CONTEMPORARY LEARNING THEORIES:
Instrumental Conditioning Theory and the Impact of Biological Constraints on Learning

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Traditional learning research frequently treated organisms as unorganized bundles of reflexes and random responses. Organized behavior was attributed to the selective strengthening of particular responses by the temporally contiguous presentation of unique events called reinforcers. According to Lloyd Morgan (1896), "Just as a sculptor carves a statue out of a block of marble, so does acquisition carve an activity out of a mass of random movements" (p. 23). Hull (1943) added, "An ideally adequate theory . . . ought to begin with colorless movement and mere receptor impulses . . . and from these build up step by step both adaptive and maladaptive behavior" (p. 25). Skinner (1953) reiterated, "Learned behavior is constructed by a continual process of differential reinforcement from undifferentiated behavior" (p. 92).

Because learning was viewed as the fundamental mechanism organizing reflexes and random responses into larger functional units, it has been treated as the primary determinant of behavior. Theorists have assumed that research on learning was research into the basis of all organized behavior. Further, because aspects of learning appeared general across species, research on one species (e.g., rats or pigeons) has been assumed to apply to the behavior of all species (e.g., humans). To promote this level of generalization researchers developed standard experimental paradigms and focused on the use of presumably species-independent stimuli and responses (Galef, 1984; Schwartz, 1978; Timberlake, 1983b).

We present here an alternative behavior system approach in which an organism is viewed as a set of organized and interrelated regulatory systems that precede, support, and constrain learning (Timberlake, 1983a, 1983b, 1984). In this view learning evolved within the context of an already functioning system, such as feeding, or defense (e.g., Mayr, 1974), rather than as an autonomous general...
process suitable for constructing behavior from random movement. Specific instances of learning result from the interaction of system structures and processes with the stimulus support and contingent organization of the environment. Common aspects of learning across species imply common ontogenetic and phylogenetic selection pressures, though not necessarily common mechanisms. A major emphasis of our view is captured by the words of Garcia and Garcia Y Robertson (1985), ‘‘All organisms . . . possess the basic behavioral patterns that enable them to survive in their niches, but learning provides the fine tuning necessary for successful adaptation.’’

In the first half of this chapter we review briefly the traditional view of learned behavior, emphasizing its scientific heritage of isolation and abstraction, and some disadvantages of its dependence on methodology to define the nature of learning. We then develop the behavior system approach which conceptualizes learning in terms of the modification of functional systems. The second half of the chapter applies the behavior system approach to research in animal learning, beginning with predispositions in and constraints on learning and ending with a consideration of some traditional general principles.

I. THE TRADITIONAL APPROACH

Philosophical and Scientific Heritage

The philosophy of associationism has exerted a powerful influence on the traditional study of animal learning. Associationism was concerned with the relations among mental elements. Learning research translated these unobservable elements into overt and controllable stimuli and responses, thus distinguishing the study of learning from introspection and the collection of anecdotes. However, this fledgling science continued the associationist emphasis that learning consisted of new associations imposed on a nearly blank slate.

The sciences most influencing learning research have been reflex physiology and psychology. Reflex physiology provided a prototypical unit of behavior, the stimulus-response combination. It also provided an emphasis on abstraction and isolation of the phenomena under study. Just as nerve conduction was studied in an isolated frog’s leg using nonspecific mechanical or electrical stimulation, learning was studied in a rat or pigeon isolated in a simplified environment using arbitrary stimuli, such as lights or tones.

A desire to emulate physics also contributed to the abstract treatment of learning. Classical physical laws, such as the law of falling bodies, do not depend on extraneous or differentiated characteristics of the entities involved, such as their shape or composition. These laws depend on summary characteristics of an entity, such as its location or speed. Following a similar style of abstraction in learning led to the development of laws in which animals were treated not unlike billiard balls with memories, undifferentiated entities acted on by external forces (e.g., reinforcers), which altered some general quality of the organism (e.g., its direction or rate of movement).

Thus, the formal concepts of learning were isolated from its particulars of occurrence much as laws of falling bodies or nerve conduction were isolated from the specific entities and circumstances of their study. Thorndike (1911) in his original work on learning claimed, ‘‘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.’’ Skinner (1956) followed up with, ‘‘Of course . . . species have behavioral repertoires which are as different as their anatomies. But once you have allowed for differences in the ways in which they make contact with the environment, and in the ways which they act upon the environment, what remains of their behavior shows astonishingly similar properties’’ (p. 230).

The Importance of Methodology

Because animals differ markedly in how they contact and act upon the environment, researchers have depended on apparatus and procedures to isolate the common principles of learning from the contribution of species-typical structure. To this end, rats are most often studied in dimly lit, low-roofed chambers of modest size containing a small movable object to manipulate. Pigeons are studied in larger, well-lit chambers with punctate stimuli to peck.

A result of using methodology to isolate learning is that the nature of learning has come to be defined implicitly in terms of the apparatus and explicitly in terms of experimental paradigms, primarily operant and Pavlovian conditioning. There has been a tendency to treat the process of learning as isomorphic with the manipulations used to investigate it. Thus, if the experimenter controls the relation of a stimulus and a reinforcer (a Pavlovian paradigm), learning is most frequently attributed to S-S associations. If the experimenter controls the relation of a response and a reinforcer (an operant paradigm), learning is attributed to R-S associations. Recent theorists have questioned the restrictiveness of this procedure to the extent of suggesting that similar connections may occur in all paradigms (e.g., Colwill & Rescorla, 1986; Hearst, 1975).

A limitation of using experimental paradigms to define learning is the difficulty of dealing with naturally occurring learning in which an analyst in terms of Pavlovian or operant conditioning find it difficult or incomplete. For example, it has been awkward to deal with bird song learning or language development, in part because it is difficult to identify and control a presumed reinforcer. Further, the acquisition and production of such learning appears heavily dependent on preorganized structures that lack representation in the traditional paradigms (see Shettleworth, 1972, 1984, for many other examples of complex natural learning).

Perhaps the most telling point is the importance of ‘‘tuning’’ presumably ar-
arbitrary apparatus and procedures to produce an expected outcome. Small, seemingly innocuous changes may alter radically the form and regularity of the result. For example, Brelend and Brelend (1961) noted that small changes in the timing of reward in an operant chain could produce the sudden emergence of extensive "misbehavior" that was incompatible with the operant chain. Similarly, any experimenter constructing a lever which rats are required to press for food discovers that unless the lever has the thick, stubby, rounded end found in most commercial levers, rats frequently will bite, shake, push under with their nose, and gnaw it rather than press it.

In a classic case of tuning Skinner (personal communication, 1977) had difficulty teaching Pliny (a rat) to deposit a marble down a small chimney to obtain food. The rat would not release the marble cleanly, but would fidget and fumble it, almost releasing and then retrieving it repeatedly. Skinner solved the problem by making the chimney taller so that the rat could not see or retrieve the marble after it had been released.

The danger of the tuning process is that it assumes the appropriateness of the traditional abstract model of learning. The goal of tuning has become to select a combination of stimulus features that eliminate or reduce the intrusion of obvious species-typical responses (e.g., biting or shaking a lever by a rat), while maintaining reliable and orderly output. Presumably tuning produces a less differentiated set of stimulus reactions and motor responses and, thus, allows examination of the essence of learning unobscured by species-typical qualities. However, the importance of tuning for successful research argues for the importance of species-specific elements in learning. Tuning frequently involves detuning—changing the environment enough to obscure the contribution of the species-typical organization underlying behavior so it need not be recognized, while still taking advantage of it. At the least, the importance of tuning indicates the existence of coherent determinants of learned behavior that are not addressed in traditional theory.

In short, the analysis of learning has been divided into two parts, the principles of learning stated in textbooks, and the species-typical qualities of learning addressed in the design of the apparatus and procedures. We think that this dichotomy has hindered severely the further development of learning theory, and interfered with the application of laboratory behavior to the study of learning in natural and applied settings. We believe that what is needed is an organism-centered theory of learned behavior that combines the information present in both the abstract principles and the methodology of traditional learning.

