell where it is.

Freezing is defined as immobility of the body (except for breathing) and the absence of movement of the whiskers associated with sniffing (Bouton & Bolles, 1980). Direct measurement of freezing as an index of conditioned fear has become
popular, especially in neurobiological studies of fear (e.g., Fendt & Fanselow, 1999; Quinn & Fanselow, 2006). However, investigators also use two different indirect measures of immobility. Both involve the suppression of ongoing behavior and are therefore referred to as *conditioned suppression* procedures. In one case, the ongoing behavior that is measured is licking a drinking spout that contains water. The animals are slightly water deprived and therefore lick readily when placed in an experimental chamber. If a fear CS (e.g., tone) is presented, their licking behavior is suppressed and they take longer to make a specified number of licks. The latency to complete a certain number of licks is measured as the behavioral index of conditioned fear. The *lick-suppression procedure* was devised more than 40 years ago (e.g., Leaf & Muller, 1965) but remains popular in contemporary research (e.g., Urcelay & Miller, 2008a).

Another prominent technique for the indirect measurement of conditioned fear is the *conditioned emotional response* procedure (CER) devised by Estes and Skinner (1941). In this procedure, rats are first trained to press a response lever for food reward in a small experimental chamber (Figure 3.2A). This lever press activity provides the behavioral baseline for measurement of fear. Once the rats are lever pressing at a steady rate, fear conditioning is introduced, consisting of a tone or light paired with a brief shock. As the participants acquire the conditioned fear, they come to suppress their lever pressing during the CS (Kamin, 1965).

To measure the suppression of lever pressing, a suppression ratio is calculated. The ratio compares the number of lever presses that occur during the CS with the number that occur during a comparable baseline period before the CS is presented (the pre-CS period). The specific formula is as follows:

\[
\text{Suppression Ratio} = \frac{\text{CS responding}}{\text{CS responding} + \text{pre-CS responding}}
\]

Notice that the *suppression ratio* has a value of zero if the rat suppresses lever pressing completely during the CS, because in this case, the numerator of the formula is zero. At the other extreme, if the rat does not alter its rate of lever pressing at all when the CS is presented, the ratio has a value of 0.5. For example, let us assume that the CS is presented for two minutes and that in a typical two minute period the rat makes 30 responses. If the CS does not disrupt lever pressing, the animal will make 30 responses during the CS, so that the numerator of the ratio will be 30. The denominator will be 30 (CS responses) + 30 (pre-CS responses), or 60. Therefore, the ratio will be 30/60 or 0.5. Decreasing values of the ratio from 0.5 to 0 indicate greater degrees of response suppression, or conditioned fear. Thus, the scale is inverse. Greater disruptions of lever pressing are represented by lower values of the suppression ratio.

Figure 3.2B shows sample results of a conditioned suppression experiment with rats. Two conditioning trials were conducted on each of five days of training. Very little suppression occurred the first time the CS was presented, and not much acquisition of suppression was evident during the first day of training. However, a substantial increase in suppression occurred from the last trial on Day 1 (Trial 2) to the first trial on Day 2 (Trial 3). With continued training, responding gradually became more and more suppressed, until an asymptotic suppression ratio of about 0.2 was achieved.

Interpreting conditioned suppression data can be confusing because the scale is inverse. Keep in mind that a suppression ratio of 0 indicates zero responding during the CS, which represents the greatest possible suppression of
FIGURE 3.2
(A) Rat lever pressing for food in a conditioning chamber that also permits the presentation of an auditory cue as the CS and brief shock as the US. (B) Acquisition of conditioned suppression to a clicker CS paired with shock. Two conditioning trials were conducted each day for five days. Suppression ratios closer to zero indicate greater degrees of suppression of lever pressing during the CS and greater conditioned fear. (Based on Waddell, Morris, & Bouton, 2006.)
lever pressing. The smaller the suppression ratio, the more motionless the animal is, because the CS elicits more conditioned fear.

The conditioned suppression procedure has also been adapted for experiments with human subjects. In that case, the behavioral baseline is provided by playing a video game (e.g., Arcediano, Ortega, & Matute, 1996; Nelson & del Camen Sanjuan, 2006).

**Eyeblink Conditioning**

As I mentioned in Chapter 2, the eyeblink reflex is an early component of the startle response and occurs in a variety of species. To get someone to blink, all you have to do is clap your hands or blow a puff of air toward the eyes. If the air puff is preceded by a brief tone, the person will learn to blink when the tone comes on, in anticipation of the air puff.

Because of its simplicity, eyeblink conditioning was extensively investigated in studies with human participants early in the development of learning theory (see Hilgard & Marquis, 1940; Kimble, 1961). Eyeblink conditioning continues to be a very active area of research because it provides a powerful tool for the study of problems in development, aging, and Alzheimer's disease (Freeman & Nicholson, 2004; Woodruff-Pak, 2001; Woodruff-Pak et al., 2007). Eyeblink conditioning also has been used extensively in studies of the neurobiology of learning. This knowledge has in turn made eyeblink conditioning useful in studies of autism, fetal alcohol syndrome, and obsessive compulsive disorder (Steinmetz, Tracy, & Green, 2001).

A study of eyeblink conditioning in five-month-old infants (Ivkovich, Collins, Eckerman, Krasnegor, & Stanton, 1999) illustrates the technique. The CS was a 1,000 cps tone presented for 750 milliseconds, and the US was a gentle puff of air delivered to the right eye through a plastic tube. Each infant sat on a parent’s lap facing a platform with brightly colored objects that maintained the infant’s attention during the experimental sessions. Eyeblinks were recorded by video cameras. For one group of infants, the CS always ended with the puff of air, and these conditioning trials occurred an average of 12 seconds apart. The second group received the same number and distribution of CS and US presentations, but for them, the CSs and USs were spaced four to eight seconds apart in an explicitly unpaired fashion. Thus, the second group served as a control. Each participant received two training sessions, one week apart.

The results of the experiment are presented in Figure 3.3 in terms of the percentage of trials on which the subjects blinked during the CS. The rate of eyeblinks for the two groups did not differ statistically during the first experimental session. However, the paired group responded to the CS at a significantly higher rate from the beginning of the second session. This experiment illustrates a number of important points about learning. First, it shows that classical conditioning requires the pairing of a CS and US. Responding to the CS did not develop in the unpaired control group. Second, the learning was not observable at first. The infants in the paired group did not respond much in the first session, but they were starting to learn that the CS was related to the US. This learning was clearly evident when the subjects were returned to the experimental situation for a second session.

Recent interest in eyeblink conditioning in humans stems from the fact that substantial progress has been made in understanding the neurobiological substrates of this type of learning. Neurobiological investigations of eyeblink conditioning...
have been conducted primarily in studies with domesticated rabbits. The rabbit eyeblink preparation was developed by Gormezano (see Gormezano, 1966; Gormezano, Kehoe, & Marshall, 1983). Domesticated rabbits are ideal for this type of research because they are sedentary and rarely blink in the absence of an air puff or irritation of the eye. In an eyeblink conditioning experiment, the rabbit is placed in an enclosure and attached to equipment that enables measurement of the blink response. The US to elicit blinking is provided by a small puff of air or mild irritation of the skin below the eye with a brief (0.1 second) electrical current. The CS may be a light, a tone, or a mild vibration of the animal’s abdomen.

In the typical conditioning experiment, the CS is presented for half a second and is followed immediately by delivery of the US. The US elicits a rapid and vigorous eyelid closure. As the CS is repeatedly paired with the US, the eyeblink response is also made with the CS. Investigators record the percentage of trials in which a conditioned blink response is observed. Rabbit eyeblink conditioning is relatively slow, requiring several hundred trials for substantial levels of conditioned responding.

