



LEARNING AND MEMORY

AN INTRODUCTION



James L. McGaugh

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PREFACE

One of the most obvious facts of experience is that we are profoundly influenced by our experiences. Our ability to learn and remember allows us to alter our behavior to fit the requirements of an ever-changing environment and provides a basis for the complex processes of thought, language, and intelligence.

This book is a brief introduction to the phenomena of learning and memory. We know a great deal about the conditions under which learning occurs. But, as yet, we know little about the bases of learning. The nature of the “machinery” underlying learning, memory, and complex intellectual processes is perhaps the most intriguing as well as important scientific problem. And, of course, it is of immense practical importance that we understand these phenomena since our behavior depends so fundamentally upon the cumulative and lasting effects of our experiences.

Many individuals have influenced the development of this book and I gratefully acknowledge these influences. I thank my colleague Richard F. Thompson for his contribution to Chapter 3 (Thought and Language). Karen Dodd was responsible for preparing the several drafts of the chapters and for attending to all of the details involved in preparing the manuscript for publication. I thank her for her expert assistance. I also thank those who have permitted me to quote or reproduce material from their works. Finally, I thank my teachers and students and colleagues for their influences on my learning about learning.

JAMES L. McGAUGH

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CHAPTER ONE

LEARNING AND BEHAVIORAL ADAPTATION

As we know from our everyday observations, our behavior is profoundly influenced by our experiences. We have learned to talk, to read, to write, to plan, to hope, and to love. We have also learned to deceive, to fear, and perhaps to hate. Learning in its broadest

sense makes human socialization possible. Society is based on the training provided by subtle as well as explicit experiences, such as formal education. Because of our enormous capacity for learning, human behavior can be and is extremely varied. For example, as humans we inherit molecules that program the neurobiological processes which make it possible for us to acquire and use language. However, the language each of us learns is the language spoken by those around us. So it is with all our skills, habits, aspirations, beliefs, and prejudices. For centuries scholars have wondered what human beings would be like if they were reared in isolation from other human beings. One speculation was that children reared in cultural isolation might speak some basic or "natural" human language. In all likelihood, however, they would acquire no language at all. They would in fact lack most of the characteristics that we regard as distinctively "human." We learn to be human beings.



LEARNING

Since it is learning that enables us to adapt to the complex requirements of our environments, it might be well to begin with a biological perspective of learning. The basis of evolution is adaptation. The survival of any species depends on its ability to adapt to the requirements of its own particular environment. There are, of course, many ways in which adaptation takes place. Through the slow process of genetic mutation and selection a species can acquire the necessary form and physiological machinery for almost any environmental condition. For example, many species, such as the polar bear, have evolved a coloration that serves as camouflage in their natural surroundings. The physiology of such arctic animals is also quite different from that of desert animals. Adaptation is particularly apparent in behavior. Lower animals can, without specific training, perform many complicated tasks, such as nest building, migrating, communicating, and mating. The development of such genetically influenced responses, commonly referred to as *instincts*, provides for rather complex behavioral adaptation to special environments. However, organisms sometimes become so specialized in form or function that they are unable to survive. In a complex environment the evolution of unique morphological, physiological, or even behavioral factors can prove fatal to the species.

Evolution of the ability to respond to *changes* in the environment clearly added a new dimension to the capacity of organisms to adapt. Specialized physiological responses such as the growth of plants toward light and hibernation of some mammals in cold weather provide for some adjustment to environmental changes. However, the most flexible basis of individual adaptation was provided by evolution of the capacity of the individual organism to vary its behavioral responses in terms of different environmental requirements—that is, to learn. Learning can do quickly what evolution can do only slowly. Whereas adaptation to a single environmental condition takes generations to achieve through evolution, an organism that can learn is able to tailor its own behavior to fit a variety of environmental conditions. Of course the ability to learn provides the basis for adaptation, but not all learning is adaptive. Just as effective behavior can be learned, so ineffective or neurotic behavior can also be learned.