II. A BEHAVIOR SYSTEM APPROACH

Philosophical and Scientific Heritage

The philosophical heritage of the behavior system approach is partly in function-alism and nativism. The organism is assumed to begin with considerably more than a blank slate; learning is defined by changes in existing perceptual and response structures and the motivational processes of a functioning organism. Though largely ignored (Timberlake, 1983b), the importance of the animal's organization for its learning was emphasized by early investigators such as Kline (1898), Small (1900), and even John Broadus Watson (1914), who noted:

Before beginning upon the simplest problem in learning, it is necessary . . . to have some knowledge at least of the instinctive modes of response of the animal and of the receptors to which we are making appeal. In behavior up to the present time, we have largely put the cart before the horse. In entire ignorance of instinctive capacity and sense organ functions, we have plunged in mediocris res and attempted to do satisfactory work on learning. (p. 45)

The scientific heritage of the behavior system approach is primarily in evolutionary and organismic biology. The emphasis is on ecologically relevant regulation and structure. As a result the behavior system approach is more compatible with classic chemistry than physics in that it emphasizes structures and interregulation (equilibria) of entities rather than their undifferentiated causal properties. Traditional learning models appear sophisticated from the viewpoint of classical physics, but from the viewpoint of biology or chemistry they are incomplete because they fail to model organic structures and processes related to learning.

In the next several sections, we outline a behavior system approach that attempts to account for both the functional organization of the organism and its relation to learning. This approach is compatible with and owes a debt to a number of prior theorists who are not adequately acknowledged including Bindra (1976), Bolles (1970), Davey (in press), Garcia, McGowan, and Green (1972), Hogan (in press), Holland (1984), Hollis (1982), Johnston (1981), Kamil and Yoerg (1982), Rozin and Kalat (1971), Rozin and Schull (1987), Seligman (1970), Shuttleworth (1972), Staddon (1975, 1983), and Williams (1981).

The Nature of Behavior Systems

A behavior system is a complex control structure related to a particular function or need of the organism, such as feeding (Timberlake, 1983b), reproduction (Baerends & Drent, 1982), defense (Bolles 1970; Bolles & Farselow, 1980), or body care (Fentress, 1973). The critical features of a behavior system are: (1) motivational processes that prime other structures and help organize and maintain the sequence of their expression, and (2) perceptual-motor structures (modules) that relate specific stimulus sensitivities to particular response components. The response components in a module are often sequentially and temporally related, and they are readily elicited, initiated, controlled, and terminated by stimuli resembling effective stimuli in natural settings.

Figure 9.1 shows a first attempt by Timberlake (1983b) to describe a behavior
system analysis of feeding in the rat. This organization was derived from reports by Barnett (1975), Ewer (1971), Galef and Clark (1972), Steiniger (1950), Telle (1966), and from personal observation. The feeding system is divided into relatively independent functional groupings of stimulus sensitivities and associated response components (perceptual-motor modules) including searching, investigating, predating, and food handling. These modules are loosely organized in several sequences that lead from searching for food to handling and consuming food.

A Control Structure. Figure 9.2 shows a more comprehensive representation of the same feeding system (see Davey, in press, for an even more complex account). Several concepts implicit in Fig. 9.1 have been made explicit here by using four hierarchically arranged levels of control: systems, subsystems, modes, and perceptual-motor modules. The four levels serve to select and coordinate the expression of individual responses (action patterns). The figure shows only the static structure of what are actually levels of ongoing processes.

The overall structure resembles the top-half of the hierarchical motivation model of Tinbergen (1951). The higher levels (shown on the left of this diagram) are concerned with motivation and global organization, while the lower levels (to the right of the diagram) are primarily concerned with local organization and form of expression. Despite similarities, the present conception differs from Tinbergen's (1951) model in several important ways. First, as becomes apparent in the next section, the system structures and processes are not as fixed, but as a framework that supports and is altered by learning. We are as interested in the flexibility and incompleteness of these structures as in their invariance. Second, the structure of appetitive behavior (Craig, 1918) is represented along with the structure of presumably more stereotyped consummatory behavior. Third, sequencing of responses is explicitly dealt with by the addition of the concept of modes. In our example, the modes range from general search to handling and consuming food, and depend on the probability of food and the nature of other cues present. Fourth, the hierarchical organization is represented as a lattice hierarchy to emphasize that the same component may be controlled by different higher order states within and even across systems (e.g., Gallistel, 1980).

It is important to note that the "levels" of organization proposed here are functional concepts that designate characteristic combinations of determinants and class-

es of outcome, not specific neural locations. Continued research will clarify the number, hierarchy, and independence of control levels required to account for particular instances of behavior (e.g., Fentress, 1983). In addition, as these concepts are mapped onto neural and hormonal mechanisms (e.g., Davis, 1984; Thompson, 1986), we anticipate that their operation will be uniquely constrained by the architecture of the nervous system in ways we cannot now predict. In the long run, this separation between function and physiology provides the possibility of using behavioral and physiological analyses as limiters and guides for each other. For the present, the structures shown in Figs. 9.1 and 9.2 are best viewed as working hypotheses about the functional organization with which a rat confronts foraging for food.

The highest level of control, the system, accounts for the tendency of behavior to be organized around important functions. Feeding, drinking, mating, body care, social bonding, care of young, defense, and territoriality are functions that have been assumed to comprise partially independent systems of behavior in most mammalian species (Scott, 1958; Tinbergen, 1951). Systems can be viewed as gener-

FIG. 9.2. A more detailed representation of the control hierarchy underlying the feeding system in the rat. Vertical lines with flat ends represent an inhibitory relation. For other information see text.
al motivational states (actually processes) that prime a set of underlying substates and modules related to a particular function. For example, the feeding system is a collection of perceptual-motor modules, modes, and subsystems related to obtaining and ingesting food. Different systems, such as feeding and drinking, may overlap in terms of control, instigation, and expression. Phenomena such as displacement behavior and polydipsia probably depend on such overlap (e.g., Lucas, Timberlake, & Gawley, 1988).

Subsystems, the next lower level of motivational control, refer to coherent strategies that serve the general function of the system. The activation of a subsystem should sensitize the animal to particular types of stimuli and potentiate particular subsets of modes and modules and their expression in coherent sets of action patterns. In the feeding systems of the rat different subsystems are presumed to control behavior related to markedly different food types. For example the predatory subsystem organizes motivational and stimulus-response structures relevant to locating and capturing moving prey. Thus, when the animal is “in” the predatory subsystem, small moving stimuli should be more salient and likely to trigger behaviors such as chasing. In contrast, a “browsing” subsystem is related to procuring stationary food items and has different stimulus sensitivities and response components.

The next level of control is modes. Modes are motivational substates related to the sequential and temporal organization of action patterns with respect to terminal stimuli in the system. In the feeding system modes are based in part on the local probability of finding food. For example, a feeding sequence typically begins in a general search mode, characterized by attention to novelty and search for food-related cues. When cues highly predictive of immediate food are encountered, the animal enters a focal search mode, in which action patterns are more focused and related to the immediate procurement of food. When food is certain, the animal enters a handling/consuming mode in which action patterns are focused on dealing with the food item. As the certainty of food declines following ingestion, the animal first reenters the focal search mode looking for more food. If this postfood focal search proves unsuccessful, then the probability of finding food locally declines further, and the animal re-enters a general search mode.

Thus, in foraging for scattered food the rat’s behavior will reflect repeated cycles of food-related modes that mirror the local distribution of food. This cycling will continue until quiescence or interruption. Note that the relation between modes and probability of food and the differential priming of modes related to the current mode will produce a sequence of action patterns with purposive character. To the extent that successive modes and modules can be instigated with little or no specific experience with the controlling stimuli, “inmate” strings of behavior will occur. Such a succession of modes helps explain the rapid organization of apparently purposive sequences of behavior, like rat-killing in inexperienced cats, or caring for newborn pups by inexperienced mother rats. It can also explain variations in prey behavior (e.g., avoidance, freezing, and attack) as a function of distance from predatory strike (Fanselow & Lester, 1987). We consider it possible that modes from different subsystems and systems share some common characteristics related to a general “arousal” (e.g., Killeen, 1982, though see Bolles & Fanselow, 1980).

Modes can be viewed as subdivisions of the appetitive-consumatory dimension of behavior proposed by Craig (1918). The general search mode represents the appetitive end of this dimension, whereas focal search and handling/consuming modes reflect the consumatory end of the dimension. Note that the appetitive-consumatory sequence is sometimes characterized as a sequence of variable to stereotyped behavior. This occurs largely because general search components are frequently less focused and more influenced by a variety of stimuli. However, we suggest that stereotypy is not the critical factor distinguishing appetitive and consumatory action patterns. Some appetitive patterns such as stalking or searching can be very stereotyped, while consumatory patterns have variable aspects (e.g., ingesting different types of food by pigeons—Zweers, 1982). The more important distinction is the extent to which action patterns are controlled by a final set of goal related stimuli.

The lowest level of control consists of perceptual-motor modules (see Davey, in press; Hogan, in press), predispositions to respond to particular stimuli with particular response components. It is worth reiterating that modules, like other behavior system concepts, are functional not physiological. At a neural level motor control is not localized in a specific brain area, and distribution of input processing is, if anything, even more diffuse.