Eyeblink conditioning in five-month-old infants. For the infants in the paired group, a tone CS ended in a gentle puff of air to the eye. For the infants in the unpaired group, the tone and air puff never occurred together. (Adapted from D. Ivlovich, K. L. Collins, C. O. Eckerman, N. A. Krasnegor, and M. E. Stanton (1999). Classical delay eyeblink conditioning in four and five month old human infants. Psychological Science, 10, Figure 1, p. 6. Adapted with permission from Blackwell Publishing.)

**FIGURE 3.3**
**BOX 3.2**

**Eyeblink Conditioning and the Search for the Engram**

When an organism learns something, the results of this learning must be stored within the brain. Somehow, the network of neurons that makes up our central nervous system is able to encode the relationship between biologically significant events and use this information to guide the selection of responses the subject will perform. This biological memory is known as an engram. The traditional view is that the engram for a discrete CR is stored in localized regions of the brain. This raises a basic question in neurobiology: Where is the engram located?

This question has been pursued for nearly four decades by Richard Thompson and his collaborators (for recent reviews see Fanselow & Poulos, 2005; Steinmetz, Gluck, & Solomon, 2001; Thompson, 2005). Thompson recognized that locating the engram would require a well-defined behavioral system in which both the conditions for learning and the motor output were precisely specified. These considerations led him to study the mechanisms that underlie eyeblink conditioning. In the eyeblink conditioning situation, a CS (e.g., a tone) is repeatedly paired with an air puff to the eye (the US) and acquires the ability to elicit a defensive eyeblink response. To pursue his neurobiological investigations, Thompson studied eyeblink conditioning in rabbits.

The search for the engram began with the hippocampus. Studies of humans with damage to this region revealed that the ability to consciously remember a recent event requires that the hippocampus remain intact. In animal subjects, small electrodes were lowered into the hippocampus and neural activity was recorded during eyeblink conditioning. These studies revealed that cells in this region reflect the learning of a CS-US association. However, to the surprise of many investigators, removing the hippocampus did not eliminate the animal's ability to acquire and retain a conditioned eyeblink response. In fact, removing all of the brain structures above the midbrain (see Figure 3.4A) had little effect on eyeblink conditioning with a delayed conditioning procedure. This suggests that the essential circuitry for eyeblink conditioning lies within the lower neural structures of the brainstem and cerebellum. Subsequent experiments clearly showed that the acquisition of a well-timed conditioned eyeblink response depends on a neural circuit that lies within the cerebellum (Ohayama, Nores, Morphy, & Mank, 2003; Steinmetz et al., 2001).

The UR elicited by an air puff to the eye is mediated by neurons that project to a region of the brainstem known as the trigeminal nucleus (see Figure 3.4B). From there, neurons travel along two routes, either directly or through the reticular formation, to the cranial motor nucleus where the behavioral output is organized. Three basic techniques were used to define this pathway. The first involved electrophysiological recordings to verify that neurons in this neural circuit are engaged in response to the US. The second technique involved inactivating the neural circuit, either permanently (by killing the cells) or temporarily (by means of a drug or cooling), to show that the circuit plays an essential role in the eyeblink UR. If the circuit is necessary, disrupting its function should eliminate the behavioral output. Finally, the circuit was artificially stimulated to show that activity in this circuit is sufficient to produce the behavioral response.

The same techniques (electrical recording, inactivation, and stimulation) have been used to define the neural pathway that mediates the acquisition and performance of the CR. As illustrated in Figure 3.4B, the CS input travels to a region of the brainstem known as the pontine nucleus. From there, it is carried by mossy fibers that convey the signal to the cerebellum. The US signal is carried into the cerebellum through the climbing fibers. These two signals meet in the cerebellar cortex where coincident activity brings about a synaptic modification that alters the neural output from the cerebellum. In essence, the climbing fibers act as teachers, selecting a subset of connections to be modified. This change defines the stimulus properties (the characteristics of the CS) that engage a discrete motor output. This output is mediated by neurons that project from the interpositus nucleus to the red nucleus, and finally, to the cranial motor nucleus.

As an eyeblink CR is acquired, conditioned activity develops within the interpositus nucleus. Neurons from the interpositus nucleus project back to the US pathway and inhibit the US signal within the inferior olive. This provides a form of negative feedback that decreases the effectiveness of the US. Many researchers believe that phenomena such as blocking and overshadowing occur because a predicted CS is less effective. In the eyeblink paradigm, this might occur

*(continued)*
because the US input is inhibited within the inferior olive. Consistent with that prediction, Kim et al. (1998) showed that eliminating this source of inhibition eliminated the blocking effect.

Earlier we noted that the hippocampus is not needed for simple delayed conditioning. It is, however, required for more complex forms of learning. An example is provided by trace conditioning, in which a temporal delay is inserted between the end of the CS and the start of the US. A normal animal can readily acquire a conditioned eyelink to a CS that ends 0.5 seconds before the US. However, it cannot span this gap if the hippocampus is removed. A similar pattern of results is observed in amnesic patients who have damage to the hippocampus (Clark & Squire, 1998). These patients cannot consciously remember the CS-US relation. In the absence of this explicit memory, they fail to learn with a trace conditioning procedure. Learning in the delayed procedure is not affected, even though the patient cannot consciously remember the CS-US relation from one session to the next. Interestingly, disrupting conscious awareness in a normal subject undermines the appreciation of the CS-US relation with the trace procedure. Again, subjects who cannot explicitly report the relation, fail to learn.

J. W. Grau
Sign Tracking

Pavlov's research concentrated on salivation and other highly reflexive responses. This encouraged the belief that classical conditioning occurs only in reflex response systems. In recent years, however, such a restrictive view of Pavlovian conditioning has been abandoned (e.g., Hollis, 1997). One experimental paradigm that has contributed significantly to modern conceptions of Pavlovian conditioning is the sign tracking, or autoshaping, paradigm (Hearst, 1975; Hearst & Jenkins, 1974; Locurto, Terrace, & Gibbon, 1981).

Animals tend to approach and contact stimuli that signal the availability of food. In the natural environment, the availability of food can be predicted by some aspect of the food itself, such as its appearance at a distance. For a hawk, the sight and noises of a mouse some distance away are cues indicating the possibility of a meal. By approaching and contacting these cues, the hawk can end up with a meal.

Sign tracking is investigated in the laboratory by presenting a discrete, localized visual stimulus just before each delivery of a small amount of food. The first experiment of this sort was performed by Brown and Jenkins (1968) with pigeons. The pigeons were placed in an experimental chamber that had a small circular key that could be illuminated and that the pigeons could peck. Periodically, the birds were given access to food for a few seconds. The key light was illuminated for 8 seconds immediately before each food delivery.

The birds did not have to do anything for the food to be delivered. Since they were hungry, one might predict that when they saw the key light, they would go to the food dish and wait for the food that was coming. Interestingly, that is not what happened. Instead of using the key light to tell them when they should go to the food dish, the pigeons started pecking the key itself. This behavior was remarkable because it was not required to gain access to the food. Presenting the keylight at random times or unpaired with food does not lead to pecking (e.g., Gamzu & Williams, 1971, 1973).

Since its discovery, many experiments have been done on sign tracking in a variety of species, including chicks, quail, goldfish, lizards, rats, rhesus monkeys, squirrel monkeys, and human adults and children (see Tomie, Brooks, & Zito, 1989). Research is also underway to develop sign tracking as a model system for studying the role of incentive motivation in drug addiction (e.g., Flagel, Akil, & Robinson, 2008).

The tracking of signals for food is dramatically illustrated by instances in which the signal is located far away from the food cup. In the first such experiment (see Hearst & Jenkins, 1974), the food cup was located about three feet (90 cm) from the key light. Nevertheless, the pigeons went to the key light rather than the food cup when the CS was presented. Burns and Domjan (2000) extended this “long-box” procedure in sexual conditioning with male quail. Domesticated quail, which copulate readily in captivity, were used in the experiment. The CS was a wood block lowered from the ceiling 30 seconds before a female copulation partner was released. The unusual feature of the experiment was that the CS and the female were presented at opposite ends of an eight foot long chamber (see Figure 3.5). Despite this long distance, the birds approached the CS rather than the location of the female before the female was released. Association of the CS with sexual reinforcement made it such an attractive stimulus that the birds were drawn to it nearly eight feet away, even
though approaching the CS took them away from where their sexual partner would appear on each trial.