For years psychologists and other biological scientists have attempted to develop a general definition of learning. Learning is most often defined as a more or less permanent change in behavior produced by experience. Although this is a useful working definition, it is admittedly imprecise. We will not have an adequate definition of learning until we know more about the varieties of behavioral plasticity that are considered examples of learning. For example, we use the phrase, “more or less permanent” as a hedge, because we do not yet know whether all the effects of experience are permanent. Certainly we and the other animals forget, and until we completely understand the nature of forgetting we cannot be certain whether, in the legendary words of William James, “nothing we ever do is, in strict scientific literalness, wiped out” [James, 1890, p. 127].

In analyzing behavior it is difficult to sort out the various influences which cause behavior to change. Learning does not take place in a vacuum, and the basic problem lies in distinguishing learning from other influences on behavior, such as fatigue, sensory adaptation, disease, injury, aging, and genetic contributions to the development of responses. For centuries man has trained animals of many species, including his own, by reward and punishment, or *instrumental conditioning*. A number of years ago two psychologists, Breland and Breland, developed a program of instrumental learning to train animal acts for county fairs and amusement parks. In general they were quite successful, but they encountered some interesting difficulties. For example, they trained a pig to pick up wooden coins and deposit them in a large “piggy bank” by rewarding it for successful responses [Breland and Breland, 1961, p. 683]:

At first the pig would eagerly pick up one dollar, carry it to the bank, run back, get another, . . . and so on. . . . Thereafter, over a period of weeks the behavior would become slower and slower. He might run over eagerly for each dollar, but on the way back, instead of carrying

the dollar and depositing it simply and cleanly, he would repeatedly drop it, root it [that is, push it with his nose], drop it again, root it along the way, pick it up, toss it up in the air, drop it, [and] root it some more.

This pattern persisted even when the pig became extremely hungry because it worked too slowly to get enough to eat over the course of the day. Why did the learned behavior deteriorate? Breland and Breland suggested that the rooting behavior competed with the learned behavior because rooting is built into this species as part of the food-getting repertoire. On the basis of many similar observations with various other species, they reached the important conclusion that "the behavior of any species cannot be adequately understood, predicted, or controlled without knowledge of its institutional patterns, evolutionary history and ecological niche" [Breland and Breland, 1961, p. 684]. This point has bearing on many of the aspects of learning we shall discuss.

It is often assumed that only one or perhaps two forms of behavioral modification can properly be called learning. It is becoming increasingly apparent, however, that there are a number of types of behavioral modifications produced by experience. A complete understanding of learning must be based on an examination of each type. There is reason to believe that much of the variety simply reflects differences in the training procedures. However, there may well be actual differences in the neurobiological mechanisms of some types of learning.

One form of learning observed in all species, from the single-celled protozoan to man, is *habituation*, the decrease in response to a specific stimulus with repeated stimulation. When we hear an unexpected noise our attention is aroused and directed toward its

HABITUATION

source. If the noise is repeated, we habituate to it; we cease paying attention to it and eventually may not even be aware of it. For example, as we sit by a highway we often quickly come to ignore the sounds of passing automobiles. Responsiveness to repeated stimulation can decrease for other reasons which we must be careful to distinguish from habituation. In habituation the decrease in responsiveness is fairly specific to a particular stimulus. Following habituation of a response to a specific stimulus the response can still be elicited by stimuli other than the specific one to which it was habituated. This is in contrast to *sensory adaptation*, which affects sensitivity to all stimuli within a given sensory modality. Habituation must also be differentiated from *fatigue*, which decreases responsiveness to *all* stimulation. Under some circumstances repeated stimulation can also lead to increased responsiveness, or *sensitization*. However, the increased responsiveness is not necessarily

TABLE 1-1 *Average number of trials required for habituation in spirostomum to mechanical stimulation repeated at 5-minute intervals [Applewhite, 1968].*

	AVERAGE NO. OF TRIALS
Whole naïve animals	9.0
Halves of habituated animals	
Anterior	3.1
Posterior	3.6
Halves of naïve animals	
Anterior	7.1
Posterior	9.6

stimulus specific. Habituation is often termed the simplest form of behavioral plasticity. It is obviously an adaptive function, and it is possible that the evolution of altered responsiveness in simple animals may have provided a basis of subsequent evolution of more complex learning processes.