The stimulus sensitivities in a module can be treated as sensory filters that gate or sharpen particular stimulus dimensions or configurations (Baerends & Krujft, 1973). In classical ethological literature, the sensitivity of gull chicks to contrasting spots on long thin objects held vertically and moved horizontally is typically attributed to such filters (Tinbergen & Perdeck, 1950). As Hallman (1967) has clearly shown, such filtering often begins with relatively broad tuning that is narrowed with experience and maturation. Thus, gull chicks initially peck at a variety of contrasting punctate stimuli independently of the configural stimuli around them. With experience they focus more on the source of food and the resemblance of the configural stimuli to their actual parents. We take this as a prototype of the stimulus tuning that occurs in many instances of learning.

The motor organization in a module is treated as resulting from motor “programs” that are related to particular stimulus sensitivities and to other motor programs. The importance of motor organization in behavior has become increasingly clear as research has progressed from observation to physiological analysis (e.g., Camhi, 1982; Gallistel, 1980). In human research, researchers as early as Lashley (1951) pointed out that highly skilled finger movements like those found in piano playing frequently occur with such speed that the ordering of the sequence by feedback circuitry in the nervous system was not possible.
Functional Aspects of Responses and Stimuli. The concepts of systems, subsystems, modes, and modules contact the environment through stimuli and responses. The basic unit of output is termed here an action pattern. The most salient aspect of action patterns is that they are typically recognizable as coherent, relatively stereotyped movement topographies, although fine-grained analysis often reveals a range of variability (e.g., Barlow, 1977). The environment is involved in the definition of an action pattern, but so are limb and body position, and temporal patterning.

Action patterns vary in strength of coupling with particular modules. Some action patterns may be controlled by different modules, and frequently more than one recognizable action pattern can be controlled by the same module. For this reason, measurements are frequently referenced to functional categories more appropriate to the level of the module (or higher) than to the topography of a single action pattern. Anyone who has watched a rat digging (a set of behaviors we assume to be controlled by input to a single module) will note that several action patterns work together to produce the digging unit. For example, the forefeet are alternated in a scraping motion to loosen the substrate (one action pattern) while the rear feet are regularly brought forward together to shovel the loosened material behind (a second action pattern). The critical point in measurement is to maintain access to the underlying structure and processes.

Another important characteristic of action patterns is that those coherent and relatively stereotyped they are not permanently fixed in number of form. Modules that underlie action patterns can be refined, combined and even reassembled as part of learning. However, once such alterations have taken place the result will be an action pattern that like others is coherent, relatively stereotyped, and usually functional.

The basic input functions to a behavior system are the effects of external stimuli. Stimuli have multiple effects both at the higher and lower levels of the system. First, external stimuli serve to increase or decrease the strength, extent, or perseverence of motivational processes ranging from the system down to the mode. The increasing function we will term instigation, the decreasing function we will term reduction. In general the influence of external stimuli will vary with the functional level. At the system level, the strength of the motivational processes typically will be more related to internal rather than external stimuli, while at the lower levels the contribution of external stimuli will be greater.

External stimuli also elicit, initiate, entrain, and control behavior at the level of modules. Elicitation refers to the ability of a stimulus to produce a relatively short latency and short duration action pattern, the basis of a reflex. Initiation refers to the ability of a stimulus to produce a longer duration organized sequence of action patterns. This effect of stimuli has been termed a trigger or releasing function (Davey, in press; Tinbergen, 1951). Entrainment refers to the ability of a stimulus to coordinate a complex set of temporally organized action patterns preceding and following its occurrence. Thus, the periodic availability of food can entrain a complex and coordinated set of rhythmic action patterns around it (e.g., Bolles & Moot, 1973; Lucas et al., 1988). Finally, control refers to the dual functions of local guidance and support of action patterns as they occur. For example, when a rat runs in a running wheel the movement of the wheel and its feedback serve to sustain running, and the side walls of the wheel provide orientation for running.

Behavior Systems and Learning

Having provided the conceptual context of a functioning organism, we can turn now to learning. Perhaps the most salient characteristic of learning in the behavior system approach is its complexity and diversity. Both attributes follow from the view that learning evolved as a modifier of an already functioning system (e.g., Nottebohm, 1972). Learning emerged where there was a loosening of the structures and processes involved in a system to provide a particular kind of window or template for the environment to influence the final form and control of behavior (e.g., Mayr, 1974).

Because of the complexities of a functioning system of behavior there are a remarkable number of ways in which learning can occur. For example, learning can occur as changes in the integration, differentiation, tuning, instigation, elicitation, and linkage within and across entities in the system. Most modifications take place within and between modules, but similar effects may occur at higher system levels, particularly, it appears, in development (Hogan, in press). Subsystems and systems may be integrated, differentiated, linked, and their instigation tuned with certain forms of experience (e.g., Alberts & Gubernick, 1984; Fentress, 1983; Hogan, 1984).

Rather than learning being restricted to one or two fundamental paradigms, the procedural conditions for learning include simple motor repetition, stimulus exposure and withdrawal, as well as response or stimulus contingent, noncontingent, and independent delivery of a reinforcer. Thus, from a behavior system view, the answer to Tolman's (1932) classic question, "Is there more than one kind of learning?," is a resounding yes. There are as many potential kinds of learning as there are ways evolved to modify the functioning of a system through experience.

This potential complexity of learning may appear overwhelming and unnecessary in a research area still dominated by questions about stimulus-stimulus versus stimulus-response control of keypecking in pigeons. But researchers have long known that current models are not a complete account of the necessary and sufficient conditions for learning; such models can be used only because agreed upon apparatus and procedures have been used to constrain their application. These agreements have been sustained by orderly data, the appealing view of learning as connection or response strengthening, and the belief that learning as studied in traditional paradigms forms the basis of all behavior. Though these agreements
have begun to fail, there seems every reason to keep the traditional goal of integrating learning and behavior. In the long run a theory of behavior that incorporates learning is more powerful than a theory of learning or behavior alone.

The behavior system approach reopens the issue of how learning occurs by asking how it fits within the structure and processes of the organism. For example, the stimulus-stimulus connections presumably formed in a Pavlovian paradigm are, at the least, connections between modules rather than between stimuli. The outcome is also likely to depend on relations between modules and even systems. Further, connections between modules are not unique to Pavlovian procedures, nor do they represent adequately all the forms of learning that occur. The presence of food activates the entire feeding system; the quality and density of food activate particular subsystems and modes. Repetition of stimuli will tune filters, integrate and link modules, and instigate motivational substrates. This level of complexity is important for understanding learning in the context of evolution, physiology, and behavior.

A final important question about behavior systems concerns their origin and development. A behavior system has a developmental history that can be modified (e.g., Alberts & Gubernick, 1984; Hogan, 1984, Tierney, 1986). For our purposes the critical issue is the nature of the system structures and processes at a particular time, and how that is modified. Thus, we refer to the system as preorganized, emphasizing that the organism always enters a learning circumstance with considerable structure already present.

It should be clear that preorganized systems do not mean that structures are either innate or learned. Genes and environment are coevolved. As John Emlen (1973) noted, "No animal learns without genetic guidance. To do so would be to change phenotype without regard to its consequences for fitness." To which we would add, "Similarly, no genetic guidance evolves without an assumed environment, for this would require that a genotype evolve and be expressed without regard to its means of expression, and, thus, also without regard for its fitness."

Experimental Paradigms and Behavior Systems

Once it is understood that learning occurs as changes in the functioning of a behavior system, the distinction between types of learning no longer depends primarily on methodology (apparatus and procedures). Instead, learning is determined by how the apparatus and procedures interact with the available motivational states, stimulus sensitivities, and response components. This realization has several far-reaching advantages.

The initial advantage is that this reconceptualization provides a framework for opening the analysis of learning to a concern with ecological requirements and phylogenetic resources. It is no longer necessary to fit learning into the standard laboratory paradigms of operant or Pavlovian conditioning in order to study or model it in common terms. For example, bird song learning can be studied (as it has been) without identifying a putative reinforcer. Such studies suggest that song learning in many species depends on the presence of auditory templates that link the species song with production templates that guide singing. In some species the auditory template can be altered most readily in early life, while in others the species song is insensitive to early experience, but can be modified later (King & West, 1984; Logan, 1983; Marler & Peters, 1982; Nottebohm, 1972). Many other cases of learning in natural environments (see Shuttleworth, 1972, 1984), are also amenable to study in a behavior system framework.

