Handbook of Contemporary Learning Theories

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A recent development in the study of learning and behavior is the emergence of a behavior systems approach, based on both the laboratory and field behavior of animals (Domjan, 1994; Fanselow, 1994; Hogan, 1994; Shettleworth, 1994; Timberlake, 1994). The behavior systems approach combines an ethologist's emphasis on the evolutionary foundation of the form and control of functional behavior with a psychologist's concern with the role of learning in creating new responses and controlling stimuli.

The importance and potential power of integrating ethological and laboratory approaches to learning and behavior has been argued with persuasiveness (e.g., Kamil, 1988; D. B. Miller, 1977; Tinbergen, 1951). Unfortunately, differences between the two approaches have proved surprisingly difficult to reconcile (Timberlake & K. M. Silva, 1995). For example, even though laboratory research on memory for stored food in birds has both face validity and rigor (e.g., Brodbeck, 1994; Kamil &
Balda, 1985; Krebs, Healy, & Shettleworth, 1990; Olson, Kamil, Balda, & Nims, 1995; Sherry, 1984), a given piece of research rarely satisfies both field biologists interested in foraging and psychologists concerned with the traditional concepts and procedures of laboratory learning. In short, although more has been discovered about how learning contributes to solving specific functional problems, there remains surprisingly little contact between the study of functional behavior in animals and the laboratory learning research accumulated over the last 100 years (e.g., Hearst, 1988; Kimble, 1961; Mackintosh, 1974).

BEHAVIOR SYSTEMS

The behavior systems approach has worked toward resolving the separation between laboratory learning and ethological analysis by relating all behavior to a common functional behavior system. A behavior system is constructed initially by integrating observations of the sensorimotor organization and motivational processes of a species in both the laboratory and field (Timberlake, 1999). Then the system is tested and developed further using the procedures and phenomena of laboratory learning. Assumptions underlying the behavior systems approach include: (a) the same systems organize behavior and stimulus processing in all circumstances, no matter how “natural” or “artificial”; and (b) the effect of an experimental manipulation is rarely direct or simple, but results from interactions among the manipulation, the supporting stimulus environment, and the mechanisms and ongoing processes of the relevant behavior systems.

A behavior system is composed of multiple levels of stimulus and response structures and motivational processes (see Fig. 5.1). The system level accounts for the organization of processing and control around important functions such as feeding (Timberlake, 1983a, 1983b, 1983c; Timberlake & Lucas, 1989), reproduction (Baerends & Drent, 1982; Domjan & Hollis, 1988), defense (Bolles, 1970; Fanselow, 1994; Fanselow & Lester, 1986), and body care (Fentress, 1973). Subsystems refer to a coherent subset of stimulus sensitivities, response components, and regulatory strategies that relate to the system function. Figure 5.1 shows an example of a predatory subsystem of the feeding system in rats. This hypothesized organization is culled from observations of relatively unconstrained laboratory rats and free-ranging wild rats (Barnett, 1975; Blanchard & Blanchard, 1990; Calhoun, 1962; Ewer, 1971; Galef, 1990; Steininger, 1950; Telle, 1966; Timberlake & F. J. Silva, 1994).

The vertical column of modes near the center of Fig. 5.1 represents a sequence of motivational substrates ranging from a general search mode at the top of the column to a consummatory search mode at the bottom.

Engaging a mode engages a repertoire of preorganized perceptual-motor modules (shown to the right) that increase sensitivities to particular stimuli (e.g., Baerends & Krujf, 1973; Barlow, 1977) and tendencies to respond with particular motor components (Fentress, 1976; Hogan, 1988; Tinbergen, 1951). These perceptual-motor units are dubbed preorganized because they have been both selected over generations and modified by previous individual experience to increase the possibilities of successful search behavior in a variety of circumstances.
A typical feeding sequence begins with a rat in general search mode, showing locomotor search and increased sensitivity to spatial and social stimuli that are likely to lead closer to food. The sight of a small moving object at a distance readily elicits chasing. As the prey becomes proximate, a focal search mode is elicited, engaging a repertoire of perceptual-motor units related to capturing and subduing the prey. Tactual and olfactory cues from the prey should then evoke the handling-consuming mode and sensitizes a repertoire of biting, manipulation, chewing, and swallowing. Following consumption of a small prey item, a postfood focal search mode predominates as the animal engages in area-restricted search; then, if food is not forthcoming, the general search mode and repertoire will reemerge. (For a similar analysis of modes in a defensive system, see Fanselow, 1994.)

Returning to Fig. 5.1, a combination of system, subsystem, mode, and module, in conjunction with the environment, facilitates and coordinates individual responses (action patterns). It is worth noting that the levels and units of organization within a behavior system are functional concepts based on characteristic combinations of determinants and classes of outcome rather than on known neural mechanisms (although connections between these levels of analysis would be expected to emerge; e.g., Fanselow, 1991, 1994; Tinsley, Rebec, & Timberlake, 1999).

Finally, the interface of the system with the environment by means of specific action patterns and environmental support stimuli is at the far right of the diagram.

Behavior Systems and Learning

Learning in a behavior system is potentially complex and extensive, including changes in perceptual processing, responses, modes, and systems and their relation to each other and to the environment. Such a view seems at variance with the traditional tendency to conceptualize Pavlovian and operant conditioning as strengthening simple associations or responses. In a behavior systems view, Pavlovian and operant conditioning are better viewed as experimental procedures than as fundamental building blocks of behavior. These procedures interact with aspects of the environment system structures and processes to produce behavior and many sorts of learning (Timberlake, 1995), including: learning about the timing of daily sessions and subsequent feedings in both local and circadian frames (e.g., Timberlake, Gawley, & Lucas, 1987; White & Timberlake, 1999), the adaptation of novelty and stress reactions to the apparatus, differentiating and generalizing stimuli on the basis of available modules, the conditioning of systems and modes, and the incorporation of food intake into the overall regulation of energy. Conceptualizing these changes using the elements and processes of a behavior system seems preferable to modeling outcomes using only a single response strengthening process, or a small set of associative links.

This is not to say that distinctions are lacking among the outcomes of Pavlovian and operant conditioning procedures, but differences that arise result from more than the procedures. Because responding is created at the interface of the procedure, the supporting environment, and the system, the result will depend on their interaction. An additional critical determinant of the outcome of a conditioning procedure is the experimenter's choice of a response measure. To the extent that operant and Pavlovian procedures interact differently with the organism's structures and processes, and the experimenter's measures highlight those differences, the procedures will produce different outcomes. To the extent that interactions are similar despite differences in experimenter manipulations, and the experimenter's measures bring out these similarities, the results will be similar.

THIS CHAPTER

The initial emphasis of research on behavior systems and learning was to explore the contribution of preorganized perceptual-motor modules to the form of learned behavior in the laboratory (e.g., Timberlake & Lucas, 1989). The importance of such modules is particularly apparent in the Pavlovian conditioning paradigm (as well as under minimal response requirements in the operant paradigm) because animals are not required to perform a specific response to produce food. Instead they "fill in" with response forms from their available repertoire. The interested reader should consult Timberlake and Lucas (1989) and Timberlake (1983b, 1990, 1994) for reviews of these studies. I briefly mention a few examples here.