Sign tracking occurs only in situations where the CS is localized and therefore can be approached and tracked. In one study, the CS was provided by diffuse spatial and contextual cues of the chamber in which pigeons were given food periodically. With the diffuse contextual cues, the learning of an association was evident in an increase in general activity, rather than in a specific approach response (Rescorla, Durlach, & Grau, 1985). In another experiment (conducted with laboratory rats), a localized light and a sound were compared as conditioned stimuli for food (Cleland & Davey, 1983). Only the light CS generated sign tracking behavior. The auditory CS elicited approach to the food cup rather than approach to the sound source. These experiments illustrate that for sign tracking to occur, the CS has to be of the proper modality and configuration.

**Learning What Tastes Good or Bad**

The normal course of eating provides numerous opportunities for the learning of associations. Rozin and Zellner (1985) concluded a review of the role of Pavlovian conditioning in the foods people come to like or dislike with the comment that “Pavlovian conditioning is alive and well, in the flavor-flavor associations of the billions of meals eaten each day...in the associations of foods and offensive objects, and in the associations of foods with some of their consequences” (p. 199).

A conditioned taste aversion is learned if ingestion of a novel flavor is followed by an aversive consequence such as indigestion or food poisoning. In contrast, a taste preference may be learned if a flavor is paired with nutritional
repletion or other positive consequences (e.g., Capaldi, Hunter, & Lyn, 1997; Ramirez, 1997). The learning of taste-aversions and taste-preferences has been investigated extensively in various animal species (Reilly & Schachtman, 2008; Riley & Freeman, 2008; Pérez, Fanizza, & Sclafani, 1999; Sclafani, 1997). A growing body of evidence indicates that many human taste aversions are also the result of Pavlovian conditioning (Scalera, 2002). Much of this evidence has been provided by questionnaire studies (Logue, Ophir, & Strauss, 1981; Logue, 1985, 1988a). People report having acquired at least one food aversion during their lives. The typical aversion learning experience involves eating a distinctively flavored food and then getting sick. Such a flavor-illness experience can produce a conditioned food aversion in just one trial, and the learning can occur even if the illness is delayed several hours after ingestion of the food. Another interesting finding is that in about 20% of the cases, the individuals were certain that their illness was not caused by the food they ate. Nevertheless, they learned an aversion to the food. This indicates that food aversion learning can be independent of rational thought processes and can go against a person’s conclusions about the causes of their illness.

Questionnaire studies can provide provocative data, but systematic experimental research is required to isolate the mechanism of learning. Experimental studies of taste-aversion learning have been conducted with people in situations where they encounter illness during the course of medical treatment. Chemotherapy for cancer is one such situation. Chemotherapy often causes nausea as a side effect. Both child and adult cancer patients have been shown to acquire aversions to foods eaten before a chemotherapy session (Bernstein, 1978, 1991; Bernstein & Webster, 1980; Carrell, Cannon, Best, & Stone, 1986). Such conditioned aversions may contribute to the lack of appetite that is a common side-effect of chemotherapy. (For laboratory studies on the role of nausea in the conditioning of taste aversions, see Parker, 2003.)

Conditioned food aversions also may contribute to the suppression of food intake or anorexia observed in other clinical situations (Bernstein & Borson, 1986; Scalera & Bavieri, 2008). The anorexia that accompanies the growth of some tumors may result from food-aversion learning. Animal research indicates that the growth of tumors can result in the conditioning of aversions to food ingested during the disease. Food-aversion learning may also contribute to anorexia nervosa, a disorder characterized by severe and chronic weight loss. Suggestive evidence indicates that people suffering from anorexia nervosa experience digestive disorders that may increase their likelihood of learning food aversions. Increased susceptibility to food-aversion learning may also contribute to loss of appetite seen in people suffering from severe depression.

Many of our ideas about food-aversion learning in people have their roots in research with laboratory animals. In the typical procedure, the subjects receive a distinctively flavored food or drink and are then made to feel sick by the injection of a drug or exposure to radiation. As a result of the taste-illness pairing, the animals acquire an aversion to the taste and suppress their subsequent intake of that flavor (Reilly & Schachtman, 2008).

Taste-aversion learning is a result of the pairing of a CS (in this case, a taste) and a US (drug injection or radiation exposure) in much the same manner as in other examples of classical conditioning, and follows standard rules of learning in many respects (e.g., Domjan, 1980, 1983). However, it also has
some special features. First, strong taste aversions can be learned with just one pairing of the flavor and illness. Although one-trial learning also occurs in fear conditioning, such rapid learning is rarely observed in eyeblink conditioning, salivary conditioning, or sign tracking.

The second unique feature of taste-aversion learning is that it occurs even if the illness does not occur until several hours after exposure to the novel taste (Garcia, Ervin, & Koelling, 1966; Revusky & Garcia, 1970). Dangerous substances in food often do not have their poisonous effects until the food has been digested, absorbed in the bloodstream, and distributed to various body tissues. This process takes time. Long-delay learning of taste aversions probably evolved to enable human and other animals to avoid poisonous foods that have delayed ill effects.

Long-delay taste-aversion learning was reported in an early study by Smith and Roll (1967). Laboratory rats were first adapted to a water deprivation schedule so that they would readily drink when a water bottle was placed on their cage. On the conditioning day, the water was flavored with the artificial sweetener saccharin (to make a 0.1% saccharin solution). At various times after the saccharin presentation ranging from 0 to 24 hours, different groups of rats were exposed to radiation from an X-ray machine to induce illness. Control groups of rats were also taken to the X-ray machine but were not irradiated. They were called the sham-irradiated groups. Starting a day after the radiation or sham treatment, each rat was given a choice of the saccharin solution or plain water to drink for two days.

The preference of each group of rats for the saccharin solution is shown in Figure 3.6. Animals exposed to radiation within six hours after tasting the

![Figure 3.6](image-url)

**FIGURE 3.6**
Mean percent preference for the saccharin CS flavor during a test session conducted after the CS flavor was paired with X irradiation (the US) or sham exposure. Percent preference is the percentage of the participant’s total fluid intake (saccharin solution plus water) that consisted of the saccharin solution. During conditioning, the interval between exposure to the CS and the US ranged from 0 to 24 hours for different groups of rats. (From “Trace Conditioning with X-rays as an Aversive Stimulus,” by J. C. Smith and D. L. Roll, *Psychonomic Science*, 1967, 9, pp. 11–12. Copyright © 1967 by Psychonomic Society. Reprinted by permission.)
saccharin solution showed a profound aversion to the saccharin flavor in the postconditioning test. They drank less than 20% of their total fluid intake from the saccharin drinking tube. Much less of an aversion was evident in animals irradiated 12 hours after the saccharin exposure, and hardly any aversion was observed in rats irradiated 24 hours after the taste exposure. In contrast to this gradient of saccharin avoidance observed in the irradiated rats, all the sham-irradiated groups strongly preferred the saccharin solution. They drank more than 70% of their total fluid intake from the saccharin drinking tube.

A flavor can also be made unpalatable by pairing it with another taste that is already disliked. In an analogous fashion, the pairing of a neutral flavor with a taste that is already liked will make that flavor preferable. For example, in a recent study with undergraduate students, Dickinson and Brown (2007) used banana and vanilla as neutral flavors. To induce a flavor aversion or preference, the undergraduates received these flavors mixed with a bitter substance (to condition an aversion) or sugar (to condition a preference). In subsequent tests with the CS flavors, subjects reported increased liking of the flavor that had been paired with sugar and decreased liking of the flavor that had been paired with the bitter taste. In another study, coffee drinkers reported increased liking of a flavor that was paired with the taste of coffee (Yeomans, Durlach, & Tinley, 2005).