A second advantage is the realization that current learning paradigms can be very useful in the continued analysis of learning. Though no longer the end-points of investigation, learning paradigms are relatively standardized tools that can be used to contact and explore the components of functional systems of behavior. For example, Pavlovian conditioning can provide information about the nature of stimulus filters and the opportunity to study the response organization available in a particular module. Operant conditioning provides a means for differentiating structures within a module and linking structures from different modules.

A third advantage of separating the conceptualization of learning from its paradigms of study is that a behavior system can be used as a common framework for analyzing and extending the accumulated results of traditional learning research. From the behavior system view regular data are likely to be based on contact with a functional system. What is missing is a specific understanding of how laboratory procedures and apparatus design contact elements of the relevant system. In general, the more closely an experimental circumstance copies the stimulus conditions of an animal's selection environment, the more accurately will a conditioning procedure entrain naturally occurring episodes of behavior (e.g., Jenkins, Barrera, Ireland, & Woodsdell, 1978).

A final issue in analyzing and extending laboratory results is how to treat the typical distinction between learning and performance. Without question a primary focus of the behavior system approach is on behavior (performance). This is an appropriate focus for an evolution-based theory because ultimately it is behavior that determines survival. Nonetheless, the behavior system approach is an account of behavior including learning, rather than an account of behavior alone. Thus, it is quite appropriate to use current criteria for separating learning from performance, though as our understanding of learning becomes more integrated and complex present distinctions and control groups may well change.

The remainder of this chapter examines several phenomena of traditional laboratory learning to show how a behavior system analysis can account for these phenomena and contribute to their further development. This endeavor provides an opportunity to show that the behavior system approach, provided moderate knowledge of the species, readily generates specific explanations and predictions. The next section focuses on several instances of predispositions and constraints in learning. The final section attempts to interpret and clarify examples of general learning principles.
III PREDISPOSITIONS AND CONSTRAINTS IN LEARNING

Because learning is presumed to occur within the preorganized structures and processes of a behavior system, it follows that learning should show considerable variation in ease, stimulus responsiveness, and response content. Marked examples of this variation traditionally have been categorized as predispositions and constraints on learning (see Chapter 6 by LoLordo & Drougas of this volume). Predispositions refer to instances in which the organism learns more rapidly or in a different form than expected. Constraints refer to those cases in which the organism learns less rapidly or less completely than expected. Predispositions and constraints, though seemingly causal entities, are in reality only descriptions of outcomes.

In the behavior system approach predispositions and constraints have content because they are based on behavior system structures and processes. But one cannot specify a predisposition or constraint only in terms of particular structures and processes. It is necessary to consider the contribution of the environment as well. Predispositions occur when the environmental circumstances fit well with the structures and processes the animal brings to the situation. Constraints occur when the circumstances do not fit the structures and processes of the animal. Thus, predispositions and constraints do not exist within the organism, but in the combination of the behavior system with the environment. We review several examples of predispositions and constraints and show how the contribution of a behavior system can be tested and its organization explored.

Predispositions

In traditional learning research it is difficult to appreciate the importance of the appetitive structure of the animal because it is incorporated into the design of the apparatus and procedures. This has allowed researchers to focus on stimulus manipulations as causal. Thus, when keypecking develops to a lighted key as a function of contingent presentation of a food hopper, many researchers conclude that the response contingency did all the important work. However, we review here several phenomena that question this view, including autoshaped keypecking, unrewarded maze learning, misbehavior, and superstition. In each of these cases complex behavior emerges either without an explicit reward or without an appropriate response contingency. These phenomena are difficult to explain in traditional learning terms, but their persistence and robustness underscores the importance of preorganized appetitive structures and processes in determining responding.

Autoshaping. Brown and Jenkins (1968) surprised most operant learning researchers by showing that keypecking in hungry pigeons could be reliably produced simply by illuminating the response key for 8 sec before the aperiodic delivery of food (see Tomie, Brooks, & Zito, 1989 for a review of this literature). The procedure was termed "autoshaping" because keypecking was automatically shaped (elicited or initiated) by the pairing of keylight and food. Though autoshaping has become a fixture of current learning research, its occurrence was unexpected: first, because a Pavlovian procedure produced positive conditioning of a directed skeletal (voluntary) response; and second, because the particular skeletal responses conditioned were those that previously had been carefully (and often laboriously) shaped as arbitrary operators.

Though a surprise in the context of traditional models of learning, autoshaped keypecking fits well within a behavior system approach. The pigeon, a visually guided feeder, is presented with a highly salient punctate visual stimulus that is a reliable predictor of food. In many cases the keylight also shares with the food hopper the common feature of being brightly illuminated. These qualities of the keylight should be adequate initially to engage specific modules related to search and exploratory pecking. The interval between the keylight and food is made sufficiently short that the certainty of food availability coupled with the characteristics of the keylight will support pecking related to focal search and handling-consuming modes. But the interval is kept long enough and the hopper left dark to prevent domination of responding by focal search activity directed to the hopper.

As noted before, the autoshaping paradigm can be a very useful tool for investigating the structure of a behavior system. The animal is free to show any form of response and the CS and US can be readily manipulated. For example, by choosing different USs it should be possible to compare the nature of pecking modules in different systems. In the pigeon a keylight paired with imminent food produces forceful, open-beak pecks much as though the animal were attempting to grasp a piece of grain from the key (although the pecks are usually too forceful to be successful—Timberlake & Lucas, 1985). In contrast, a keylight paired with water produces mumbbling and bowing to the key similar to the responses pigeons use in obtaining water (Jenkins & Moore, 1973; Woodruff & Williams, 1976).

Similarly, by choosing different CSs and different species and using food reward one should be able to engage other modules appropriate to the food system for a particular species. An illustration of these effects was provided by Timberlake (1983b) in analyzing the social-feeding structures of rats. Based on data from Ewer (1971) and Galef and Clark (1972) it was hypothesized that a set of social modules should exist in the feeding system of rats. Rats are social feeders. They follow each other to food sources; they investigate and steal food items from the mouths of other rats (Whishaw & Tomie, 1987); and they also learn to distinguish appropriate foods based on the feeding location and odors of other rats. We assumed that a rat CS predicting food would engage a social-feeding module and, thus, produce enhanced social behaviors.
Timberlake and Grant (1975) supported this hypothesis by showing that a rat predicting food elicited a variety of social behaviors including orienting, approaching, sniffing the mouth and ano-genital area, and contacting, including pawing, grooming and crawling over the stimulus rat. As seen in Fig. 9.3 these action patterns increased rapidly when a rat predicted food (panel A), but not so when the rat appeared alone (B), or was randomly paired with food (C). When a ratsize wood block predicted food (D) rats oriented toward the block but rarely approached or contacted it. Timberlake (1983b) summarizes a variety of other experiments testing predictions contrasting the treatment of social predictive stimuli by rats and hamsters.

**Maze Running.** Small (1900) selected maze running as an instrumental behavior because in his estimation it “conformed to the psychobiological character of the rat.” If he was right, the rat should have a well organized appetitive structure for maze running appropriate to finding its way rapidly around burrows and subterranean paths (Calhoun, 1962). Classic latent learning studies support this view in showing that rats learn about the maze in the absence of food reward (Blodgett, 1929; Tolman & Honzig, 1930). More recent research has analyzed some of the nature of the appetitive structure underlying maze running.

Following the lead of a number of investigators, Timberlake (1983a) showed that improvements in straight-alley running developed in the absence of explicit reward for completing the alley. In addition, he found that the acquisition of alley running was retarded by bright lights, by the presence of novel odors in the alley, by short alleys or open spaces with few vertical walls, by delaying release from the start box, and by removing the rat from the alley immediately after it completed the run. Alley running was facilitated by darkness, unusual stimuli at the end of the tunnel, long alleys, and allowing the rat to roam the alley after traversing it. Timberlake (1983a) argued that alley running was a released behavior, initiated and controlled by vertical edges, facilitated by the presence of long uninterrupted paths, and improved by habituation of exploratory and fear reactions to local alley cues.

Figure 9.4 compares run and start times in rats given 0, 1, or 10 pellets of food. It is clear that food had an effect, particularly in reducing start times. However, improved alley running emerged more in parallel in the groups. As Timberlake (1983a) noted, “Alley running was for many years a key instrumental response in the development of general, context-free theories of learning. The present results suggest we did not adequately understand it. Reward in the goal box of an alley is not the only or even the primary determinant of alley running in rats” (p. 214).

These results are not limited to straight alleys or rats. Brant and Kavanau (1965) showed rapid and marked acquisition of running speed and error reduction in canyon mice exposed to a 75 x 75 foot complex maze attached to their home environment. Such findings together with the straight-alley research raise the possibility that latent learning occurs largely because rats and mice are predisposed to identify and traverse long uninterrupted pathways in their environment.