Based on prey consumed in the field and the reactions of laboratory-reared animals to live crickets, Timberlake and Washburne (1989) hypothesized differences among six rodent species in preorganized perceptual-motor units relevant to predation. Based on these observations, we predicted the relative probability and form with which prey-naive members of each species would interact with a prey surrogate (a moving ball bearing related to food) in the laboratory. As predicted, the more predatory species contacted the ball bearings more frequently and all species showed responses to the bearings similar to those occurring during interaction with the live crickets. For example, the species Peromyscus californicus attacked both crickets and ball bearings by lunging toward them, sliding along the substrate with paws outstretched on either side of the prey item and mouth open to bite.
We confirmed several more predictions of the relevance of preorganized perceptual-motor organization to learned behavior, including differences in rats' interactions with a moving bearing predicting food versus water (Timberlake, 1986), differences between the behavior of rats versus hamsters to conspecifics predicting food (Timberlake, 1983b; Timberlake & Grant, 1975), and difference in the type of behavior directed toward a ball bearing predicting acceptable versus poisoned food (Timberlake & Melcer, 1988). Similar evidence for the importance of preorganized perceptual-motor units in other species included differences in the autosized key pecking of pigeons as a function of food versus water reward (Jenkins & Moore, 1973), aggressive behavior directed at conspecifics by territorial gouramis (Hollis, 1990), and sexual behavior directed by male quail at models (Domjan, 1994).

The purpose of this chapter is to extend the work on behavior systems by focusing primarily on the contribution of search modes to learned behavior in the feeding system of the rat. As noted previously, search modes are motivational states involving particular repertoires of modules (response components and stimulus sensitivities). There appear to be four types of mode: general search, focal search, handling and consuming, and postfood focal search. Activation of a search mode increases the probability that perceptual-motor structures comprising it will be evoked by appropriate environmental stimuli or conditioned by appropriate environmental contingencies. Most important, we assume that search modes themselves can be conditioned to cues that are related to receipt of an unconditioned stimulus (US; a reward). Unlike the conditioning of specific stimuli and responses, the conditioning of search modes should produce a more general motivational quality that supports their entire repertoire of perceptual-motor modules.

This chapter explores evidence for search modes and their characteristics, how they are produced, and how they combine with specific cues and contextual support to determine learning. We will continue to focus on Pavlovian conditioning procedures and phenomena for the same reasons we used Pavlovian procedures to explore the existence of characteristic perceptual-motor (module) organization. The animal must "fill in" behaviors related to the system of the US, the environmental support, and the relation of the CS to the US. As a result, the behaviors that emerge can be used to identify the dominant search modes present.

In the first section of this chapter, I consider whether we can account for both naturally occurring and learned strings of appetitive responses using only a sequence of stimulus-response units (perceptual-motor modules), or if an extra layer of causation in the form of search modes is required. In the second section, I evaluate the ways in which the characteristics of the conditioned stimulus (CS)-US relation in a Pavlovian procedure can influence the dominant search mode. In the third section, I explore the temporal characteristics of search modes in interfood intervals. In the fourth section, I consider how search modes may contribute to complex Pavlovian conditioning phenomena, such as backward conditioning, context blocking, and conditioned inhibition. I conclude with a discussion of the usefulness and coherence of search modes as revealed in these data and their possible relation to other conceptions of motivational states (Brown & Jenkins, 1968; Hearst & Jenkins, 1974; Konorski, 1967; Rescorla & Solomon, 1967; Solomon & Corbit, 1974).

POSSIBLE DIFFICULTIES

To some researchers it may seem unlikely that an ethologically based model like behavior systems can account for phenomena occurring within the artificial environments and seemingly arbitrary problems of laboratory learning research. Several arguments, however, support this attempt. First, laboratory experimenters have invested considerable time in tapping (iteratively changing and checking the effects of) their apparatus and procedures to produce reliable and vigorous responding (Timberlake, 1990). I assume that such learning engages the existing appetitive organization of the animal (e.g., Timberlake, 1990, 1997). As evidence for this view, note that the dominant learning responses—manipulation and locomotion in rats, and pecking in pigeons—are important parts of naturally occurring foraging behavior in these species.

Second, because animals have not been selected to deal with artificial laboratory environments, they must necessarily fall back on the same stimulus processing and response repertoire engaged in more natural settings. As Tinbergen (1951) and Lorenz (1981) so artfully documented, artificial stimuli and controlled environments can be of great advantage in revealing the causation of naturally occurring behavior. Finally, the laboratory rat, presumably an artificial creature perverted by domestication, has been shown to have the same perceptual-motor repertoire as its wild cousins, but with altered thresholds for expression (e.g., Blanchard & Blanchard, 1990; Boice, 1972; Galef, 1990).

BEHAVIOR CHAINS AND SEARCH MODES

A major focus in both ethology and laboratory learning has been on the production of behavior chains, a sequence of perceptual-motor modules leading to a consummatory response. Ethologists such as Tinbergen (1951) showed how courtship behavior in sticklebacks and bee hunting in wasps could be explained as a sequence of releaser/fixed-action-pattern units. Psychologists have created similar complex chains of behavior
by conditioning a sequence of novel discriminative-stimulus/operant-response units. For example, Skinner (1937) trained the rat, Pliny, to pull a long chain to obtain a marble, which the rat then carried across the cage and deposited down a chimney before returning to the food tray to obtain food. In both types of behavior chain the observed sequence of responses is presumed to be linked by the fact that the performance of one pattern places the animal in position to receive the stimulus controlling the next response.

A basic premise of the behavior systems approach is that underlying and supporting a behavior chain is a sequence of search modes, each related to a large repertoire of perceptual-motor organization on the basis of both learning and natural selection. A critical assumption is that each search mode can be conditioned to environmental stimuli and internal timing cues related to the US. The major question to be answered in this section is whether there is a need to assume the existence of a sequence of modes underlying behavior chains, or if behavior can be explained completely without this assumption. I examine this question separately within the approaches of ethology and laboratory learning. This analysis is based on noting that behavior chains are not so stereotyped as may have been first thought, and that this variability in responding appears to occur in clumps that fall within the temporal purview of different modes.

**Ethology**

The view that appetitive behavior can be accounted for strictly in terms of chains of sensorimotor units probably began with the study by physiologists of chained reactions like the peristalsis that occurs in swallowing or regurgitation. The chain reaction concept was used to account for more complex repetitive behavior like swimming in eels (Fearing, 1930; Hinde, 1970). Then, despite data supporting more central control of repetitive behaviors (e.g., von Holst, 1937/1973), the concept of reaction chains was extended to complex behavior such as reproduction (Tinbergen, 1951) and hunting (Leyhausen, 1979).

The extension of behavior chains to ethology involved positing independent releaser/ fixed-action-pattern units that were linked by the environmentally based result that one response led to receipt of the next releasing stimulus. For example, Tinbergen (1951) used a reaction chain of releaser/ fixed-action-pattern units to account for courtship behavior in sticklebacks. When the female appeared, the male swam toward her, which released a head-up posture in the female, which released nest-leading behavior on the part of the male, following by the female, nest-showing by the male, entry by the female, quivering by the male, spawning by the female, milting (fertilization) by the male, the exit of the female, and the return to guard duty by the male. In each case, the action pattern response to one releaser put the animal in position to receive the releasing stimulus for the next action pattern.