Several examples will illustrate the pervasiveness of habituation. The protozoan *spirostomum* responds to stimulation by contracting. Applewhite [1968] found that when these single-celled animals were repeatedly stimulated by a mild jarring vibration every 5 seconds their response progressively decreased. In one experiment the animals ceased all contractions after only nine jarrings. After training the animals were cut in half, and the two sections (anterior and posterior) were given additional habituation training. Rehabilitation of the severed halves took fewer than four trials (see Table 1-1). When naïve animals were cut in half the sections habituated in approximately the same number of trials as the intact animals (7 to 10 trials). Further tests showed that the decrease in responsiveness was not due either to fatigue or to local sensory adaptation. Clearly habituation in simple organisms does not require an organized nervous system.

Habituation of responses, including responses to socially significant stimuli, has been studied extensively in more complex species [Thorpe, 1963]. According to Lorenz [1969], wildfowl react to the approach of a furry animal such as a dog at the edge of their pond by escaping and “cautious mobbing” of the animal. However, birds that remain in the same region become habituated to specific dogs—that is, their responsiveness to them decreases. This habituation is highly stimulus specific; the birds respond readily when a strange dog wanders into the area. Some of the clearest evidence of habituation is seen in fish. The male three-spined stickleback will defend its newly constructed nest by attacking other males which intrude into its territory [Tinbergen, 1951]. Peeke [1969] studied the habituation of these aggressive responses by placing either a wooden model of a male fish or a live male stickleback (restrained in a clear plastic tube) directly into an aquarium each day for

10 days. Figure 1-1 shows the decrease with repeated exposure in attacks on the “intruder.” The live fish elicited many more responses than the model. Note that the biting response decreased during each day but that some recovery occurred between each pair of days, although the responsiveness clearly decreased over a 10-day period. As is the case with other forms of behavioral plasticity, habituation is frequently short-lasting, as it is with the protozoan discussed above, and under other circumstances it can be quite persistent.

It is generally, and no doubt properly, assumed that in multicellular animals the plasticity underlying learning is due to changes in neural tissue. There is considerable controversy over whether learning can occur in restricted portions of the nervous systems of vertebrates, particularly in the spinal cord. Research by Thompson has provided conclusive affirmative evidence [Thompson, 1967; Thompson and Spencer, 1966; Groves and Thompson, 1970]. Habituation of a flexion response to repeated stimulation was obtained in laboratory animals in which the spinal cord had been surgically severed from the brain. The stimulus was a shock applied to the animal’s skin and the response was a muscle contraction. The amplitude of the response decreased with stimulus repetition, recovered with time, and was then readily rehabituated. The electrical activity of nerve cells within the spinal cord, termed *interneurons*, was recorded by means of microelectrodes during habituation trials (see Fig. 1-2). Interestingly, three types of cells were found—cells which showed no changes in frequency of firing with repetition, cells which initially showed increased activity with repetition, and cells which showed decreased activity with repetition. The three types of cells are referred to as type *N* (nonplastic), type *H* (habituation), and type *S* (sensitization). In addition to differing in frequency of firing with repeated stimulation, the cells differ in their speed of response