**Misbehavior.** Like autoshaped pecking and unrewarded maze running, misbehavior emerges without an appropriate response-reward contingency (refer to Chapter 7 of this volume by Garcia, Brett, and Rusiniak). But more strikingly its occurrence represents the failure of an explicit response contingency to control behavior (Breland & Breland, 1961). In the two most frequently cited examples, pigs and raccoons were first trained to pick up, transport, and deposit a token in a container to obtain reward. When the number of tokens to be transported and deposited prior to reward was increased, organized interfering responses began to emerge. The raccoon instead of releasing the tokens into the container “... spent seconds, even minutes rubbing them together... and dipping them into the container.” The pig “... instead of carrying the dollar and

![Figure 9.3](image-url) Median percent trials with oriented, approaches, sniffs, and social contacts to stimulus rats by four groups of subject rats. In Group Paired (A) the stimulus rat predicted food in Group Social (B) the stimulus rat was presented alone. In Group Random (C) the stimulus rat and food were randomly presented. In Group Wood Block (D) a rat-sized wood block predicted food. From Timberlake & Grant (1975).
Depositing it simply and cleanly... would repeatedly drop it, root it, drop it again, root it along the way, pick it up, toss it up in the air, drop it, root it some more, and so on.” As Breland and Breland (1961) remarked, “These egregious ailments came as a rather considerable shock to us... the animal simply did not do what it had been conditioned to do.”

These effects appear straightforward from a behavior system view. The feeding system was activated by the presence of food. As training of the instrumental response progressed, regular pairings were produced between the token and food. The hard small token when paired with food apparently fit stimulus filters connected with components of food-related action patterns, rooting responses for the rig, and crustacean washing for the raccoon. It appears to be important that the token-food interval in these pairings was relatively long, because the misbehavior did not emerge until an increase in the instrumental requirement lengthened this interval. Such an outcome would follow if the imminent delivery of food produced focal search mode related to immediate feeding that blocked acquisition or expression of search patterns more related to discovering and capturing food. When the delay between food items became longer, more complex search patterns emerged directed toward the predictive tokens.

Several predictions about misbehavior follow from a behavior system account. First, if misbehavior occurs because of the pairing between appropriate stimuli and reward, then it should emerge without an operant requirement, simply as the result of pairing an appropriate stimulus and food. Second, most forms of misbehavior should be much less likely under short CS-US intervals because focal search responses directed to the food location will supersede responses directed to the predictive stimulus. Finally, differences in misbehavior should occur to the same predictive stimulus as a function of the system engaged because different modules should be involved.

All these predictions were tested using a rolling ball bearing as a predictor of food (or water) for rats. Because rats prey on insects and small vertebrates, a small moving object should fit stimulus filters for modules related to prey capture. Figure 9.5 shows that rats exposed to a rolling ball bearing followed by food readily increased orient, approach, and contact to the bearing compared to a group of rats receiving random pairings of the ball bearing and food. The modal pattern of interaction with the bearing involved the predatory responses of digging it out of the entrance hole, seizing it in the mouth and paws, carrying it to a corner of the apparatus, and alternately chewing, releasing, and retrieving it.

As to the effects of CS-US interval, Figure 9.6 shows that the percentage of trials with a bearing contact varied directly with the length of the interval. When food was presented at a short interval (approximately 1.6 sec after the bearing entered the chamber—group Before-Exit), very little bearing-directed behavior occurred; instead the animal went to the food tray. When food delivery was delayed until the bearing exited the chamber (group Actual-Exit) or until 2.5 sec after an unpimied bearing would have exited (group After-Exit), considerably more behavior was directed to the bearing.

The third study in this group (Timberlake, 1983c) examined the prediction that handling modules related to food should produce more extensive and complex interaction with a bearing than handling modules related to water. Figure 9.7 shows that the duration of contact was significantly longer and more complex (measured by carrying and chewing) to bearings predicting food than to bearings predicting water. It’s worth noting that these results do not support the stimulus substitution view in Pavlovian conditioning because the rats were never observed to lick the bearing predicting water (cf. Davey & Cleland, 1982).

Superstition. The classical superstition paradigm is a short fixed-time (FT) schedule of food delivery (Skinner, 1948). The action patterns that result are of interest because they represent behavior in the absence of either response contingencies or specific predictive cues. Therefore, in a behavior system view, resultant action patterns should be related to modes and modules activated by the
stimulus circumstances and the inter-food interval, and, thus, should be recognizable species-typical.

In apparent contrast to this expectation Skinner (1948) reported that pigeons exposed to a short FT schedule developed unpredictable (supersitious) responses presumably based on repeated accidental pairings of that response with food. However, later research has not supported Skinner’s interpretation. Staddon and Simmelhag (1971) reported that most of their birds showed the same final behavior under a fixed-time schedule, namely pecking the magazine wall just prior to food delivery. Timberlake and Lucas (1985) and Innes, Simmelhag, and Staddon (1983) reported a related pattern of wall-directed behavior (without pecking) for most of their birds (see also Reberg, Innes, Mann, & Eizenga, 1978).

Timberlake and Lucas (1985) further tested the accidental response contingency explanation by explicitly pretraining pecking or turning. Birds were trained to either peck or turn on a short interval schedule for 3 days before receiving response-independent food. Because of their high probability, pecking and turn-

FIG. 9.5. The mean percentage of trials with contacts to a moving ball bearing by two groups of rats. In Group Actual-Exit food was presented when the ball bearing exited the test chamber. In Group Random the ball bearing and food were presented randomly. Adapted from Timberlake, Wahl, & King (1982).

FIG. 9.6. The mean percentage of trials with contacts to a moving ball bearing by three groups of rats. In Group Before-Ext food was presented 1.6 sec after the ball bearing entered the chamber. In Group Actual-Exit food was presented when the ball bearing actually left the chamber. If the bearing was delayed in the chamber, so was the delivery of food. In Group After-Ext food was presented 2.5 sec after an unimpeded ball-bearing would have exited the test chamber (approximately 5.6 sec after it first entered the chamber). Adapted from Timberlake, Wahl, & King (1982).

FIG. 9.7. Panel A shows the mean duration of contact and mean latency to contact a moving ball bearing presented alone in baseline (BL), or after pairing with either food (FD) or water (WT). Panel B shows the percentage of total contact trials in which carrying or chewing of the ball bearing occurred as a function of these same training conditions. Adapted from Timberlake (1983c).
ing should have been very likely to be rewarded by chance during the FT schedule. However, as shown in Fig. 9.8, though turning and pecking were increased in initial probability by pretraining, they rapidly dropped out in favor of wall-directed and "stand away" behavior under the FT schedule.

From a behavior system view superstitious behaviors should reflect aspects of food-search behavior supported by the interfood interval and the physical characteristics of the chamber. The interpretation is straight-forward for floor or wall pecking, but more difficult for wall-directed bumping and stepping. Timberlake and Lucas (1983) offered the possibility that the wall directed behavior was related to food begging behavior in mobile squab. In fact, observations of 14-20 day-old squab begging show that they step back and forth in front of a newly encountered parent, frequently pressing their breast against them, and moving their head repeatedly near the parent's beak.

Constraints

In the behavior system view constraints on learning are formally the same as predispositions. They both reflect a combination of system structures and processes

with a particular environment. Thus, by changing the stimulus circumstances to either facilitate or oppose the expression of the structures engaged by the environment, predispositions become constraints, and vice versa. For example, if a light key is paired with food for a pigeon, there is ample evidence of a predisposition to learn to peck, but if a response contingency is added that omits food if the keylight is pecked, a constraint on learning not to peck will be shown (Williams & Williams, 1969). Similarly, signaling illness with a gustatory cue produces ready learning to avoid that cue, but signaling shock with the same gustatory cue does not produce such ready learning (Garcia & Koelling, 1966).

At a mode level, constraints can be shown by entraining mode-appropriate action patterns to a situation and then presenting stimuli or requiring responses typical of a different mode. For example, Timberlake (1986) conditioned focal search patterns to the food tray by frequent periodic presentation of food to hungry rats. This focal search mode interfered with the emergence of more general search responses to a moving bearing predicting food.

At a system level constraints can be produced by imposing a contingency relation between the expression of modules from different systems. A classic example of this type of constraint is Sevenster's (1973) attempt to train a stickleback (a small territorial fish) to swim through a ring or bite a rod in order to court a female or aggressively display to a rival. In the stickleback's natural repertoire swimming through a ring resembles swimming through a nest, a well organized response sequence in courtship that entices the female to deposit eggs in the nest. On the other hand, biting and tugging a rod are behaviors related to aggression toward rivals. The expression of courtship and aggression systems are mutually incompatible. In fact one function of courtship appears to be to decrease aggression toward an invading female.