At first glance such behavior chains do not appear to require the presence of an underlying sequence of motivational modes and their repertoires. However, on closer examination, evidence for underlying modes and repertoires of stimulus sensitivities and motor components seems more compelling. One type of evidence is that responses in a behavior chain appear to drop out in a sequence of groupings as overall motivation decreases. Leyhausen provided a particularly clear qualitative account of the organized waning of hunting behavior in a cat (recounted in Lorenz, 1981). When placed in a room full of mice, a cat initially hunted captured, killed, and ate them. After a time, the cat would chase and capture but not kill the mice. Finally, the cat would simply lie still and follow the moving mice with its eyes. Such data support the presence of a series of motivational substrates that require successively higher levels of motivation and/or stimulus support to make the transition to the next mode in the sequence and related responses (see also Tugendhat, 1960).

A second form of evidence for specific motivational modes and repertoires lies in the local flexibility of appetitive strings. A hunting cat shows many variations in its specific sequences of responses. The variation is often particularly striking in the early stages of prey finding, although variable responding accompanies and follows prey capture as well. Most important, the variation appears to occur within general repertoire classes, like locating prey, stalking or chasing prey, capturing and dispatching prey, and consuming prey. Within a repertoire class, behaviors repeat and change with the environment, while transitions between classes are related to single behaviors like sighting or capturing the prey. Hinde (1970) reviewed data showing similar constrained interchangeability and transitions in a variety of appetitive strings and species.

Related evidence arises from carefully examining strings of behavior in the courtship behavior of sticklebacks. Tinbergen (1951) outlined a prototypical behavior chain leading the animals from start to finish of an egg-laying and fertilization sequence. However, Morris (1958) analyzed actual strings of behaviors, revealing an initial clump of appearing and dancing on the part of the male accompanied by presenting and orienting on the part of the female. Male leading was a transitional behavior for the female from dancing to behaviors related to approaching and entering the nest, which in turn were accompanied by a "clump" of nest-related behaviors by the male. Finally, once the female was in position, the male "trembled" with his snout near her tail, precipitating spawning and a transition to another set of behaviors by each.
The existence of such "clumps" of variable and interchangeable behaviors, separated by transitional responses, suggests a relatively small number of underlying motivational modes in both feeding and reproduction behavior chains. Each mode and its accompanying repertoire, combined with environmental support, allow repetitions and loops of behavior within them. Pivotal behaviors and changes in the environment and levels of motivation appear to mark transitions to a different mode.

Laboratory Learning

Like ethology, the laboratory study of learning also focused on stereotyped stimulus-response chains, but of the sort apparently acquired by the sequential conditioning of individual units. This view emerged first in the study of maze learning in which animals were hypothesized to learn a chain of motor responses that allowed them to choose the appropriate sequence of turns (Hull, 1932; Munn, 1950). A more general chaining approach was articulated by Skinner (1937) and used by him to train complex sequences of responses, such as the slot machine behavior of the rat Pliny that was featured in the national press.

Variability in the Context of Trained Stereotypy. There seems little question that stereotyped units of behavior can be trained by consistent reward and then combined with other units to form stereotyped chains, yet this is not the complete story. That variation still occurs in both individual responses and in overall chains suggests the existence of more complex underlying repertoires associated with search modes. A clear illustration of the presence of underlying repertoires occurs in the misbehavior examples of Brelan and Brelan (1961). For example, using operant procedures with food reward, the Brelans carefully trained a pig to perform a chain of responses; picking up, transporting, and depositing a surrogate coin in a container (a "piggy" bank). However, when they lengthened the chain by requiring the pig to deposit two coins in the bank, the previously unexpressed foraging response of rooting (applied to the coin) suddenly emerged. This sudden intrusion of an obviously preorganized response into a carefully trained operant chain is readily explained by positing the existence of alternative perceptual-motor units related to an underlying mode.

Misbehavior is only a particularly arresting example of a larger repertoire of alternative responses in conditioning. In a more standard procedure, Muenzinger (1928) observed guinea pigs operate a lever for food on more than 700 trials and documented a complex set of behaviors used to operate the lever that slowly varied over trials, including pressing with the paw, moving the bar with the head, biting the bar, and so on (see also Stokes & Balsam, 1991). In the case of mazes, researchers have reported that in a single-choice maze rats tend to alternate choices (Hughes, 1998), in a Dashiel maze they routinely alter their route to food (Munn, 1950), and in a radial maze they tend to enter arms in an unpredictable order whether food is present or not (Timberlake & White, 1990).

In short, constrained variability is often the rule rather than the exception, and such a rule makes sense as a means of ensuring successful foraging in an environment that is similar but not identical from day to day. That such variability is not more obvious in conditioning experiments is in part a tribute to the ability of experimenters to tune their apparatus, manipulanda, and response measures to maximize apparent stability. B. F. Skinner (personal communication, 1977) appears to have been keenly aware of the importance of altering the environment to produce tighter control over behavior. He told me that he had grave difficulty in shaping the rat Pliny to carry a marble over to a chimney and drop it cleanly in. Instead, the rat would manipulate the marble, hesitate to release it, and then try to retrieve it as it disappeared down the chimney. To reduce this problem, Skinner simply made the chimney taller so that the rat could not see or feel with its whiskers the bearing disappear.

In a better known example of how the environment can support stereotyped learned behavior, Skinner (1938, 1956) recounted how he successfully modified his operant chamber and lever to promote lever pressing, including lowering the ceiling, moving the lever higher on the wall and closer to the feeder, and, eventually, rounding the end of a lever that barely protruded from the wall. The importance of Skinner's efforts for the reliability of lever pressing can best be appreciated by attempting to manufacture your own lever, as we did. By slightly changing the lever's dimensions and location, we could (inadvertently) support noseing underneath, biting, grasping, shaking, or two- and one-handed presses. Together, these results support the existence of an underlying repertoire of perceptual-motor units that can emerge and change, tracking changes in the stimulus conditions despite a long history of reinforcement for the previous response in this context.

Temporal Patterns of Variability. In addition to examples of alternative responses, there are also data that suggest transitions between different repertoires, points at which the animal moves from one group of responses and stimulus sensitivities to another. Delivering small amounts of reward at a fixed time in the absence of response requirements or environmental signals provides a particularly rich source of data for such transitions. The curves in Fig. 5.2 illustrate how search modes are hypothesized to map onto the interfractional interval between deliveries of food. Repeated food deliveries at the point shown in the middle of the horizontal axis should organize a sequence of overlapping
search modes preceding and following food. The dominance of a particular search mode at a particular time will depend probabilistically on its relative strength (height on the vertical axis), and the response shown will depend on the supporting stimulus environment as well as the strength of the mode selected.

For example, researchers commonly treat the results of the superstitious procedure, in which food is presented each 12 to 15 sec (regardless of responding), as evidence for the arbitrary effectiveness of proximate reward in strengthening a response (Skinner, 1948). However, when behavior in the superstitious procedure is examined more carefully, further points emerge that are compatible with a version of Fig. 5.2 compressed horizontally so that general search has relatively little time for expression.