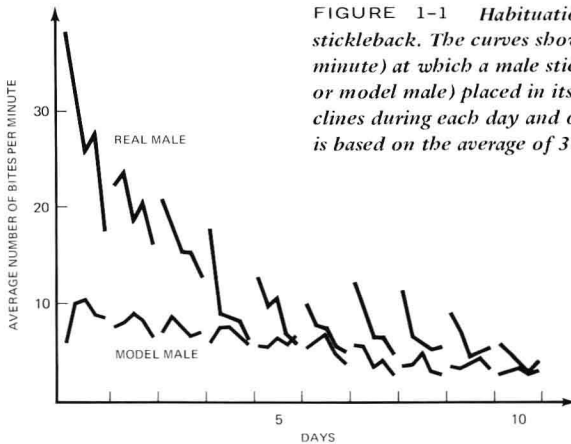


FIGURE 1-1 *Habituation of an aggressive response by male stickleback. The curves show the decline in average rate (bites per minute) at which a male stickleback bites another male (real male or model male) placed in its territory. The rate of attacking declines during each day and over a period of 10 days. Each point is based on the average of 3 successive minutes. [Peeke, 1969]*

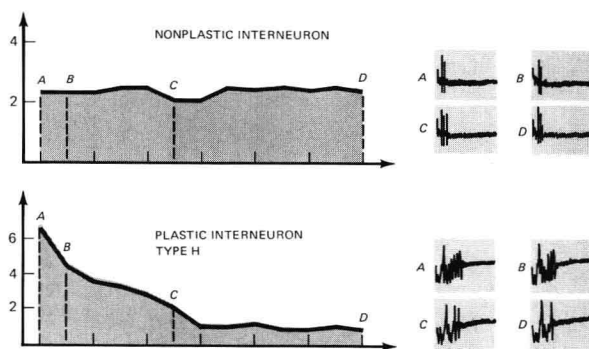


FIGURE 1-2 *Three types of spinal interneurons. The curves show responsiveness to sensory stimulation (mean number of spikes per stimulus) with increasing number of trials. A through D on the right of each curve show the electrical response of a typical cell—A before habituation, B on the first several trials, C after a number of trials, and D at the end of the*

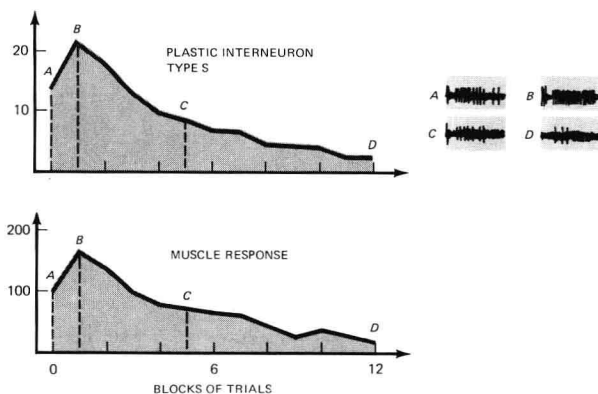
following stimulation. Furthermore, the different types of cells are located in different regions of the spinal cord. Neurons in this phylogenetically old region of the nervous system appear to be specialized for different types of responses to stimulation.

These findings are not too surprising in view of the evidence that habituation can occur even in single-celled animals. Analysis of the features of single cells which make such plasticity possible may lead to an understanding of the neurobiological bases of more complex forms of learning—but again, this is a complex and controversial issue. Some of the reasons for the controversy will become clear as we consider other forms of learning which have been studied in man and the other animals.

CLASSICAL AND INSTRUMENTAL CONDITIONING

Although animal training has been practiced for many centuries and naturalistic observations of learning have been made by scholars since recorded history, experimental studies of learning began only in the latter part of the last century. Ebbinghaus' classical research

on memory was published in 1885. The Russian physiologist Pavlov and the American psychologist Thorndike both began laboratory studies of learning in animals just at the turn of the century. For decades the research and writings of these pioneer investigators were dominant influences in the development of theories and experimental analyses of learning. Many contemporary techniques, problems, and theories stem directly from these influences.



habituation session. In nonplastic interneurons responsiveness does not change with repeated stimulation. In plastic type-H interneurons responsiveness decreases with stimulation. In plastic type-S interneurons responsiveness first increases, and then habituates. [Groves and Thompson, 1970]