These examples of how people learn to like or dislike initially neutral flavors is part of the general phenomenon of evaluative conditioning (De Houwer, Thomas, & Baeyens, 2001). In evaluative conditioning, our evaluation or liking of a stimulus changes by virtue of having that stimulus associated with something we already like or dislike. Evaluative conditioning is used extensively in the advertising industry. The product the advertiser is trying to sell is presented with things people already like in an effort to induce a preference for the product.

EXCITATORY PAVLOVIAN CONDITIONING PROCEDURES

What we have been discussing so far are instances of excitatory Pavlovian conditioning. In excitatory conditioning, organisms learn an association between the conditioned and unconditioned stimuli. As a result of this association, presentation of the CS activates behavioral and neural activity related to the US in the absence of the actual presentation of the US. Thus, dogs come to salivate in response to the sight of sand or colored water, pigeons learn to approach and peck a key light that is followed by food, rats learn to freeze to a sound that precedes foot shock, babies learn to blink in response to a tone that precedes a puff of air, and people learn to avoid a flavor that is followed by illness.

Common Pavlovian Conditioning Procedures

One of the major factors that determines the course of classical conditioning is the relative timing of the CS and the US. In most conditioning situations, seemingly small and trivial variations in how a CS is paired with a US can have profound effects on how vigorously the CR occurs, and when the CR occurs.
Five common classical conditioning procedures are illustrated in Figure 3.7. The horizontal distance in each diagram represents the passage of time; vertical displacements represent when a stimulus begins and ends. Each configuration of CS and US represents a single conditioning trial.

In a typical classical conditioning experiment, CS-US episodes are repeated a number of times during an experimental session. The time from the end of one conditioning trial to the start of the next trial is called the intertrial interval. By contrast, the time from the start of the CS to the start of the US within a conditioning trial is called the interstimulus interval or CS-US interval. For conditioned responding to develop, it is advisable to make the interstimulus interval much shorter than the intertrial interval (e.g., Sunsay & Bouton, 2008). In many experiments the interstimulus interval is less than 1 minute, whereas the intertrial interval may be 5 minutes or more. (A more detailed discussion of these parameters is provided in Chapter 4.)

1. **Short-delayed conditioning.** The most frequently used procedure for Pavlovian conditioning involves delaying the start of the US slightly after the start of the CS on each trial. This procedure is called short-delayed conditioning. The critical feature of short-delayed conditioning is that the CS
starts each trial and the US is presented after a brief (less than one minute) delay. The CS may continue during the US or end when the US begins.

2. **Trace conditioning.** The trace conditioning procedure is similar to the short-delayed procedure in that the CS is presented first and is followed by the US. However, in trace conditioning, the US is not presented until some time after the CS has ended. This leaves a gap between the CS and US. The gap is called the **trace interval.**

3. **Long-delayed conditioning.** The long-delayed conditioning procedure is also similar to the short-delayed conditioning in that the CS starts before the US. However, in this case the US is delayed much longer (5-10 minutes) than in the short-delay procedure. Importantly, the long-delayed procedure does not include a trace interval. The CS lasts until the US begins.

4. **Simultaneous conditioning.** Perhaps the most obvious way to expose subjects to a CS and a US is to present the two stimuli at the same time. This procedure is called **simultaneous conditioning.** The critical feature of simultaneous conditioning is that the conditioned and unconditioned stimuli are presented concurrently.

5. **Backward conditioning.** The last procedure depicted in Figure 3.7 differs from the others in that the US occurs shortly before, rather than after, the CS. This technique is called **backward conditioning** because the CS and US are presented in a “backward” order compared to the other procedures.

### Measuring Conditioned Responses

Pavlov and others after him have conducted systematic investigations of procedures like those depicted in Figure 3.7 to find out how the conditioning of a CS depends on the temporal relation between CS and US presentations. To make comparisons among the various procedures, one has to use a method for measuring conditioning that is equally applicable to all the procedures. This is typically done with the use of a **test trial.** A test trial consists of presenting the CS by itself (without the US). Responses elicited by the CS can then be observed without contamination from responses elicited by the US. Such CS-alone test trials can be introduced periodically during the course of training to track the progress of learning.

Behavior during the CS can be quantified in several ways. One aspect of conditioned behavior is how much of it occurs. This is called the **magnitude** of the CR. Pavlov, for example, measured the number of drops of saliva that were elicited by a CS. Other examples of the magnitude of CRs are the amount of response suppression that occurs in the CER procedure (see Figure 3.2) and the degree of depressed flavor preference that is observed in taste-aversion learning (see Figure 3.6).

The vigor of responding can also be measured by how often the CS elicits a CR. For example, we can measure the percentage of trials on which a CR is elicited by the CS. This measure is frequently used in studies of eyeblink conditioning (see Figure 3.3) and reflects the likelihood, or **probability** of responding.

A third aspect of conditioned responding is how soon the CR occurs after presentation of the CS. This measure of the vigor of conditioned behavior is called the **latency** of the CR. Latency is the amount of time that elapses between the start of the CS and the occurrence of the CR.
In the delayed and trace-conditioning procedures, the CS occurs by itself at the start of each trial (see Figure 3.7). Any conditioned behavior that occurs during this initial CS-alone period is uncontaminated by behavior elicited by the US and therefore can be used as a measure of learning. In contrast, responding during the CS in simultaneous and backward conditioning trials is bound to be contaminated by responding to the US or the recent presentation of the US. Therefore, test trials are critical for assessing learning in simultaneous and backward conditioning.

Control Procedures for Classical Conditioning

Devising an effective test trial is not enough to obtain conclusive evidence of classical conditioning. As I noted in Chapter 1, learning is an inference about the causes of behavior based on a comparison of at least two conditions. To be certain that a conditioning procedure is responsible for certain changes in behavior, those changes must be compared to the effects of a control procedure. What should the control procedure be? In studies of habituation and sensitization, we were interested only in the effects of prior exposure to a stimulus. Therefore, the comparison or control procedure was rather simple: it consisted of no prior stimulus exposure. In studies of classical conditioning, our interest is in how conditioned and unconditioned stimuli become associated. Concluding that an association has been established requires more carefully designed control procedures.

An association between a CS and a US implies that the two events have become connected in some way. After an association has been established, the CS is able to activate processes related to the US. An association requires more than just familiarity with the CS and US. It presumably depends on having the two stimuli experienced in connection with each other. Therefore, to conclude that an association has been established, one has to make sure that the observed change in behavior could not have been produced by prior separate presentations of the CS or the US.

As I described in Chapter 2, increased responding to a stimulus can be a result of sensitization, which is not an associative process. Presentations of an arousing stimulus, such as food to a hungry animal, can increase the behavior elicited by a more innocuous stimulus, such as a tone, without an association having been established between the two stimuli. Increases in responding observed with repeated CS-US pairings can sometimes result from exposure to just the US. If exposure to just the US produces increased responding to a previously ineffective stimulus, this is called pseudo-conditioning. Control procedures are required to determine whether responses that develop to a CS represent a genuine CS-US association, or just pseudo-conditioning.

Investigators have debated the proper control procedure for classical conditioning at length. Ideally, a control procedure should have the same number and distribution of CS and US presentations as the experimental procedure, but with the CSs and USs arranged so that they do not become associated. One possibility is to present the US periodically during both the CS and the intertrial interval, making sure that the probability of the US is the same during the intertrial interval as it is during the CS. Such a procedure is called a random control procedure. In a random control procedure, the CS does not signal an increase or change in the probability that the US will occur. The
random control was promising when it was first proposed (Rescorla, 1967b), but it has not turned out to be a useful control procedure for classical conditioning. Evidence from a variety of sources indicates that having the same probability of US presentations during the CS and the intertrial interval does not prevent the development of conditioned responding (Kirkpatrick & Church, 2004; Papini & Bitterman, 1990; Rescorla, 2000a; Williams, Lawson, Cook, & Johns, 2008).