First, responding appears to involve several inflection points. Following eating, there is a postfood set of behaviors by the bird (postfood focal search), followed frequently by turning away from and then back toward the wall (more general search), followed typically by a pattern of stepping or pecking focused near the feeder (this focus is more obvious in a large box than in a small one). The transitions between these different repertoires become even clearer when the interval between food presentations grows longer (Innis, Simmelhag-Grant, & Staddon, 1983). In particular the turning response develops into much more extensive walking and pacing.

Second, the behavior shown within each repertoire has some variability in it and can be altered by the nature of the supporting stimuli around the hopper (Timberlake & Lucas, 1985). In other words, there is constrained variability within and between trials. The typical interpretation of superstitious behavior as accidental strengthening of responding can account for the (surprisingly sparse) individual differences (Staddon & Simmelhag, 1971; Timberlake & Lucas, 1985), but it has a much harder time with the regular temporal transitions between repertoires and the less regular changes within them.

The adjunctive behavior procedure differs from the superstitious procedure in that the interval between food deliveries is generally much longer, and the subjects typically are rats. Again, however, there is ample evidence of constrained variability in responding falling within repertoires organized by transitions from one repertoire to another (Lucas, Timberlake, & Gawley, 1988; Staddon, 1977; Timberlake & Lucas, 1991). The first repertoire of behavior after food is consumed consists of postfood focal search represented by head in feeder, local restless activity, and rearing around the food hopper. A second large repertoire extends across a great deal of the interval and involves running in the wheel, passing in and out of the nest, and locomotion about the chamber, behaviors that appear related to general search. Preceding food is a
focal search repertoire, the majority of which consists of head in feeder and inspection around it.

Our classification of interfood repertoires into general search, focal search, and postfood focal search reflects, expands, and integrates classification schemes by Staddon (1977) and Cohen, Looney, Campagnoni, and Lawler (1985). Two questions, though, arise for all these models. The first is why highly excessive drinking occurs primarily at interfood intervals of greater than 90 sec, and the second concerns how to explain the variability in particular response sequences. I consider these questions at a little length to show how a behavior systems framework can integrate both general and specific mechanisms underlying behavior.

Four observations support a unique transitional status for drinking between postfood focal search and the general search repertoire. First, drinking resembles the postfood focal search repertoire in peaking at a relatively fixed time after food (Lucas et al., 1988). Second, at shorter interfood intervals neither drinking nor general search occur with much frequency. Only as the interfood interval increases do both sorts of response emerge and take over increasing parts of the interval. Third, the amount of drinking relative to the regulatory demands of eating is, to say the least, excessive. Fourth, the occurrence of such excessive behavior does not occur with other rewards, like water (Timberlake & Lucas, 1991).

Additional relevant evidence was provided by Lucas et al. (1988), who showed that the interfood interval at which excess drinking starts to emerge is close to the interval at which free-feeding rats start to drink following their voluntary termination of a meal. Postmeal water intake is usually attributed to its ability to lower the cost of metabolizing the food by substituting for water that would otherwise be retrieved from the intercellular and intracellular stores, requiring additional energy to withdraw and later replace (Mook, 1996). Evidence for the critical importance of postmeal drinking is provided by observations that rats rarely drink in the middle of a meal, and by the experimental demonstration that rats are unable to drink before meals in anticipation of reduced in postmeal water availability (Lucas, Timberlake, & Gawley, 1989).

Together these data suggest that rats have a mechanism eliciting water intake that begins to act if food is interrupted for longer than approximately a minute. This explanation requires the meal terminating mechanism to operate at the same time the rat is expecting more food at a later point, but such independence is not unusual in a complex system. Given the cost of bringing water out of the intracellular store (Mook, 1996), a mechanism that evoked drinking after a certain period without food makes sense. Whether fully correct or not, this hypothesis invites further testing and relates closely to the structure and mechanisms of foraging behavior and energy regulation rather than to mysterious side-effects of reinforcement.

A second issue for theories positing motivational substates underlying interfood behavior was raised by the report of Reid, Bacha, and Moran (1993). They reported that although the average sequence of behaviors in the interfood interval is stable, the sequence of responses within individual interfood intervals is quite variable. I have similar data that are not published. Actually, the predictability of average sequences and the variability of sequences of individual responses appears to fit reasonably well the present hypothesis of a sequence of overlapping search modes entrained to the period of the interfood interval. If there are probabilistic aspects to the time at which a mode is evoked and which behavior within a mode is sampled, we should expect stable distributions of response repertoires in time, but not necessarily stable sequences of particular responses within intervals.

Other Paradigms. Evidence potentially compatible with the distinction between general and focal search states also occurs in self-control paradigms (Logue, 1988). Self-control procedures offer subjects a choice between responding for a temporally proximate but smaller reward and responding for a more temporally distant but larger reward. When food on average is imminent, the animal predominantly responds for the closer but smaller reward with rapid strong responding. However, when food on average is more distant, the choices are more frequently directed to the more distant, larger reward, and the rate and intensity of responding is considerably lower. These differences can be explained by the difference between search states conditioned to different delays to food (Timberlake, 1988). For proximate rewards the subject is in a focal search state in which less choice flexibility is possible, whereas the distant rewards initially heighten a general search state in which more choice flexibility exists.

Stereotyped Response Chains. None of this evidence is intended to deny the existence of stereotypy in learned chains of behavior. For example consider the reports of mice running into runway walls when they are moved, or plowing by piles of pellets on the way to the goal box (Clton, 1979). It seems, though, that the majority of such stereotypy occurs when the organism is very close to reward or to the receipt of a stimulus that has been closely correlated with reward in time and space; in other words, when the focal search mode is likely to be well engaged. In support of this view, even when an animal is being rewarded for variability in responding, the degree of variation decreases with proximity of reward (Cherot, Jones, & Neuringer, 1996).
Summary
In short, there seems to be considerable evidence that a sequence of search modes and repertoires underlies both naturally occurring and trained sequences of behavior. Evidence for constrained variability both within repertoires and across repertoires and differences in flexibility of responding exists in naturally occurring sequences such as courtship in sticklebacks and in conditioned behavior produced by the periodic delivery of food in laboratory rats. Interestingly, even well-trained operant responses appear to show transitions in response patterns across the intertrial interval. For example, animals performing on fixed-interval schedules show no responding following food, then low response rates, followed by rapid acceleration to a higher rate as food approaches (Ferster & Skinner, 1957).

CS CHARACTERISTICS AND SEARCH MODES
Protoypical examples of laboratory work on Pavlovian conditioning traditionally focused on autonomic responses (like salivation or eye blinks) to neutral CSs using short CS–US intervals of a few seconds or less. Doubt was cast on the completeness of this view by a number of phenomena, including the ready conditioning of skeletal avoidance responses (Liddell, 1934), and operant conditioning of autonomic responses (N. E. Miller, 1969). However, the most generally bothersome problem has been the phenomenon of autoshaping—the acquisition of extensive skeletal responding in freely moving animals using CS–US intervals much longer than usual, (e.g., 5–20 sec; Hearst & Jenkins, 1974).