CLASSICAL PAVLOVIAN CONDITIONING

The methods used by Pavlov in his studies of conditioning in dogs were based on his earlier work on the physiology of digestion (for which he was awarded the Nobel prize in 1904). Some of his basic findings are common knowledge. When meat powder is placed on a dog's tongue, the dog salivates. If some other stimulus, such as a bell or sound of a ticking metronome, is presented along with the meat powder on several occasions, the other stimulus will eventually elicit salivation when presented without the food. The process of pairing the meat powder with the bell is termed *reinforcement*. The stimulus which elicits the response is termed the *unconditioned stimulus*, and the initial response is called the *unconditioned response*. The signal is referred to as the *conditioned stimulus* and the learned response is called the *conditioned response*. An essential feature of this *classical* conditioning procedure is that the conditioned stimulus and unconditioned stimulus are controlled by the experimenter; the dog has no control over the delivery of the meat powder. The speed of acquisition of the conditioned response in classical conditioning is influenced by many factors. One of the most important of these is the time at which the conditioned stimulus is presented. Optimal conditioning occurs when the conditioned stimulus terminates shortly (0.5 second) before the onset of the unconditioned stimulus. Conditioning probably does not occur when the unconditioned stimulus precedes the conditioned stimulus.

Pavlov also observed a number of other interesting phenomena, which are summarized in Fig. 1-3. After conditioning, if the conditioned stimulus is presented alone, the response will decrease, or *extinguish*. In

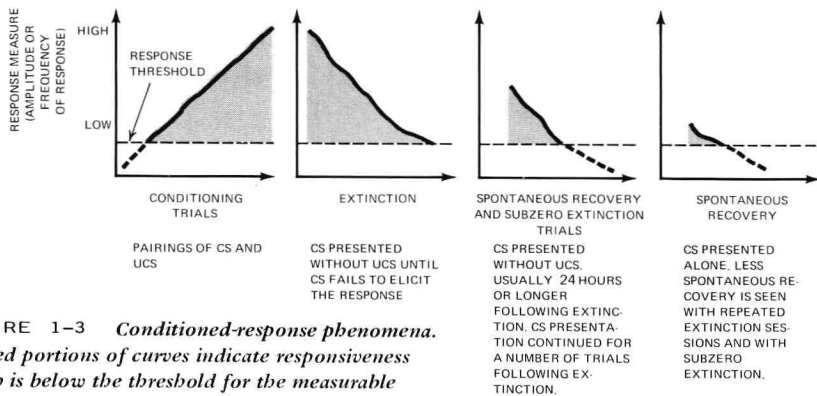


FIGURE 1-3 *Conditioned-response phenomena.* Dashed portions of curves indicate responsiveness which is below the threshold for the measurable response.

the session following extinction the response recovers to a higher level, a phenomenon termed *spontaneous recovery*. Spontaneous recovery can be decreased by presenting the conditioned stimulus alone even after complete extinction has occurred; this is called *subzero extinction*. Following conditioning training with a conditioned stimulus such as a bell, *higher-order conditioning* can be obtained by pairing that conditioned stimulus with another conditioned stimulus such as a light, even though the food is no longer given. Higher-order conditioning is difficult to obtain, and without reinforcement with the unconditioned stimulus it is readily extinguished. Animals conditioned to respond to a specific unconditioned stimulus such as a 200-hertz tone will subsequently respond to other tones. This phenomenon is called *generalization*. Degree of generalization decreases as the difference between the conditioned stimulus and the test stimuli are increased.

These are some of the major phenomena studied by Pavlov. In numerous experiments, by Pavlov as well as other investigators, many stimuli have been used as conditioned stimuli, many responses other than salivation have been studied, and other stimuli, such as electric shock, have been used as unconditioned stimuli.