A more successful control procedure involves presenting the conditioned and unconditioned stimuli on separate trials. Such a procedure is called the explicitly unpaired control. In the explicitly unpaired control, the CS and US are presented far enough apart to prevent their association. How much time has to elapse between them depends on the response system. In taste-aversion learning, much longer separation is necessary between the CS and US than in other forms of conditioning. In one variation of the explicitly unpaired control, only CSs are presented during one session and only USs are presented during a second session.

**Effectiveness of Common Conditioning Procedures**

There has been considerable interest in determining which of the procedures depicted in Figure 3.7 produces the strongest evidence of learning. The outcome of many early studies of the five conditioning procedures depicted in Figure 3.7 can be summarized by focusing on the interval between the start of the CS and the start of the US: the *interstimulus interval* or *CS-US interval*. Generally, little conditioned responding was observed in simultaneous conditioning procedures, where the CS-US interval was zero (e.g., Bitterman, 1964; Smith, Coleman, & Gormezano, 1969). Delaying the presentation of the US just a bit after the CS often facilitated conditioned responding. However, this facilitation was fairly limited (Ost & Lauer, 1965; Schneiderman & Gormezano, 1964). If the CS-US interval was increased further, conditioned responding declined, as is illustrated in Figure 3.8. Even in the taste-aversion conditioning procedure, where learning is possible with CS-US intervals of an hour or two, conditioned responding declines as the CS-US interval is increased (see Figure 3.6).

Trace conditioning procedures are interesting because they can have the same CS-US interval as delayed conditioning procedures. However, in trace procedures the CS is turned off a short time before the US occurs, resulting in a *trace interval*. Traditionally, trace conditioning has been considered to be less effective than delayed conditioning (Ellison, 1964; Kamin, 1965), because of the trace interval (Kaplan & Hearst, 1982; Rescorla, 1982). As with delayed conditioning, however, less conditioned responding is evident with a trace procedure if the interval between the CS and US is increased (Kehoe, Cool, & Gormezano, 1991).

The above findings encouraged the conclusion that conditioning is most effective when the CS is a good signal for the impending delivery of the US. The signal value of the CS is best in the short-delayed procedure, where the US occurs shortly after the onset of the CS. The CS becomes a less effective signal for the impending delivery of the US as the CS-US interval is increased. The CS is also a poor predictor of the US in simultaneous and trace procedures. In simultaneous conditioning, the US occurs at the same time as the CS and is therefore not signaled by the CS. In trace conditioning, the CS is
followed by the trace interval rather than the US. Hence the trace interval is the best predictor of the US.

The one procedure whose results were difficult to interpret in terms of CS signal value was backward conditioning. Backward conditioning produced mixed results. Some investigators observed excitatory responding with backward pairings of a CS and US (e.g., Ayres, Haddad, & Albert, 1987; Spetch, Wilkie, & Pinel, 1981). Others reported primarily inhibition of conditioned responding with backward conditioning (e.g., Maier, Rapaport, & Wheatley, 1976; Siegel & Domjan, 1971; see also Chang, Blaisdell, & Miller, 2003). To make matters even more confusing, in a rather remarkable experiment, Tait and Saladin (1986) found both excitatory and inhibitory conditioning effects resulting from the same backward conditioning procedure (see also, McNish, Betts, Brandon, & Wagner, 1997).

The simple assumption that CS signal value determines whether a procedure will produce conditioned responding clearly cannot explain the complexity of findings that have been obtained in backward conditioning. The idea that there is a unitary hypothetical construct such as signal value or associative strength that varies as a function of the CS-US interval has also been challenged by the results of more recent experiments that have employed more sophisticated and diverse measures of learning. These studies have documented that delayed, simultaneous, trace, and backward conditioning can all produce strong learning and vigorous conditioned responding (e.g., Albert & Ayres, 1997; Akins & Domjan, 1996; Marchand & Kamper, 2000; Romaniuk & Williams, 2000; Schreurs, 1998; Williams & Hurlburt,
2000). However, different behavioral processes are engaged by these variations in procedure, and the learning that occurs is mediated by different neural circuits (e.g., Han et al., 2003; Kalmbach et al., 2008; Waddell, Morris, & Bouton, 2006). In a study of fear conditioning (Esmoris-Arranz, Pardo-Vázquez, & Vázquez-Garcia, 2003), with a short-delayed procedure, the CS came to elicit conditioned freezing, but with a simultaneous procedure, the CR was movement away from the CS, or escape. As I will describe in greater detail in Chapter 4, the nature of the CR also varies between short-delayed and long-delayed conditioning procedures.

An important reason why animals come to perform different responses with different procedures is that instead of learning just a CS-US association, participants also learn when the US occurs in relation to the CS (Balsam, Drew, & Yang, 2001; Balsam & Gallistel, in press; Ohyama & Mauk, 2001). For example, in a recent study (Williams et al., 2008), rats received a pellet of food either 30 seconds or 90 seconds after the onset of an auditory CS. The investigators monitored when the rat poked its head into the food cup as a measure of conditioned behavior. Food-cup entries peaked at the scheduled time of food delivery: 30 or 90 seconds after the onset of the CS. The view that classical conditioning involves not only learning what to expect but when to expect it is called the temporal coding hypothesis (Amundson & Miller, 2008; Barnet, Cole, & Miller, 1997; Brown, Hemmes, & de Vaca, 1997; Cole, Barnet, & Miller, 1995; Savastano & Miller, 1998). I will revisit this issue in Chapter 4.

INHIBITORY PAVLOVIAN CONDITIONING

So far I have been discussing Pavlovian conditioning in terms of learning to predict when a significant event or US will occur. But, there is another type of Pavlovian conditioning, inhibitory conditioning, in which you learn to predict the absence of the US. Why would you want to predict the absence of something?

Consider being in an environment where bad things happen to you without warning. Civilians in a war zone can encounter road-side bombs or suicide bombers without much warning. A child in an abusive home also experiences unpredictable aversive events (yelling, slamming doors, and getting hit) for no particular reason. Getting pushed and shoved in a crowd also involves danger that arises without much warning and independent of what you might be doing. Research with laboratory animals has shown that exposure to unpredictable aversive stimulation is highly aversive and results in stomach ulcers and other physiological symptoms of stress. If one has to be exposed to aversive stimulation, predictable or signaled aversive stimuli are preferable to unpredictable aversive stimulation (Mineka & Henderson, 1985).

The benefit of predictability is evident even in the case of a panic attack. A panic attack is a sudden sense of fear or discomfort, accompanied by physical symptoms (e.g., heart palpitations) and a sense of impending doom. If such attacks are fairly frequent and become the source of considerable anxiety, the individual is said to suffer from panic disorder. At some point in their lives, 3.5% of the population has panic disorder (Kessler et al., 1994). Sometimes individuals with panic disorder are able to predict the onset of a panic attack. At other times, they may experience an attack without warning. In a study of individuals who experienced both predictable and unpredictable panic attacks,
Craske, Glover, and DeCola (1995) measured the general anxiety of the participants before and after each type of attack. The results are summarized in Figure 3.9. Before the attack, anxiety ratings were similar whether the attack was predictable or not. Interestingly, however, anxiety significantly increased after an unpredicted panic attack and decreased after a predicted attack. Such results indicate that the anxiety that is generated by the experience of panic attacks occurs primarily because of the unpredictability of the attacks.