In contrast to attempts made to separate autoshaping phenomena from “true” Pavlovian conditioning (e.g., Gormezano, 1966), the behavior systems analysis views both “forms” of conditioning as part of the same appetitive sequence, attributing their apparent differences to a combination of different underlying modes and repertoires, environmental support, and measurement choices by the experimenter. Figure 5.2 can be used to illustrate how motivational modes are assumed to relate to each other and to the procedures of Pavlovian conditioning. For our purposes here the abscissa represents the relatedness of the CS and the US in dimensions such as time, spatial proximity, correlation, and evolutionary association. Examples of how short and long forward CSs relate to motivational modes are shown below the abscissa.

The ordinate corresponds to the strength of the mode. It can be seen that the modes have characteristic distances from the US along the relatedness dimension, but overlap considerably. A CS that falls predominantly within one search mode would be expected to most strongly

condition that mode. One or more perceptual-motor units in the repertoire comprising the search mode and supported by the nature of the CS and the environment should be conditioned as well.

This view of Pavlovian procedures raises the intriguing possibility of using manipulations of the CS–US relation to test and provide evidence for the nature of motivational search modes and related perceptual-motor repertoires. At the same time, this view makes clear that traditional Pavlovian experiments typically use only a small part of the possible space of relations between the CS and US, namely short CS–US intervals, high spatial proximity, high correlation, and low evolutionary relatedness. In the first part of this section, I look at evidence for differences in response repertoires as a function of the interval between the CS and the US. In the second part of this section, I look at the role of spatial proximity between the CS and US. The third part briefly examines how the correlation between CS and US affects behavior, and the fourth part tests how the qualities (evolutionary relatedness) of a CS and a given US influence the effects of the CS–US interval.

CS–US Interval and Response Measures
A basic prediction of the behavior systems approach as represented in Fig. 5.2 is that different CS–US intervals should differentially condition different modes along with examples of their repertoires of stimulus sensitivities and response components. Several experiments have provided supporting evidence for the behavior systems view. For example, Schneiderman (1972) showed that the optimal intertrial interval for conditioning varied with the response being measured. CSs predicting a puff of air to the eye of a rabbit showed an optimal CS–US interval of less than 1 sec for the eye blink response, but an optimal CS–US interval of 5 to 6 sec for a change in heart rate. Timberlake, Wahl, and King (1982), using the CS of a rolling ball bearing to predict food for hungry rats, showed that when the ball bearing was presented more than 6 sec before food, rats typically engaged in responses related to the emergence of the bearing, then chasing and capturing it. However, when the same ball bearing was presented just 2 sec before food, rats in that group responded to the bearing as a signal for behavior related to focal search alone, such as nosing in the food tray.

Similar evidence of different response repertoires under different CS–US intervals comes from the work of Holland (1980) and Hilliard, Domjan, Nguyen, and Cusato (1998). A particularly clear example is found in the work of Akins, Domjan, and Gutierrez (1994), who presented a light CS of 30 or 1,200 sec to a male quail as a predictor of access
to a receptive female US. The CS was presented near the alcove where the female was to appear. The 30-sec CS produced approach and attention to the alcove with the light CS. A 1,200-sec CS failed to increase approach, but considerably increased locomotion about the apparatus compared to that shown by a yoked control group. This finding is compatible with the existence of a focal search mode conditioned to the shorter CS and a general search mode conditioned to the longer CS.

Matthews and Lerner (1987) used yet another technique to test the effects of CS-US interval on conditioning in pigeons. They introduced a sequence of three 10-sec clock stimuli (three different colored key lights) that completely filled a 30-sec interfood interval, and showed that the behavior of the pigeons varied during each 10-sec segment. The pigeons predominantly turned around the chamber during the first segment, paced near the hopper wall during the second, and kept pecking during the final segment. Strong stimulus control of these effects was demonstrated when the segments of the interfood clock were randomized or extended in duration; in all cases the pigeons showed behavior more appropriate to the typical location of the cue than to the current postfood interval.

Taken together, such data strongly indicate that a major determinant of the traditional results of Pavlovian conditioning is the combination of the CS, the CS-US interval, and the choice of what response is measured. It appears that the view of Pavlovian conditioning as related to autonomic responses with maximum conditioning at short CS-US intervals was based primarily on the choice of responses and CSs. To see conditioned responses at longer intervals with a food US it is necessary to remove physical and temporal constraints and focus on search responses related to discovering and capturing food and CSs that should support them. It follows that if Pavlov had allowed his dogs to roam free in the presence of the CS he would have discovered begging behavior to longer CSs, similar to that shown by Jenkins, Barrera, Ireland, and Woodside (1978), and seemingly to that reported by Zener (1937) and perhaps Konorski (1967).

The behavior systems view of the conditioning of search modes and related perceptual-motor units makes good sense of these data, yet learning researchers are typically quite cautious in extending traditional views further than necessary. Thus, it is possible to attribute many of these results simply to the empirical fact that different CS-US intervals condition different responses, without any need to presume the additional conditioning of a search mode. Although this empirical use of the traditional view does not explain why the same CS should best condition different responses at different intervals (or for that matter predict the occurrence and form of autoshaping, superstitious behavior, misbehavior, and adjunctive behavior), nonetheless this empirical interpretation highlights the absence of an explicit separate test for the motivational search states presumably being conditioned and supporting the conditioning of the perceptual-motor unit. The data in the next section attempt to test more directly for the presence of a general search mode.

Unconditioned Probes of the General Search Mode. A classic way to test for the conditioning of a motivational state like a search mode is to first present a CS to evoke or prime the state and then present an unconditioned probe stimulus that elicits a response presumably related to the state. That a response to the unconditioned probe stimulus is facilitated relative to its baseline level by the presentation of a conditioned CS strongly supports the existence of a motivational state tied to the CS. An example of this procedure is to compare the unconditioned startle response to a loud sound with and without the prior presentation of a putative fear CS. If the startle response following presentation of the CS is enhanced relative to baseline and the presentation of other CSs, one assumes the presence of a fear state related to the CS.

Our studies first paired presentations of a tone CS with the delivery of food to condition a motivational mode, and in a subsequent test condition we used a rolling ball bearing as an unconditioned probe stimulus related primarily to general search. To the extent that prior pairings of the CS with food condition a general search state, then presenting the CS prior to the ball bearing should facilitate bearing contact relative to baseline levels, in the absence of any possibility of second-order conditioning. To the extent that prior pairings conditioned a focal search state, we expected no increase (or a decrease) in bearing contact as a function of presentation of the CS prior to the ball bearing.

K. M. Silva and Timberlake (1997) presented separate groups of animals with a tone CS with a duration either long (16 or 18 sec) or short (2 or 4 sec). Following training, the animals were first exposed to 6 days of 12 presentations of unconditioned presentations of a rolling ball bearing to reliably assess the unconditioned strength of the probe as well as extinguish responding to the context of the food tray; then the CS was presented 2 sec before the bearing to see its effect on bearing contact. The results (shown in the top of Fig. 5.3) supported the existence of a general search state conditioned to the CS under the longer interval but not the short interval. Contact with the bearing increased significantly over baseline only in the case of the long CS-US interval. In contrast, the bottom of Fig. 5.3 shows that both long and short groups increased nosing in the feeder following presentation of the CS, though, as would be expected, the short group increased more.