What conclusions can be drawn about classical conditioning? Pavlov regarded conditioning as the fundamental process of association and regarded the conditioning experiments as providing a means of investigating the mechanisms of brain functioning underlying complex behavior. According to Pavlov [1957, pp. 197-198] :

The conditioned reflex is a common and widespread phenomenon. It is, evidently, what we recognize in ourselves and in animals under such names as training, discipline, education, habits; these are nothing but connections established in the course of individual existence, connections between definite external stimuli and corresponding reactions. Thus the conditioned reflex opens to the physiologist the door to investigation of a considerable part, and possibly, even of the entire higher nervous activity.

Other investigators have regarded classical conditioning as one of two, or perhaps several, types of learning. However the facts of conditioning are interpreted, it is clear that classical conditioning is a specific method of training animals. In view of this, some of the phenomena obtained with classical conditioning may differ from those obtained with other methods. However, it seems likely that the neurobiological bases of classical conditioning do not differ fundamentally from those of other forms of learning. It is sometimes assumed that classical conditioning consists only of training an animal to make a specific conditioned response, say salivation, to a specific stimulus, say a 200-hertz tone, and that the conditioned response is identical to the unconditioned response [Pavlov, 1957]. If this were true, we would need only to understand how a conditioned stimulus can substitute for an unconditioned stimulus in order to explain conditioning. The facts of conditioning are somewhat different from this concept. Zener reported his experiments in using a bell as a conditioned stimulus and salivation as an unconditioned response [1937, p. 393] :

Except for the component of salivary secretion the conditioned and unconditioned behavior is not identical. The *CR* [conditioned response] . . . is a different reaction from the *UCR* [unconditioned response] anthropomorphically describable as looking, expecting, the fall of food with a readiness to perform the eating behavior which will occur when the food falls. The effector pattern is not identical with the *UCR* [unconditioned response] .

Another more complex and interesting observation was made by Liddell while he was working in Pavlov's laboratory. A dog which had been conditioned to salivate at the acceleration of the beat of a metronome was freed from its harness. As reported by Lorenz [1969, p. 47] :

The dog at once ran to the machine, wagged its tail at it, tried to jump up to it, barked, and so on; in other words, it showed as clearly as possible the whole system of behavior patterns serving, in a number of *canidae*, to beg food. . . . It is, in fact, this whole system that is being conditioned in the classical experiment.

Obviously when animals are trained with classical conditioning procedures they learn much more than the specific response which is measured during the training. This is one of the basic facts of learning which has made it difficult to develop an adequate general theory of learning. It is relatively easy to control behavior through training. However, it is not easy to specify the nature of the changes produced by the training.

INSTRUMENTAL CONDITIONING

The learning obtained with reward-and-punishment training procedures, termed *instrumental conditioning*, was first studied by Thorndike during his graduate work under William James. These studies, like Pavlov's, were

begun just before the turn of the century. Thorndike placed laboratory animals, usually cats, in a small cage which could be opened, providing escape and a food reward, only if the cats made a specific response such as turning a latch or pulling a string. On the first few trials the animals made a variety of responses prior to making the "correct" one. As training continued, the irrelevant, or "incorrect," responses decreased, and the animals escaped within a short time after being placed in the problem box [Thorndike, 1932]. These procedures are, of course, the same as those we use to train our dog to "shake hands" or "roll over." In instrumental conditioning, in contrast to classical conditioning, the animal's behavior is "instrumental" in influencing the consequences of behavior; the reward is not given, or the punishment is not avoided, unless the animal makes the appropriate response. The environmental consequences—rewards and punishments—"select" adaptive responses, and the behavior of individual animals can thus become shaped to the requirements of the environment. From the animal's standpoint learning enables it to gain some degree of control over its environment.