The ability to predict bad things is very helpful because it also enables you to predict when bad things will not happen. Consistent with this reasoning, many effective stress-reduction techniques, such as relaxation training or meditation, involve creating a predictable period of safety or a time when you can be certain that nothing bad will happen. Stress management consultants recognize that it is impossible to eliminate aversive events from one’s life altogether. For example, a teacher supervising a playground with pre-school children is bound to encounter the unexpected stress of a child falling or hitting another child. One cannot prevent accidents or avoid having children hurt each other. However, introducing even short periods of predictable safety (e.g., by allowing the teacher to take a break) can substantially reduce stress. That is where conditioned inhibition comes in. A conditioned inhibitor is a signal for the absence of the US.

Although Pavlov discovered inhibitory conditioning early in the twentieth century, this type of learning did not command the serious attention of
psychologists until decades later (Boakes & Halliday, 1972; Rescorla, 1969b; Savastano, Cole, Barnet, & Miller, 1999; Williams, Overmier, & LoLordo, 1992). I will describe two major procedures used to produce conditioned inhibition and the special tests that are necessary to detect and measure conditioned inhibition.

**Procedures for Inhibitory Conditioning**

Unlike excitatory conditioning, which can proceed without special preconditions, conditioned inhibition has an important prerequisite. For the absence of a US to be a significant event, the US has to occur periodically in the situation. There are many signals for the absence of events in our daily lives. Signs such as “Closed,” “Out of Order,” and “No Entry” are all of this type. However, these signs provide meaningful information and influence what we do only if they indicate the absence of something we otherwise expect to see. For example, if we encounter the sign “Out of Gas” at a service station, we may become frustrated and disappointed. The sign “Out of Gas” provides important information here because we expect service stations to have fuel. The same sign does not tell us anything of interest if it is in the window of a lumber yard, and it is not likely to discourage us from going to buy lumber. This illustrates the general rule that inhibitory conditioning and inhibitory control of behavior occur only if there is an excitatory context for the US in question (e.g., Chang, Blaisdell, & Miller, 2003; LoLordo & Fairless, 1985). This principle makes inhibitory conditioning very different from excitatory conditioning which has no such prerequisites.

**Pavlov’s Procedure for Conditioned Inhibition**

Pavlov recognized the importance of an excitatory context for the conditioning of inhibition and was careful to provide such a context in his standard inhibitory training procedure (Pavlov, 1927). The procedure he used, diagrammed in Figure 3.10, involves two conditioned stimuli and two kinds of conditioning trials, one for excitatory conditioning and the other for inhibitory conditioning. The US is presented on excitatory conditioning trials (Trial Type A in Figure 3.10), and whenever the US occurs, it is announced by a stimulus labeled CS+ (e.g., a tone). Because of its pairings with the US, the CS+ becomes a signal for the US and can then provide the excitatory context for the development of conditioned inhibition.

During inhibitory conditioning trials (Trial Type B in Figure 3.10), the CS+ is presented together with the second stimulus called the CS− (e.g., a light), and the US does not occur. Thus, the CS− is presented in the excitatory context provided by the CS+ but the CS− is not paired with the US. This makes the CS− a conditioned inhibitor. During the course of training, A-type and B-type trials are alternated randomly. As the participant receives repeated trials of CS+ followed by the US and CS+/CS− followed by no US, the CS− gradually acquires inhibitory properties. (For recent studies with Pavlov’s conditioned inhibition procedure, see Campolattaro, Schnitker, & Freeman, 2008; Urcelay & Miller, 2008a).

Pavlov’s conditioned inhibition procedure is analogous to a situation in which something is introduced that prevents an outcome that would occur otherwise. A red traffic light at a busy intersection is a signal for potential
danger because running the light could get you into an accident. However, if a police officer indicates that you should cross the intersection despite the red light (perhaps because the traffic light is malfunctioning), you will probably not have an accident. Here the red light is the CS+ and the gestures of the officer constitute the CS−. The gestures inhibit, or block, your hesitation to cross the intersection because of the red light.

A CS− acts as a safety signal in the context of danger. Children who are afraid will take refuge in the arms of a parent because the parent serves as a safety signal. Adults who are anxious also use safety signals to reduce or inhibit their fear or anxiety. People rely on prayer, a friend, a therapist, or a comforting food at times of stress (Barlow, 1988). These work in part because we have learned that bad things don’t happen in their presence.

**Negative CS-US Contingency or Correlation**

Another common procedure for producing conditioned inhibition does not involve an explicit excitatory stimulus or CS+. Rather, it involves just a CS− that is negatively correlated with the US. A negative correlation or contingency means that the US is less likely to occur after the CS than at other times. Thus, the CS signals a reduction in the probability that the US will occur. A sample arrangement that meets this requirement is diagrammed in Figure 3.11. The US is periodically presented by itself. However, each occurrence of the CS is followed by the predictable absence of the US for a while.

Consider a child who periodically gets picked on by his classmates when the teacher is out of the room. This is like periodically receiving an aversive stimulus or US. When the teacher returns, the child can be sure he will not be bothered. Thus, the teacher serves as a CS− that signals a period free from harassment, or the absence of the US.

Conditioned inhibition is reliably observed in procedures in which the only explicit CS is negatively correlated with the US (Rescorla, 1969a). What provides the excitatory context for this inhibition? In this case, the environmental cues of the experimental chamber provide the excitatory context (Dweck & Wagner, 1970). Because the US occurs periodically in the experimental situation, the contextual cues of the experimental chamber acquire excitatory properties. This in turn permits the acquisition of inhibitory properties
by the CS. (For a recent study on the role context in inhibitory conditioning, see Chang, Blaisdell, & Miller, 2003).

In a negative CS-US contingency procedure, the aversive US may occur shortly after the CS occasionally but it is much more likely to occur in the absence of the CS; that is what defines the negative CS-US contingency. However, even in the absence of the CS, the exact timing of the US cannot be predicted precisely because the US occurs at various times probabilistically. This is in contrast to Pavlov’s procedure for conditioned inhibition. In Pavlov’s procedure, the US always occurs at the end of the CS+ and does not occur when the CS− is presented together with the CS+. Since Pavlov’s procedure permits predicting the exact timing of the US, it also permits predicting exactly when the US will not occur. The US will not occur at the end of CS+ if the CS+ is presented with the CS−. Tests of temporal learning have shown that in Pavlov’s procedure for conditioned inhibition participants learn exactly when the US will be omitted (Denniston, Blaisdell, & Miller, 2004; Williams, Johns, & Brindas, 2008).

**Measuring Conditioned Inhibition**

How are conditioned inhibitory processes manifested in behavior? For conditioned excitation, the answer to this type of question is straightforward. Conditioned excitatory stimuli come to elicit new responses such as salivation, approach, or eye blinking, depending on what the US was. One might expect that conditioned inhibitory stimuli would elicit the opposites of these reactions—namely, suppression of salivation, approach, or eye blinking—but how are we to measure such response opposites?

**Bi-Directional Response Systems**

Identification of opposing response tendencies is easy with response systems that can change in opposite directions from baseline or normal performance. Heart rate, respiration, and temperature can all increase or decrease from a baseline level. Certain behavioral responses are also bi-directional. For example, animals can either approach or withdraw from a stimulus or drink more or less of a flavored solution. In these cases, conditioned excitation results in a change in behavior in one direction and conditioned inhibition results in a change in behavior in the opposite direction.

Unfortunately, many responses are not bi-directional. Consider freezing or response suppression as a measure of conditioned fear. A conditioned excitatory stimulus will elicit freezing, but a conditioned inhibitor will not produce
activity above normal levels. A similar problem arises in eyeblink conditioning. A CS+ will elicit increased blinking, but the inhibitory effects of a CS− are difficult to detect because the baseline rate of blinking is low to begin with. It is hard to see inhibition of blinking below an already low baseline. Because of these limitations, conditioned inhibition is typically measured indirectly using the compound stimulus test and the retardation of acquisition test.

The Compound-Stimulus, or Summation, Test

The compound-stimulus (or summation) test was particularly popular with Pavlov and remains one of the most widely accepted procedures for the measurement of conditioned inhibition. The test is based on the simple idea that conditioned inhibition counteracts or inhibits conditioned excitation. Therefore, to observe conditioned inhibition, one has to measure how the presentation of a CS− disrupts or suppresses responding that would normally be elicited by a CS+.