In sum, there is considerable evidence compatible with the behavior systems prediction that search modes and parts of their repertoires can
be conditioned to a CS, and that the modes most strongly conditioned will vary with the CS-US interval. Longer CS-US intervals appear to differentially condition a general search mode and related general search behaviors, whereas shorter CS-US intervals appear to differentially condition a focal search mode and related behaviors. The use of a ball bearing as an unconditioned probe for a general search state strongly supported our conclusion that long CS-US intervals condition a motivational mode rather than only a stimulus–response unit.

CS-US Spatial Proximity

Given that motivational modes can be mapped to the temporal separation between the CS and the US, it would seem reasonable that the mapping of motivational modes may also be a function of the spatial separation of the CS and the US. The view presented here predicts that both a spatially distant CS and a temporally distant CS should better condition a general search mode and related responses, whereas both a spatially and a temporally proximate CS should better condition a focal search mode and related responses. To understand the following experiment it is also necessary to assume that a serial CS can differentially condition different modes to different elements of the CS.

Consider the case of a two-element forward serial CS consisting of an 8-sec sequence of lever insertions, one lever on each side of the food tray and at different distances from it. Temporally the first lever should differentially condition a general search mode and the second lever should differentially condition a focal mode. Spatially, the farther lever should differentially condition general search mode and the closer lever should differentially condition focal mode (see F. J. Silva, Timberlake, & Koehler, 1996). Both of these predictions can be seen from Fig. 5.2 by imagining a sequence of two CSs preceding the food, and assigning the dimension of either space or time to the abscissa.

F. J. Silva, Timberlake, and Gont (1998) tested these predictions by presenting rats with either congruent or incongruent combinations of temporal and spatial characteristics of the elements of a serial CS. Two levers were presented in succession for 4 sec each followed by food. In the congruent (far–near) case the far lever was followed by the near lever to predict food (the spatial dimension and the temporal dimension for Fig. 5.2 predict the same outcome). In the incongruent (near–far) case the near lever was first, followed by the far lever and food (the spatial dimension and the temporal dimension predict opposite outcomes). At an intuitive level we expected the animal to “follow” the levers to food in the far–near case because both the temporal and spatial cues supported the appropriate sequence of search modes, more general fol-

![Graphs showing differences in percentage trials and duration nosing in food tray per 2 sec for CS-BB trials and BB-alone trials between Group Long and Group Short.](image-url)
lowed by focal. In the near–far case, the animal could not “follow” the levers to food spatially because the far lever in the second position lead them away from food, so we expected less contact of the far lever (We previously had discovered that rats were extremely sensitive to the relative spatial differences between two levers near food.)

The results supported our predictions, showing that the congruent (far–near) sequence of Group FN evoked attention to each element of the CS sequence followed by nose in the food site just prior to food (see Fig. 5.4, top and bottom). In contrast, rats in Group NF, receiving the near–far sequence, attended to the first lever but then to the food site, skipping the second (far) lever almost entirely; they even spent more time nose during the first lever than Group FN.

It is possible again to argue (after the fact) that this outcome occurred because of the particular stimuli presented, not because any modes were involved. However, a further prediction was made also based on the assumption of the presence of underlying modes. Assume the reason for minimal contact with the second lever by Group NF was that the contradiction between its relative spatial and temporal positions resulted in a conflict between general and focal search modes resolved in favor of the dominance of the focal search mode and nosing in the hopper. Then it should be possible to resolve this conflict in favor of the general search mode and contact with the lever by increasing the temporal distance of the second lever onset to food.

Increasing the duration of the second lever should increase the relative strength of the general search mode and produce more contact with the second lever and less nosing in the feeder. This prediction that responding to the spatially far lever in the near temporal position (the incongruent, near–far sequence) should be increased markedly by increasing its duration was confirmed (F. J. Silva, Timberlake, & Gont, 1998, Experiments 3 & 4). In short, both spatial and temporal proximity to reward appear important in determining the conditioning of search modes.

CS–US Correlation (Partial Reinforcement)

We realize that based on the work of Kamin (1969) and Rescorla (1967) the concept of correlation has expanded considerably beyond the manipulation of partial reinforcement (percent CSs followed by a US). However, the testing of mode predictions seems clearest and the potential complexities fewest if we limit our concern to partial reinforcement. To this end we presented food on either 100%, 50%, 25%, or 12.5% of the CS presentations. Our question was to what extent the partial reinforcement correlation between the CS and US would map differentially to search modes, producing responding above baseline levels. We as-

![Graph](image-url)

**FIG 5.4.** (Top) Average duration of contact per 4-sec access to the first and second levers for Group FN (far–near order of levers) and Group NF (near–far order of levers). (Bottom) Average duration per 4-sec lever access for nosing in the feeder during the first and second levers for Group FN (far–near order of levers) and Group NF (near–far order of levers; F. J. Silva, Timberlake, & Gont, 1998).
assumed that other things being equal, partial correlations would map onto the abscissa of Fig. 5.2 such that a high positive correlation would act like a short CS–US interval in differentially conditioning a focal search mode and related behavior. In contrast, a low positive correlation between CS and US should act more like a long CS–US interval and differentially condition a general search mode.

The behavior system view was tested more completely by using four CSs: ball bearings, an insertable rat, an insertable lever, and a jewel light proximate to the food tray. Supported by our observations and previous data, we predicted an interaction between CS type and percentage reward. In essence when the CS and the percentage reward both predict differential conditioning of the same search mode, the result should be the maximum expression of that mode. When the CS and the percentage reward predict differential conditioning of different search modes an intermediate level of responding should occur.

Translated into the current experiment, we predicted that ball bearings, because of their shared characteristics with moving prey items, would differentially condition a general search mode (and, thus, maximum responding at a lower percentage reward), whereas a punctate jewel light proximate to the feeder should differentially condition a focal search mode (and, thus, show maximum responding at the highest reward percentages). Levers and rats should condition general and focal search more evenly, and, thus, show peaks of attentional responding at intermediate percentages of reward. Finally, nosing in the hopper (a focal search behavior) should be maximal at the highest reward percentages and fall off rapidly at lower levels.

Rats were divided into 16 groups of six rats each formed by crossing the four CSs (light, insertable lever, rat, and ball bearing), and the four percentage reward levels (100%, 50%, 25%, and 12.5%). Baselines to the CSs alone were collected prior to conditioning for each group. The results shown in the top of Fig. 5.5 for the last 2-day block of acquisition and the first 2-day block of extinction are compatible with our predictions, most clearly on the two extinction tests: trials. Extinction trials have the advantage of no direct conflict with food or handling behaviors; they also tend to highlight general search behaviors because in the absence of food the focal search mode begins to weaken and the general search mode to predominate.

The ball bearing groups peaked at the lowest reward percentages, still contacting on more than 80% of the trials at 12.5% reward. The light groups peaked at 100% reward (extinction data). The rat group had very high responding throughout 25% reward and the lever had highest responding at 50% reward. The bottom of Fig. 5.5 shows that (except for the rat CS groups) head in feeder at the end of acquisition showed highest responding at 100% reward, falling rapidly from there. Lever and

light CS groups also showed greater levels of nosing than the rat and ball bearing groups.