In the artificial environment of the laboratory animals have been taught an enormous variety of responses. Instrumental-conditioning procedures have been successfully used to teach tricks to animals. Instrumental conditioning is also referred to as *operant conditioning*. This term was introduced by Skinner [1938], who also developed the well-known training apparatus—called the Skinner box—in which animals are given a small reward, or *reinforcement*, for pressing a lever. This technique enables us to study the effects of various rewards and other influences on the rate of response and has provided a means of investigating such things as sensory processes in animals. For example, an animal can be taught to press a lever only in the presence of a particular stimulus, and by varying the stimulus intensity, its sensory threshold for that stimulus can be measured. Studies of instrumental, or operant, conditioning have also revealed a number of interesting phenomena not observed in classical conditioning. For example, the pattern of responding is influenced by the frequency and pattern of rewards. Rewards can be given after each response, or they can be given only intermittently—that is, after either a fixed or random number of responses or after a fixed or random interval. Examples of the effects of different schedules of reward are shown in Fig. 1-4.

Operant conditioning in which response rate is the critical observation should be regarded as a special variety of instrumental conditioning. Most kinds of instrumental-learning tasks use measures of the time required for a response or of the number of errors made with repeated trials. A variety of other procedures are used in studies of instrumental learning. They all employ reward or punishment to induce animals to respond or stop responding (inhibitory avoidance). In some cases the response may produce a reward, and in others it may lead to the escape from or avoidance of a punishing stimulus. Each procedure produces a different type of behavioral modification—but all these procedures result in learning.

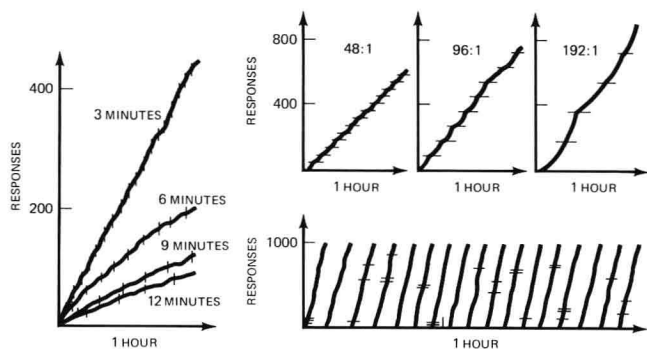


FIGURE 1-4 Cumulative-response curves obtained with various schedules of rewards. Lines through the curves indicate delivery of reward. Left, fixed interval, the cumulative responses over a 1-hour period when rats are rewarded for the first lever pressing response made after 3, 6, 9, or 12 minutes. Center, fixed ratio, the cumulative responses of rats rewarded for every 48, 96, or 192 responses. Right, variable interval, the cumulative pecking responses of a pigeon rewarded at intervals ranging from 10 seconds to 21 minutes, with an average of five rewards per hour. Note that the rate of response varies with the type of reward schedule used. [Skinner, 1938; 1950]

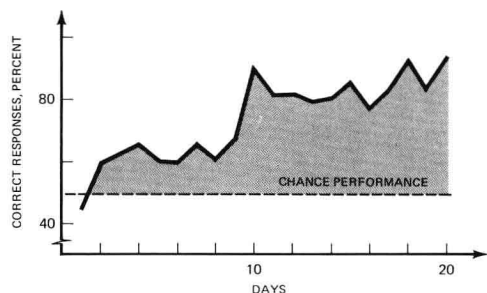


FIGURE 1-5 Visual-discrimination learning by monkeys for visual exploration reward. Correct responses were rewarded only by an opportunity to look at a complex visual stimulus. [Butler, 1953]

For some years researchers attempted to see whether events which are rewarding and punishing, termed *reinforcements*, might have a common basis. For example, Hull [1943] proposed that reinforcements act by decreasing biological drives such as hunger and thirst, and that such reinforcement was essential for learning to occur. One difficulty with this view is that an enormous variety of stimuli can act as reinforcers, that is, modify performance—and many appear to be unrelated to drives such as hunger and thirst. Animals will work for such rewards as variation in sensory stimulation. Neither beast nor man works for bread alone. Some examples of the reward effects of various visual stimuli are shown in Fig. 1-5.

The story is told of the researcher who, curious to find out what laboratory monkeys do when they are not being observed by psychol-