A particularly well controlled demonstration of conditioned inhibition using the compound-stimulus or summation test was reported by Cole, Barnett, and Miller (1997). The experiment was conducted using the lick-suppression procedure with laboratory rats. The subjects received inhibitory conditioning in which the presentation of a flashing light by itself always ended in a brief shock (A+), and the presentation of an auditory cue (X) together with the light ended without shock (AX−). Thus, Pavlov’s procedure for conditioned inhibition was used and X was predicted to become an inhibitor of fear. A total of 28 A+ trials and 56 AX− trials were conducted over 7 sessions. The participants also received training with another auditory stimulus (B) in a different experimental chamber, and this stimulus always ended in the brief shock (B+). The intent of these procedures was to establish conditioned excitation to A and B and conditioned inhibition to X.

Cole et al. then asked whether the presumed inhibitor X would suppress responding to the excitatory stimuli A and B. The results of those tests are summarized in Figure 3.12. How long the participants took to accumulate five seconds of uninterrupted drinking was measured. Notice that when the excitatory stimuli, A and B, were presented by themselves, the rats required substantial amounts of time to complete the five second drinking criterion. In contrast, when the excitatory stimuli were presented together with the conditioned inhibitor (AX and BX tests), the drinking requirement was completed much faster. Thus, presenting stimulus X with A and B reduced the drinking suppression that occurred when A and B were presented by themselves. X inhibited conditioned fear elicited by A and B.

Figure 3.12 includes another test condition, stimulus B, tested with another auditory cue, Y. Stimulus Y was not previously conditioned as an inhibitor and was presented to be sure that introducing a new stimulus with stimulus B would not cause disruption of the conditioned fear response. As Figure 3.12 illustrates, no such disruption occurred with stimulus Y. Thus, the inhibition of conditioned fear was limited to the stimulus (X) that received conditioned inhibition training. Another important aspect of these results is that X was able to inhibit conditioned fear not only to the exciter with which it was trained (A) but also to another exciter (B) that had never been presented with X during training.
The compound-stimulus test for conditioned inhibition indicates that the presentation of a conditioned inhibitor or safety signal can reduce the stressful effects of an aversive experience. This prediction was tested with patients who were prone to experience panic attacks (Carter, Hollon, Carson, & Shelton, 1995). Panic attack patients were invited to the laboratory and accompanied by someone with whom they felt safe. Panic was experimentally induced in the participants by having them inhale a mixture of gas containing elevated levels of carbon dioxide. The participants were then asked to report on their perceived levels of anxiety and catastrophic ideation triggered by the carbon dioxide exposure. The experimental manipulation was the presence of another person with whom the participants felt safe (the conditioned inhibitor). Half the participants were allowed to have their trusted acquaintance in the room with them during the experiment, whereas the remaining participants took part in the experiment alone. The results indicated that the presence of a safe acquaintance reduced the anxiety and catastrophic ideation associated
with the panic attack. These results explain why children are less fearful during a medical examination if they are accompanied by a trusted parent or guardian. (For a review of panic disorder including the role of learning, see Craske & Waters, 2005.)

**The Retardation of Acquisition Test**

Another frequently used indirect test of conditioned inhibition is the retardation of acquisition test (Rescorla, 1969b). The rationale for this test is straightforward. If a stimulus actively inhibits a particular response, then it should be especially difficult to condition that stimulus to elicit the behavior. In other words, the rate of excitatory conditioning should be retarded if the CS is a conditioned inhibitor. This prediction was tested by Cole et al. (1997) in an experiment very similar to their summation test study described above.

After the same kind of inhibitory conditioning that produced the results summarized in Figure 3.12, Cole et al. took stimulus X (which had been conditioned as an inhibitor) and stimulus Y (which had not been used in a conditioning procedure before) and conducted a retardation of acquisition test by pairing each stimulus with shock on three occasions. (Three acquisition trials were sufficient since conditioned fear is learned faster than the inhibition of fear.) After the three acquisition trials, each stimulus was tested to see which would cause greater suppression of drinking. The results are presented in Figure 3.13. The time to complete five seconds of drinking took much longer in the presence of the control stimulus Y than in the presence of stimulus X, which had previously been trained as a conditioned inhibitor. Thus, the initial inhibitory training of X retarded its acquisition of excitatory conditioned fear properties.

Conditioned inhibition can be difficult to distinguish from other behavioral processes. Therefore, the best strategy is to use more than one test and be sure that all of the results point to the same conclusion. Rescorla (1969b) advocated using both the compound stimulus test and the retardation of acquisition test. This dual test strategy has remained popular ever since (Campolattaro, Schnitker, & Freeman, 2008; Savastano et al., 1999; Williams et al., 1992).

**PREVALENCE OF CLASSICAL CONDITIONING**

Classical conditioning is typically investigated in laboratory situations. However, we do not have to know much about classical conditioning to realize that it also occurs in a wide range of situations outside the laboratory. Classical conditioning is most likely to develop when one event reliably precedes another in a short-delayed CS-US pairing. This occurs in many aspects of life. As I mentioned at the beginning of the chapter, stimuli in the environment occur in an orderly temporal sequence, largely because of the physical constraints of causation. Some events simply cannot happen before other things have occurred. Eggs won’t be hard boiled until they have been put in boiling water. Social institutions and customs also ensure that things happen in a predictable order. Whenever one stimulus reliably precedes another, classical conditioning may take place.

One area of research that has been of particular interest is how people come to judge one event as the cause of another. In studies of human causal judgment, participants are exposed to repeated occurrences of two events (pictures of a blooming flower and a watering can briefly presented on a computer screen) in
various temporal arrangements. In one condition, for example, the watering can may always occur before the flower; in another it may occur at random times relative to the flower. After observing numerous appearances of both objects, the subjects are asked to indicate their judgment about the strength of causal relation between them. Studies of human causal judgment are analogous to studies of Pavlovian conditioning in that both involve repeated experiences with two events and responses based on the extent to which those two events become linked to each other. Given this correspondence, one might suspect that there is considerable commonality in the outcomes of causal judgment and Pavlovian conditioning experiments. That prediction has been supported in numerous studies, suggesting that Pavlovian associative mechanisms are not limited to Pavlov’s dogs, but may play a role in the numerous judgments of causality we all make during the course of our daily lives (see Allan, 2005).

As I described earlier in the chapter, Pavlovian conditioning can result in the conditioning of food preferences and aversions. It can also result in the acquisition of fear. Conditioned fear responses have been of special interest because they may contribute significantly to anxiety disorders, phobias, and

![Diagram of Two-Test Strategy](image-url)
panic disorder (Bouton, 2001; Bouton, Mineka, & Barlow, 2001; Craske, Hermans, & Vansteenwegen, 2006). As I will discuss further in Chapter 4, Pavlovian conditioning is also involved in drug tolerance and addiction. Cues that reliably accompany drug administration can come to elicit drug-related responses through conditioning. In discussing this type of learning among crack addicts, Dr. Scott Lukas of McLean Hospital in Massachusetts described the effects of drug-conditioned stimuli by saying that “These cues turn on crack-related memories, and addicts respond like Pavlov’s dogs” (Newsweek, February 12, 2001, p. 40).

Pavlovian conditioning is also involved in infant and maternal responses in nursing. Suckling involves mutual stimulation for the infant and the mother. To successfully nurse, the mother has to hold the baby in a particular position, which provides special tactile stimuli for both the infant and the mother. The tactile stimuli experienced by the infant may become conditioned to elicit orientation and suckling responses on the part of the baby (Blass, Ganchrow, & Steiner, 1984). The tactile stimuli experienced by the mother may also become conditioned, in this case to elicit the milk let-down response of the mother in anticipation of having the infant suckle. Mothers who nurse their babies frequently experience the milk let-down reflex when the baby cries or when the usual time for breast-feeding arrives. All these stimuli (special tactile cues, the baby’s crying, and the time of normal feedings) reliably precede suckling by the infant. Therefore, they can become conditioned by the suckling stimulation and come to elicit milk secretion as a CR. The anticipatory conditioned orientation and suckling responses and the anticipatory conditioned milk let-down response make the nursing experience more successful for both the baby and the mother.