In short, both percentage reward and presumed evolutionary relatedness of the CS appeared to map to motivational modes. In general, high reward percentage was related to focal search modes and lower reward percentages to general search modes. Most interesting, CSs presumed to differentially condition a focal search mode showed higher responding to the CS at lower reward percentages relative to groups with higher reward percentages with the same CS and to the responding
of other CS groups at the same reward percentages. Similarly, CSs presumed to differentially condition a focal search mode showed higher at higher responding reward percentages.

Evolutionary Relatedness of the CS and US and the CS-US Interval

The previous results showed a strong relation between the presumed evolution-based tendency of particular CS types to condition general and focal search and the manipulation of the relation between the CS and the US in terms of partial reinforcement. This study examines the possibility of a similar relation between the CS type and the CS-US interval. Again our general hypothesis was that to the extent that the CS type and the CS-US interval conditioned the same mode, the behavior demonstrated would be the strongest focal search or the strongest general search behavior. In contrast, if the CS type and the CS-US interval predicted the conditioning of different modes, responding would be more a compromise between general and focal search behaviors.

Given the previously established CS-US interval data, we expected the ball bearing CS to peak at the longest CS-US interval where both conditioned a general search mode and related responding. In contrast, the jewel light should peak at a shorter CS-US interval where both the light and the interval should lead to the differential conditioning of focal search. The peak of responding for the rat should fall more toward the ball bearing, and for the lever more toward the light.

The experiment involved 16 groups of six rats each. We used the same CSs as in the percentage reward study discussed earlier (ball bearing, light, lever, and rat). Four groups were assigned to each CS with CS-US intervals of 2, 6, 12, or 24 sec. It is important to note that all CSs were approximately 6 sec long (the duration of the ball bearing presentation was ultimately determined by how much the rat interacted with it). This means that in the 2-sec condition the CS continued past the US, which should make it a weaker conditioner of prefood focal search behaviors. We measured approach responses as movement to within 5 cm of the object with the nose pointed at the object. The stimuli were presented on a VT 72-sec schedule and the US consisted of one 45-mg pellet. Approach responses were coded by an observer unfamiliar with the hypotheses under test and checked for reliability (Timberlake & F. J. Silva, 1994).

The results for percentage trials with a contact with a CS are shown in the top of Fig. 5.6 averaged on the left over the last two trials of acquisition and on the right over the first two trials of extinction, both plotted by CS type and CS-US interval. The results are similar in both graphs, differing primarily in the undifferentiated responding to the light at the end of acquisition, possibly interfered with by the high levels of nosing in the feeder. The peak of responding occurred at the shortest CS-US interval for the light, at intermediate CS-US intervals for the lever and rat, and at the longest CS-US intervals for the ball bearing. The bottom of Fig. 5.6 shows the expected pattern of head in feeder peaking only at the shortest intervals. The peak likely would have been pronounced if the length of the CS had not been 6 sec, so that at the 2-sec CS-US interval it extended past the US.

![Figure 5.6](image-url)

**FIG 5.6.** (Top) Average percentage trials with a CS contact during CS-US intervals of 2, 6, 12, and 24 sec with one of four CSs: proximal jewel light, insertable lever, ball bearing, or rat. The data were averaged over the last two trials of acquisition or the first two trials of extinction. (Bottom) Average percentage trials nosing in feeder during CS-US intervals of 2, 6, 12, and 24 sec with one of four CSs: proximal jewel light, insertable lever, ball bearing, or rat. The data shown were averaged over the last two trials of acquisition or the first two trials of extinction.
These results provide support for the prediction that different CSs may ultimately be most readily related to particular modes, and thus, should be differentially conditionable at different CS-US intervals. The light CS, which should have most readily evoked a focal search mode, peaked at a shorter interval than any other CS. The lever and rat essentially peaked at the same interval and showed the same levels of responding at longer intervals as well. The ball bearing stimulus peaked a little later and was sustained. It appears that even a lower degree of association between the ball bearing and food may be necessary to outline the distant limits of the general search mode.

Summary

In short, it appears that four dimensions of the CS-US relation (temporal proximity, spatial proximity, correlation, and evolutionary relatedness) share sufficient attributes to have reasonably similar effects on responding. Although I propose no clear and precise common metric of relatedness, these CSs share at least a common qualitative relation to the hypothesized sequence of search modes. In almost every case high relatedness between the CS and US produced evidence for the differential conditioning of a focal search mode, and low relatedness between the CS and US produced evidence for the differential conditioning of general search modes. These predictions can be contrasted with a traditional associative view that would have focused on short CS-US intervals, the light stimulus, and the response of nosing in the feeder.

THE TEMPORAL CHARACTERISTICS OF MOTIVATIONAL MODES

The research and observations outlined in the preceding sections provide considerable support for the presence of search modes along with some evidence of their temporal extent. The research in this section attempts to get a clearer idea of the temporal characteristics of the different search modes including the extent to which they show absolute timing versus scalar timing (timing proportional to the interreward interval), how dependent the effects of timing are on CS characteristics, and how flexible the relative timing of the modes is. The first part of this section considers briefly a series of experiments performed by Silva for her PhD thesis (K. M. Silva & Timberlake, 1998a, 1998b, 1999) that makes use of an interfood clock procedure to cast light on the temporal characteristics of search states. The second part of this section examines the results of a procedure that structures the time before and after delivery of a pellet by repeatedly delivering the CS (e.g., 10 times before the US and 10 times after the US).

Interfood Clocks and the Timing of Motivational Modes

A major advantage of the laboratory is that one can control precisely the time at which reward is delivered. To the extent that this timing is predictable, but no response is required, the simple delivery of reward provides an opportunity for the animal to organize its behavior in time, thereby indirectly casting light on how motivational modes are organized in time. The work on adjunctive behavior considered earlier in this chapter (Lucas et al., 1988) suggested that the timing of modal organization is to a great extent scalar. In other words, the time spent in a particular mode (except for the postfood focal search mode) appears to be a relatively constant proportion of the interval between rewards. The purpose of the first experiment here was to determine the extent to which behaviors associated with particular modes did show scalar performance, and how it was associated with the elements of a four-element interfood clock, each element of which occupied 25% of the interval between food deliveries. We chose four elements for the clock in part to provide the opportunity to test if there might be four discrete search modes instead of the three we had considered (handling and consuming aside). The second experiment used an unconditioned ball bearing probe to test for the conditioning of a state rather than a response, whereas the third experiment showed that the search modes had only so much flexibility in tracking the elements of the interfood clock.