Based on these system differences, it should be easy to produce biting of an intruding glass rod for access to a rival, and to produce swimming through a ring for access to a female. It should be more difficult to bite a glass rod that predicts courtship because courtship inhibits aggressive behavior.

Similar structures exist within a defensive system (Bolles, 1970; Bolles & Fanselow, 1980; Fanselow & Lester, 1988). Bolles noted that animals have special repertoires of species-specific defense reactions (SSDRs) related to running, freezing, and defensive threat. Fanselow and Lester (1987) argued that these action patterns could be controlled by the distance to the strike by the predator (an idea corresponding to our notion that modes in the feeding system control responding as a function of distance from food).

The ease of escape and avoidance learning depends on whether the environmental contingencies and stimuli promote or compete with the expression of the structures and processes of the defensive system. For example, it is easy to train a rat to jump out of a box to avoid shock, but not so easy to train the same jumping topography when it does not permit escape. In contrast it is easy to get a rat to press (manipulate) a lever to obtain food, but more difficult to train the

![Fig. 9.8](image_url)

The percentage of behavior categories recorded across 2-day blocks for 4 pigeons when grain was presented at 15 second intervals (FT 15 sec). The solid point to the left of each graph indicates the percentage occurrence of the behavior category (Peck or Turn) that was trained prior to the beginning of the FT 15 sec schedule. From Timberlake & Lucas (1985).
animal to repeatedly press a lever to turn off shock. Frequently the best that can
be obtained is freezing on the lever.

Summary

Predispositions and constraints are outcomes, not causes. They represent the in-
teraction of behavior system structures and processes with the stimulus circum-
sances and response linkages imposed by the environment. In other words, the
same system can produce either predispositions or constraints, depending on the
environment. It follows from this view that there is not a simple causal dimen-
sion of preparedness underlying learning (Seligman, 1970). For example, it is
not instructive to argue that jumping is a more prepared avoidance response than
barpressing when the relative speed of learning these responses can be reversed
by small changes in the contingency or the environment. What is of most interest
in examples of predispositions and constraints is that they provide evidence that
behavior system structures and processes are critical determinants of behavior
under typical learning paradigms.

IV. BEHAVIOR SYSTEMS AND GENERAL PRINCIPLES
OF LEARNING

The data reviewed above strongly support the importance of species-typical be-
havior systems in determining learning. However, the relevance of these data
to more typical laboratory learning may be unclear. Many investigators assume
that predispositions and constraints are simply biological boundary conditions for
the operation of general learning laws. Within these boundaries lies a large terri-
ory where unconstrained and unpredisposed learning is the rule. Other researchers
have argued that general learning principles extend even to boundary phenome-
nas. Predispositions and constraints simply require the use of different constants
in a prototypical equation describing learning (e.g., Logue, 1979). Thus, it has
been argued that taste aversion learning, despite its unique time course and stimulus
relations, follows the same laws as any other form of learning but with longer
time constants.

In the behavior system view all learning occurs as modification of the struc-
tures and processes of the relevant behavior system(s). The stimulus conditions
and constraints imposed by the experimenter or the environment are critical in
determining how a system is modified, but there is no unconstrained learning
based only on the experimenter’s operations. To be sure, there are circumstances
under which learning appears to follow the classic reinforcement model—the
reinforcer-based differentiation of responding from undifferentiated behavior.
However, close inspection of such circumstances should reveal a systematic elimi-
nation of support for response tendencies that might compete with experimenter-
designated learning, and increased support for structures and processes relevant
to the desired action patterns.

This section examines several traditional principles and processes in laborato-
ry learning for the potential contribution of specific behavior systems. Our in-
terest is not in disproving general learning principles, but rather in placing them
in an appropriate organismic context. A general principle that is not related to
an animal’s evolution and ecology is only half a principle. The rest of it is embed-
ded in the apparatus and procedures. The issues we consider include acquisition
and extinction, response form, temporal contiguity, and US predictability. These
are by no means an exhaustive list of issues, but we feel: they are representative
and important. In briefly discussing each we try to show how the behavior sys-
tem approach can account for the known effects as well as suggest exceptions
and extensions.

Acquisition and Extinction

In the most common view, acquisition is produced by the selective strengthen-
ing (probability increasing) action of an unconditioned stimulus contingent on a stim-
ulus or response. The contiguity and predictability of the unconditioned stimulus
(US) determine the degree of strengthening. In the behavior system view acqui-
sition is determined by the fit between the structures and processes of the organ-
ism and the environment. The physical characteristics of the environment and
the predictive stimuli are critically important through their roles in producing
motivation and eliciting and initiating the expression of particular modules. Con-
tiguity and predictability of the US are also important but for the same reasons.
The use of arbitrary stimuli probably means that the stimuli produce a weak fit
across several modules. In effect, the use of arbitrary stimuli reduces the contribu-
tion of their physical characteristics and emphasizes the effects of contiguity
and predictability in selecting a module.

Basic issues in acquisition can be illustrated by considering the procedure of
shaping a rat to press a lever through the “principle of successive approxima-
tion.” This principle refers to the procedure of making successive rewards con-
tingent on action patterns closer and closer to the desired response. Anyone who
has taught undergraduates to shape rats soon discovers that the process is not
simple. There are important tricks. Depending on how adept they are at such
tricks, some students are exceptional shapers, many are not. This spread in abili-
ty occurs even in professional scientists. Few can match Skinner’s talent in train-
ing animals. Such variation suggests that concern with the response-reward
contingency must be tempered by an awareness of the structures and processes
of relevant behavior systems.

A behavior system analysis of shaping a rat to leverpress suggests three general
steps: (1) Allow a hungry rat to find and eat food in the experimental chamber.
(2) Present food at a high enough density that the rat shows focused exploration
in the area of the food tray, but not so densely as to restrict search to the food tray alone. (3) Present food contingent on investigatory and handling activities that contact and move the lever.

We can minimize step 2 by withholding the lever until the animal has found the food and is engaged in postfood search. We can also provide intermediate steps such as the discriminative training of a feeder click that predicts delivery of food. This step is most useful when the lever is not very close to the feeder. However, in a carefully designed and "tuned" experimental chamber, the size, location, and movement of the lever do most of the work in bridging the gap between steps 1 and 3.

This account of shaping has little to do with a strict view of successive approximation, but careful observation of shaping suggests that shapers don't control the timing of reward delivery with sufficient accuracy to follow this rule in any precise way. Like predisposed and constrained learning, shaping appears based on a combination of the experimenter's manipulations with the rat's particular stimulus sensitivities, response components, and motivational processes. In behavior system terms, shaping activates the food system, instigates a combination of general and focal search modes primarily focused on the area of the food tray, and links modules related to food capture or handling to the movement of the lever.

As would be anticipated from this view, lever pressing does not have to be shaped by response-contingent reward; it can be produced in a Pavlovian procedure by pairing insertion of the lever with the delivery of food. Food entrains focal search responses to the area of the food tray. Insertion of the lever elicits investigation. The response-dependent movement of the lever supports the linking and expression of handling or capture modules, provided food is coming at a slow enough rate to "time-out" postfood search focused on the food tray.

The present focus on the system context of learning may clarify a classic disagreement among traditional theories of learning, whether animals learn by eliminating inappropriate behaviors or by strengthening new, appropriate behaviors (Harlow, 1949; Staddon, 1983). The obvious answer is that learning occurs in both ways. Consider the cats in Thorndike's (1911) puzzle box. Their original actions involved inappropriate squeezing and clawing directed to the bars of the box. Only after these escape reactions dropped out did the cat move on to components of search and manipulation related to food that produced elements of the response which the experimenter had picked to study.

Finally, consideration of the structures and processes of a behavior system also has ramifications for the concept of extinction, a process that classically has been viewed as the reverse of acquisition. In a behavior system extinction can occur in several forms, ranging from a decrease in the instigation of motivational states to the explicit unlinking of different modules. Timberlake (1986) has argued that many of the behavioral effects of extinction are due to shifts in modes of focal search/food handling back to more general search and finally to quiesence as the instigation of the underlying motivational processes decreases.

Thus, behaviors under simple extinction may not be so much unlearned as made less accessible by mode shifts. If the appropriate mode is reinstated through priming or delay, the extinguished behavior may reappear almost immediately (spontaneous recovery). Such a mechanism makes sense for an animal foraging in limited but renewable patches. After failing to find more food, it should not unlearn the position of the patch or the locations within it, but only learn that the patch is now depleted. Extinction should not prevent it from returning at a later point. Extinction of a different sort might be expected where the modules themselves are disrupted and incorporated in new learning. Such extinction would be slower, more permanent, and would more likely show interference effects than spontaneous recovery.