Pavlovian conditioning is also important in sexual situations. Although clinical observations indicate that human sexual behavior can be shaped by learning experiences (Akins, 2004), the most systematic evidence of sexual conditioning has been obtained in studies with laboratory animals (Pfaus, Kippin, & Centeno, 2001; Woodson, 2002). In these studies, males typically serve as participants, and the US is provided either by the sight of a sexually receptive female, or by physical access to a female (Domjan, 1998). Subjects come to approach stimuli that signal the availability of a sexual partner (Burns & Domjan, 1996; Hollis, Cadieux, & Colbert, 1989). The presentation of a sexual CS also facilitates various aspects of reproductive behavior. Studies with rats, quail, and fish have shown that after exposure to a sexual CS, males are quicker to perform copulatory responses (Zamble, Hadad, Mitchell, & Cutmore, 1985), compete more successfully with other males for access to a female (Gutiérrez & Domjan, 1996), show more courtship behavior (Hollis, Cadieux, & Colbert, 1989), release greater quantities of sperm (Domjan, Blesbois, & Williams, 1998), and show increased levels of testosterone and leuteinizing hormone (Graham & Desjardins, 1980).

Although the preceding studies of sexual conditioning are noteworthy, the ultimate payoff for sexual behavior is the number of offspring that are produced. Hollis, Pharr, Dumas, Britton, and Field (1997) were the first to show (in a fish species) that the presentation of a Pavlovian CS+ before a sexual encounter greatly increased the numbers of offspring that resulted from the reproductive behavior. This effect of Pavlovian conditioning on increased fertility has since been also demonstrated in quail (Adkins-Regan & MacKillop, 2003; Mahometta & Domjan, 2005). In a recent study, Pavlovian conditioning
also influenced the outcome of sperm competition in domesticated quail (Matthews, Domjan, Ramsey, & Crews, 2007). To observe sperm competition, two male quail were permitted to copulate with the same female. A copulatory interaction in quail can fertilize as many as 10 of the eggs the female produces after the sexual encounter. If two males copulate with the same female in succession, the male whose copulation is signaled by a Pavlovian CS+ sires significantly more of the resulting offspring. This is a very important finding because it shows that “learning and individual experience can bias genetic transmission and the evolutionary changes that result from sexual competition” (Matthews et al., 2007, p. 762).

CONCLUDING COMMENTS

Chapter 3 continued the discussion of elicited behavior by turning attention from habituation and sensitization to classical conditioning. Classical conditioning is a bit more complex in that it involves associatively-mediated elicited behavior. In fact, classical conditioning is one of the major techniques for investigating how associations are learned. As we have seen, classical conditioning may be involved in many different important aspects of behavior. Depending on the procedure used, the learning may occur quickly or slowly. With some procedures, excitatory responses are learned; with other procedures, the organism learns to inhibit an excitatory response tendency. Excitatory and inhibitory conditioning occur in many aspects of common experience and serve to help us cope with significant biological events (unconditioned stimuli).

SAMPLE QUESTIONS

1. Describe similarities and differences between habituation, sensitization, and classical conditioning.
2. What is object learning, and how is it similar or different from conventional classical conditioning?
3. What is the most effective procedure for excitatory conditioning and how is it different from other possibilities?
4. What is a control procedure for excitatory conditioning and what processes is the control procedure intended to rule out?
5. Are conditioned excitation and conditioned inhibition related? If so, how are they related?
7. Describe four reasons why classical conditioning is of interest to psychologists.

KEY TERMS

autoshaping   Same as sign tracking.
backward conditioning A procedure in which the conditioned stimulus is presented shortly after the unconditioned stimulus on each trial.
compound-stimulus test A test procedure that identifies a stimulus as a conditioned inhibitor if that stimulus reduces the responding elicited by a conditioned excitatory stimulus. Also called summation test.
conditional or conditioned response (CR)  The response that comes to be made to the conditioned stimulus as a result of classical conditioning.

conditional or conditioned stimulus (CS)  A stimulus that does not elicit a particular response initially, but comes to do so as a result of becoming associated with an unconditioned stimulus.

classical conditioning procedure

conditioned emotional response (CER)  Suppression of positively reinforced instrumental behavior (e.g., lever pressing for food pellets) caused by the presentation of a stimulus that has become associated with an aversive stimulus. Also called conditioned suppression.

conditioned suppression  Same as conditioned emotional response.

conditioning trial  A training episode involving presentation of a conditioned stimulus with (or without) an unconditioned stimulus.

CS-US interval  Same as interstimulus interval.

evaluative conditioning  Changing the hedonic value or liking of an initially neutral stimulus by having that stimulus associated with something that is already liked or disliked.

explicitly unpaired control  A procedure in which both conditioned and unconditioned stimuli are presented, but with sufficient time between them so that they do not become associated with each other.

inhibitory conditioning  A type of classical conditioning in which the conditioned stimulus becomes a signal for the absence of the unconditioned stimulus.

interstimulus interval  The amount of time that elapses between presentations of the conditioned stimulus (CS) and the unconditioned stimulus (US) during a classical conditioning trial. Also called the CS-US interval.

intertrial interval  The amount of time that elapses between two successive trials.

latency  The time elapsed between a stimulus (or the start of a trial) and the response that is made to the stimulus.

lick-suppression procedure  Similar to the conditioned emotional response (CER), or conditioned suppression procedure. However, instead of lever pressing for food serving as the behavior that is suppressed by conditioned fear, the baseline is licking a water spout by thirsty rats. The presentation of a fear-conditioned CS slows down the rate of drinking.

magnitude of a response  A measure of the size, vigor, or extent of a response.

object learning  Learning associations between different stimulus elements of an object.

probability of a response  The likelihood of making the response, usually represented in terms of the percentage of trials on which the response occurs.

pseudo-conditioning  Increased responding that may occur to a stimulus whose presentations are intermixed with presentations of an unconditioned stimulus (US) in the absence of the establishment of an association between the stimulus and the US.

random control procedure  A procedure in which the conditioned and unconditioned stimuli are presented at random times with respect to each other.

retardation of acquisition test  A test procedure that identifies a stimulus as a conditioned inhibitor if that stimulus is slower to acquire excitatory properties than a comparison stimulus.

short-delayed conditioning  A classical conditioning procedure in which the conditioned stimulus is initiated shortly before the unconditioned stimulus on each conditioning trial.
sign tracking Movement toward and possibly contact with a stimulus that signals the availability of a positive reinforcer, such as food. Also called autoshaping.

simultaneous conditioning A classical conditioning procedure in which the conditioned stimulus and the unconditioned stimulus are presented simultaneously on each conditioning trial.

summation test Same as compound-stimulus test.

temporal coding hypothesis The idea that Pavlovian conditioning procedures lead not only to learning that the US happens but exactly when it occurs in relation to the CS. The CS comes to represent (or code) the timing of the US.

test trial A trial in which the conditioned stimulus is presented without the unconditioned stimulus. This allows measurement of the conditioned response in the absence of the unconditioned response.

trace conditioning A classical conditioning procedure in which the unconditioned stimulus is presented after the conditioned stimulus has been terminated for a short period.

trace interval The interval between the end of the conditioned stimulus and the start of the unconditioned stimulus in trace-conditioning trials.

unconditional or unconditioned response (UR) A response that occurs to a stimulus without the necessity of prior training.

unconditional or unconditioned stimulus (US) A stimulus that elicits a particular response without the necessity of prior training.