Response Form:

Pavlovian Conditioning. The predominant model of response form in Pavlovian conditioning is based on the concept of stimulus substitution (Mackintosh, 1974). In simplest form this model argues that through repeated pairings the CS comes not only to predict but to substitute for the US in eliciting the UR. Thus, the conditioned response (CR) should be highly similar, if not identical, to the unconditioned response (UR) in both its form and orientation. For example, salivation that was initially produced by the presentation of meal powder in a dog's mouth comes to be elicited by a bell that has been paired with the meal powder.

In the behavior system view instances of apparent substitution should occur only under a restricted set of circumstances. The effect of the Pavlovian paradigm is to attach one or more food-system modules to the CS. Which modules are attached and the specificity of their expression will depend on the match of their stimulus filters to the physical characteristics of the CS and the timing, predictability, and type of food delivery. With the typical conditions of a very short CS-US interval, a highly predictable food US, and a presumably neutral CS, we would expect to produce behaviors closely related to handling and consuming food. Thus, salivation should occur because the high probability of contact with a particular food item places the animal in a consummatory mode and primes appropriate contact and ingestion modules thereby producing salivation.

Using longer CS-US intervals, lower predictability, or physical characteristics of the CS that fit filters for more search related modules, we would expect more general appetitive behaviors that are tied less closely to the UR. These circumstances are more typical of the autoshaping paradigm (Hearst & Jenkins, 1974), and can produce remarkably complex and flexible behavior. For example, Jenkins et al. (1978) describe a procedure with dogs in which they replicated the traditional Pavlovian stimulus procedure of pairing a head-high auditory-visual stimulus with food; but they also allowed the dogs to move about freely and initiate their own trials. During conditioning the dogs treated the stimulus less as a substitute for food than as a social surrogate. Dogs approached,
pranced, bowed, tail-wagged and barked at the CS, all behaviors related to greeting and begging food from another dog. Apparently what was conditioned were modules related to social-feeding. Jenkins et al. (1978) concluded "... the experimental CS-US episode mimics a naturally occurring episode for which preorganized behavior patterns exist. ... We propose that the artificial signal substitutes for a natural signal, not for the object being signaled as in the Pavlovian concept of substitution."

In another example, Wasserman (1973) paired the illumination of a small response key with the presentation of a heat reward to week old domestic chicks placed in a cold environment. Chicks both pecked and "snuggled" (the CRs) against the lighted response key. However, their response to the heat lamp US was one of "twittering" and then sprawling to the chamber floor with wings extended in a "curtsy" (the URs). Hogan (1974) noted that pecking at the hen by chicks is a natural signal that encourages brooding (covering and warming of chicks) by the hen, and that snuggling into the feathers is a natural response of a cold chick to the brooding hen. That is, the behaviors directed to the keylight were selected from modules appropriate for the chick's interaction with a brooding hen.

The form of the UR to the heat lamp is equally interesting. The sprawling and wing extensions seen in these week-old chicks are typical of "turning" postures in adult chickens, a behavior elicited by a bright source of heat, which presumably serves to expose feather parasites to the sun. Thus, while pairing the predictive keylight with warmth-activated search modules related to brooding, the intense light-heat of the heat lamp elicited a module related to sunning.

Instrumental (Operant) Conditioning. The classic assumption in instrumental and operant conditioning is that the response form is determined solely by the response-reward contingency. Responses followed most closely by reward are strengthened the most, thereby selecting the final form by the cumulative effects of successive rewards (e.g., Hull, 1943). From the data we have reviewed, this is not a defensible view. Instead the form of instrumental responses appears to be highly dependent on preorganized modules.

Consider that the three major forms of laboratory instrumental behaviors, key-peeking in pigeons, lever pressing in rats, and maze running in rats, have been shown to develop without explicit response-reward contingencies. Even the possibility that accidental response-reward contingencies may have helped acquisition seems unimportant given their apparent lack of effect on superstitious behavior in pigeons (Timberlake & Lucas, 1985). Further, comparisons of the form of the same response produced by Pavlovian and operant responding can show great similarities. For example, the form of a rat's behavior to a ball bearing was similar whether the bearing was simply paired with food or the rat was required to contact the bearing to receive food (Timberlake, Wahl, & King, 1982).

In short, operant behavior appears to involve the expression of preorganized response components sensitive to elicitation, initiation, support, and control by particular environmental stimuli. A clear example of the importance of environmental stimuli was provided by Moore and Stuttard's (1979) analysis of the classic puzzle box conditioning studies of cats by Guthrie and Horton (1946). Guthrie and Horton (1946) found that the response of rubbing against a pole was readily acquired and attributed it to the contingent consequence of escape. However, Moore and Stuttard (1979) showed the stereotyped rubbing was related to the grooming rubs used by cats in social contexts and was initiated by the presence of human observers. Rubbing was not likely to emerge if the human observer could not be seen by the cat.

Despite this unpromising brief review of response-reward contingencies as a determinant of response form, there appear to be several ways in which such contingencies do directly and indirectly modify responding. Response contingencies can change the interval between important stimuli and food, thereby changing the degree of instigation of a particular module, as occurs in the development of misbehavior. Modules can be refined and organized in anticipation of response-contingent reward. Modules from different systems can be linked by a response contingency, and stimulus filtering and linkages to particular behavior can be affected using reward as feedback. Also, response contingencies may affect the persistence of action patterns under evaluation of the reinforcer (see Cleland & Davey, 1982).

Finally, despite their organized quality, behavior system structures do not inevitably produce fixed responding. Oscillation between several behaviors can be produced when a stimulus fits several filters, or the filters are connected with a variety of response components. For example, Muenzinger (1928) noted that lever related responding in guinea pigs slipped in and out of several distinct forms over long time periods. Novel responses can be produced by several means, including simultaneous activation of two semi-compatible modules. For example, if contact with a wall-mounted key is required for a pigeon to obtain water, the pigeon often assumes a modified bow with its neck arched up to press the key.

A more complex example of novel behavior is the case of the dolphins rewarded with food only when they produced a response noticeably unlike any previous response (Pryor, Haag, & O'Reilly, 1969). It might be argued that such novelty disputes that system structures always constrain learning. However, as far as we can judge, the novel behaviors appear to be constructed from a repertoire of response components all potentially related to pursuing prey items. It should be noted that when dolphins are trapped in nets during commercial tuna fishing they rarely display these creative jumping abilities in service of escape. Instead they are frequently trapped with the tuna because diving, their customary escape response, is not effective.

Temporal Contiguity

Temporal contiguity is one of the original conditions for association emphasized
by philosophers. Though there is good evidence that temporal contiguity is not sufficient for reinforcement in either Pavlovian procedures (Rescorla, 1967) or operant procedures (Premack, 1965; Timberlake, 1980), it is still widely assumed that the strength of both Pavlovian and operant conditioning is positively related to the temporal contiguity of the reinforcer (Kaplan & Hearst, 1984). The argument we make here is that this association between response strength and temporal contiguity is mediated by the structures of the organism, not by the strengthening effect of the reinforcer. In this view the US acts as an entrainer of food modes, the expression of which depends on the constraints imposed by the stimuli presented and the responses required.

Pavlovian Conditioning (CS-US Interval). For many years animal learning texts noted that the optimum interstimulus interval (ISI—the time from CS onset to US onset) for Pavlovian conditioning was around .5 sec. However, this value has been shown to be relatively specific to eyelid conditioning. For example, Ost and Lauer (1965) reported that the optimal ISI for salivary conditioning in dogs was 5-10 sec. Maximum misbehavior to a ball bearing appears to occur in a slightly longer range. Kamin (1965) reported little decrement in conditioned suppression to shock cues with ISIs in the 1 to 3 min range. The optimal ISI for conditioning of wheel running in anticipation of food access may well occur at intervals approaching the hour range.

The behavior system approach accounts readily for these diverse data because it argues that the optimal interval for conditioning should vary with the mode and modules involved. This prediction follows because modes (and, thus, modules) are arranged on an aperture-consumatory dimension ranging from interaction with terminal stimuli at the consummatory end to general search at the appetitive end. In the feeding system, modules related to food handling and focal search should condition most readily at the shorter intervals, whereas modules related to more general search should condition most readily at longer CS-US intervals. Thus, modules related to salivation, food tray behavior, and keypecking (in different species) should condition more readily at intervals approaching 5 sec or less. In contrast, modules related to prey capture, systematic search, social approach, and restless activity should condition more readily at longer intervals.

There has been little systematic comparison of the optimum conditioning interval of different CSs, especially those that are likely to control different modules. An interesting test can be done using two concurrent CSs, a circumstance typically producing overshadowing of one stimulus by the other. When two stimuli are compounded at long intervals, the cue that best fits the physical filters for more general search behavior should be responded to the most. When the same two stimuli are compounded at shorter intervals, the cue that best fits the filters for more focal search should control more of the behavior.

In a specific test of this prediction in our laboratory, Shuming Cheng compared the responding in single element extinction tests of different groups of animals all receiving pairings of the stimulus compound of a flashing-light and a ball bearing with food, but trained at CS-US intervals of 2, 4, 12, or 24 sec. We hypothesized that at longer intervals a moving object (the ball bearing) would better fit stimulus filters related to predatory search and capture, while at shorter intervals the light would be a better fit for stimulus filters controlling focal search due to its location near the food tray. Figure 9.9 shows that the peak of responding to the ball bearing occurred at a CS-US interval of 12 sec whereas the peak of responding to the light occurred at 4 sec.

Instrumental (Operant) Conditioning. The basic finding with delay of reinforcement in instrumental conditioning is that minimum delay is best (e.g., Mackintosh, 1974). However, it seems likely that this result may share some restrictions in common with the results for CS-US intervals. One would anticipate that this generalization would be most accurate for behaviors closely related to handling and consuming food, or for single choice responses where considerable interference with retention is likely and the reward serves an important feedback function. With behaviors related to continuous general search, more intense and extensive responding might be produced with longer delays. Certainly delaying reward for a particular keypeck on fixed-ratio or variable-interval schedule can increase keypecking rates and amount. One would expect even a stronger effect for wheel running or locomotor exploration in rats because they are more related to general search mode. Thus, the effects of temporal delay should depend on the type of response measured, the supporting stimuli available, and the quality of the stimuli that accompany the delivery of the US.

However, it is worth noting that the use of response contingencies adds some

![FIG. 9.9. The percentage of trials on which four groups of rats approached a ball bearing or a flashing-light stimulus presented alone during extinction tests. During training the four groups were trained with the Light-Ball bearing compound presented 2, 4, 12, or 24 sec prior to food delivery.](image-url)
interesting complications to the interpretation of the effects of temporal delay. First, in operant conditioning the animal's behavior produces stimulus change in the environment. These new stimuli can fit filters for modules more closely related to obtaining food (as in the case of misbehavior). Thus, a delay may not result in increased vigor of a particular response, but in an increase in some alternative response. Second, adding a response contingency that enforces a particular delay between any examples of a particular response and reward (e.g., a DRO schedule) may increase the possibility of engaging alternative modules. The module that the schedule relates to reward is a good predictor but usually has inappropriate timing. Alternative modules are bad predictors, but with potentially better timing (given a basic rate of reward). The results should show considerable conflict between different modules.

In short, to the extent that it enhances the entrainment of a particular module, temporal contiguity is an important contributor to the emergence of learned responding in both instrumental and Pavlovian paradigms. But the key factor is the production of an appropriate interval rather than the strengthening of a particular response (Staddon, 1975). The distinction is seen in that different responses can emerge under different intervals of temporal contiguity.

Among the implications of such a view is that the juxtaposition of response and reward reflects the animal's contribution as much as the experimenter's. In other words temporal contiguity is in many respects a dependent variable. This is easiest to see when no particular response is required of the subject. For example, in the superstition study we reported earlier, we rewarded either wall pecking or turning to increase their probability, and then we released the pigeon into the condition of fixed-time delivery of food. Despite their high probabilities and resultant temporal proximity to rewards, turning and pecking were dropped in favor of temporal contiguity between an initially low probability wall-directed behavior and reward. In other words, neither pecking, turning, or wall-directed behavior followed the rules of response-contingent strengthening. Instead wall-directed behavior was organized and entrained by the periodic delivery of food.

Another example was provided by King and Timberlake (see Timberlake et al., 1982) when they set up a condition of random presentations of ball bearings and food. After a few days of exposure to this condition, several rats reliably came to seize the bearing, carry it to the food tray, and sit and chew it until the pellet arrived. The behavior of the rats at this point appeared as though it had been reinforced by the response-contingent delivery of food. But considering the developmental sequence it was clear that the appetitive structures of the rat interacting with the environment produced the final temporal ordering. Anticipated food delivery had entrained expression of the most strongly instigated feeding modules present resulting in chewing on the bearing in front of the food tray.

Predictability (Contingencies and Partial Reinforcement)

The importance of contingency relations between the CS and the US in deter-

mining responding has been a pivotal finding in learning theory (see Durlach, 1989 or Mackintosh, 1974; Rescorla, 1967). In behavior system terms, the issue of contingency translates into how behavior is entrained by responding to predictable and unpredictable rewards. In operant or instrumental conditioning the results of a decrease in the predictability of reward given the response is often an increase in the frequency, vigor, or persistence of responding during acquisition and extinction. In traditional Pavlovian conditioning the result is more often a decrease in the frequency, vigor, and persistence of the conditioned response (Mackintosh, 1974). However, autoshaped behaviors resemble operant behaviors in showing an increase in responding under partial reinforcement.

Such a mixture of results is understandable from a behavior system view using some of the same arguments applied to the effects of temporal delay. A decrease in reward predictability, like an increase in CS-US interval, should move the subject from a focal search/handling mode toward a more general search mode. To the extent that the measured behavior is related to more general search behaviors it should increase in amount or vigor; to the extent that the measured behavior is related to more focal search behaviors or food handling behaviors, it should decrease in amount and vigor.

In this view a difference in the response measured may partially account for the classic differences between the effects of partial reinforcement on responding in Pavlovian and instrumental appetitive paradigms (Mackintosh, 1974). In Pavlovian paradigms the response measured, such as salivation, is closely related to focal search/food handling. Thus, supporting a more general search mode by decreasing the predictability of reward will decrease the response. On the other hand, in instrumental paradigms the responding distant from reward is more related to general search mode. Decreasing reward predictability will increase the importance of these more reward-distant behaviors.

As might be anticipated from this analysis, partial reinforcement has been shown to increase running rate in the initial portions of a straight alley, but not near the goal box. Further support is offered by Boakes (1979) demonstration that when the appearance of a lever perfectly predicts food for hungry rats, they predominantly go to the food tray (a typical focal search response). But when food follows the lever only 50% of the time, the rats spend more time with the lever.

V. CONCLUSIONS

We have shown that the behavior system approach can be applied broadly to the current data and procedures of animal learning; it potentially encompasses both naturally occurring and laboratory learning. In the latter case it deals with anomalies, such as misbehavior, superstition, and constraints on learning, as well as with general principles. It argues that Pavlovian and operant paradigms are tools rather
than reflections of basic learning processes, that response form is based on the motor components of the modules involved, and that traditional causal variables, such as temporal contiguity and predictiveness, can be as much derivative as productive of organized behavior. Further, phenomena such as overshadowing and blocking may be critically related to particular modules and motivational states rather than to general information processing rules (Timberlake, 1986).

In the behavior system view learning occurs as modification of the structures of a behavior system, and learned responding occurs as a function of the interaction of those structures with the contingencies and support of the environment. Though we have not emphasized it, a behavior system approach is compatible with many notions of recent cognitive theory while providing a larger framework that emphasizes regulation and responding. For example, the behavior system approach leans heavily on concepts of stimulus filtering, tuning, and linkage between stimuli in the context of their relation to particular response components and modes. There appear to be potential relations between concepts of automatic and controlled processing and how stimuli are involved in learning at the level of both modules and modes (e.g., Kaye & Pearce, 1984; Shiffrin & Schneider, 1977).

The behavior system approach is still in its infancy. The pictures we have drawn and the hypotheses we have advanced will not remain unchanged. Further, our exposition has concentrated disproportionately on the single system of feeding, and is much too incomplete to assimilate the entire sweep of traditional learning phenomena built up by concentrated effort over 90 years of research. The behavior system approach is not an attempt to deny the reliability and importance of previous learning research, but is an attempt to include the major generalizations, exceptions, and methodology in a more coherent framework.

We feel confident that this approach has identified an important issue, the organism’s contribution to learning. The adaptive structures and processes that the organism brings to the learning situation have been ignored inappropriately for historical reasons ranging from rejection of introspection and internal causation to an attempt to isolate learning from issues of instinct and performance (Timberlake, 1983b). Studying learning within a behavior system organization provides a framework which relates learning to the larger scope of the animal’s behavior, including motivational changes and interactions, development and evolution, and physiological underpinnings.

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