Interfood Clocks and Scalar Search Modes. K. M. Silva and Timberlake (1998b) compared the effects of presenting an interfood clock ending with food delivery with the effects of no clock during interfood intervals (IFIs) ranging from 12 to 196 sec. Each four-clock element was one-fourth of the length of the IFI, so that in a 60-sec interval, for example, each clock element was 15 sec in duration. Our purpose was to determine whether different conditioned responses (and inferred underlying modes) showed absolute or scalar timing characteristics (scalar timing occurs when the proportion of the interval at or during which a response appears is constant across different IFIs). Figure 5.7 shows that for all rats and IFIs, the first postfood quarter was dominated by checking and remaining near the food site; the second postfood quarter was dominated by locomotion around the cage; the third quarter combined aspects of locomotion with nosing in the feeder; the final quarter was dominated by nosing in the feeder.
With the exception of postfood behavior during the first quarter of the interval, behavior from different clock intervals showed scalar (proportional) timing; that is, the same proportion of total responding was shown in each clock element by animals with different IFIs. Animals with either interfood clock stimuli or no clock stimuli increased time spent near the feeder during the last two quarters of the interval, but the clock animals showed a sharper discrimination and higher levels of nosing in the feeder during the last two clock elements. The latter finding supported stimulus control of nosing in the feeder by clock cues. In general the data supported the existence of three motivational cues, postfood focal search, general search, and focal search, each compromising different response repertoires.

Clocks and Probes. The results of the previous study supported the hypothesis that general and focal search modes showed scalar timing distributions, whereas postfood focal search showed a fixed timing. However, it seemed worthwhile to test more directly for the general search mode while trying to distinguish between a general search mode and a simple arousal effect. To this end rats were first trained to asymptotic performance using a 48-sec interfood clock with 12-sec elements, then probe stimuli were presented once in each element per day with no food following that interval. The remaining trials remained the same. For one group the probe was a rolling ball bearing that was expected to serve as a probe for the presence of a general search mode. For a second group the probe was the opening of a 4.5 in. × 9 in. door in the wall of the chamber, which provided access to a wire mesh screen for 5 sec. This manipulation was designed to test the possibility that the bearing produced a nonspecific arousal that interacted with the conditions present in the different clock elements to produce the results.

The results showed very strong facilitation of ball bearing contact in the second CS element (see Fig. 5.8) and no difference among these elements in reaction to the moving door (see K. M. Silva & Timberlake, 1998a). These data strongly suggest that an excitatory general search state not based solely on nonspecific arousal produced by the bearing is relatively most strongly conditioned to the second time period.

Mode Flexibility. Taken together, the previous two studies suggest modes have predominantly scalar timing, although there were also modifying effects based on CS presence and duration. The point of this next study (K. M. Silva & Timberlake, 1999) was to explore the possibility that the temporal distribution of the stimuli of an interfood clock could facilitate or interfere with the conditioning of particular modes and the expression of particular response repertoires. We assumed that although there should be flexibility in terms of responding following temporal durations, some distributions of clock elements in time should be closer to “naturally” occurring temporal patterning of search modes than other distributions.

To test this temporal distribution hypothesis, this study presented one group of rats (decreasing) with a four-element interfood clock that successively decreased the size of the elements in a trial (24, 12, 8, and 4 sec); a second group (increasing) received clock elements that increased in size (4, 8, 12, and 24 sec). A third (basic) group received four equal elements (12, 12, 12, and 12 sec). Presumably the more compatible the distribution of clock elements with the flexibility of the underlying modes
and response repertoires, the more clearly distributed and vigorous should be the distribution of the index responses we used, namely remaining on a platform in front of the hopper (postfood focal search), crossing a platform along the back wall (general search), and nosing in the feeder (focal search). Based on the data from our adjunctive behavior studies, we assumed that the decreasing group should be most compatible on average, the increasing group the least compatible, and the basic (equal) group should be intermediate.

Figure 5.9 shows clear differences in our three index responses as a function of the temporal distribution of the clock elements. When the clock elements increased, postfood focal search responses were facilitated by the short elements at the beginning of the interval, and other responses showed little or no change in responding with time. When the clock elements decreased, prefood focal search responses were facilitated at the end of the interval and general search responses were facilitated in the middle of the interval.

**Ball Bearing Contact**

![Bar Chart](image)

**Figure 5.8.** Average percentage trials with contact of an unconditioned ball bearing probe when it was presented during each of four equal elements of an interfood clock (K. M. Silva & Timberlake, 1998a).

**Figure 5.9.** Mean duration of head in feeder per second of presentation of a four-element clock stimulus during a 48-sec interfood interval at asymptote. In the different conditions the size of the element of the interfood clock either decreased from 24 sec to 4 sec across the interfood interval, increased from 4 sec to 24 sec, or remained at 12 sec across the interfood interval (after K. M. Silva & Timberlake, 1999).

In short, the temporal distribution of responses associated with postfood focal, general, and prefood focal search modes is sensitive to the distribution of clock cues within the IFI. Shorter clock elements, whether at the beginning or the end of the IFI showed the most articulated responding that remained relatively constant within each element.

**Periodic Probes Using Different CSs**

The focus of the previous studies in this section was on the temporal distribution of responding within an interfood "space" defined by peri-
odic presentations of food during the experimental session. In contrast, this study focused on the temporal extent (the "envelope") of the effects of a single presentation of a food US (two 45-mg pellets) on repeated unrewarded CS probes presented before and after the single CS-US pairing on the 10th min of a 20-min session. In the initial phase of the experiment there was only the single CS presentation in the middle of the session. In subsequent phases the CS was delivered first 6 additional times a session (3 before and 3 after the food pairing) and then 19 additional times a session (9 times before and 10 after the food pairing).

Three types of CS probe were used: a ball bearing, an insertable lever, and a jewel light mounted within 2 in. of the feeder. We expected the probes to reveal the temporal limits of a general search mode around the US produced by a single CS-US pairing and as revealed by reactions to the CS probes. As in previous experiments, the ball bearing was assumed to be the best probe for a general search mode and the light the worst. Thus, we predicted the largest envelope of general reactivity to CS probes should occur in the case of the ball bearing, the next for the lever, and the least for the light.

The behavior to the CS probes of the paired group (receiving the pairing between the CS and US in the 10th min) was compared to that of an unpaired group and a CS-only group. The unpaired group received the same pattern of presentation of the CSs except the CS was omitted on the 10th min when food was delivered so that no proximate pairing occurred. The CS-only group received all presentations of the CS but never was presented with food. To the extent that behavior to the CS depends on the pairing with food, we would expect more frequent and intensive interaction with the CS in the paired group than the unpaired or CS-only groups.

Two further questions arise in this design. The first is whether responding should be related to the number of CSs presented. A simple associative account would seem to argue that the most intense excitation should occur under conditions of perfect predictability of the US given the CS—namely the one-CS phase when the single CS in the 10th min predicts food perfectly. For the other two phases for the paired group either 6 out of 7 CSs or 19 out of 20 CSs never predict food. Following this logic predicts that the average excitation should be highest for the one-CS phase, followed by the 7-CS phase and the 20-CS phase. For a variety of reasons having to do with the learning of a discrimination, one would also expect no responding to CSs that follow food because food never occurs past the midpoint of the session.

From a behavioral systems view, to the extent that a cue is related to the repertoire of the general search state, presentation of the CS alone may facilitate a general search state particularly if the CS predicts food (see the partial reinforcement results earlier in the chapter). On these grounds we would expect that when responding to a cue is related to response components that characterize and even evoke a general search state, the animal should respond to most of the CSs, including some of those after the US. Thus, we would expect the general search state to be actually enhanced by presentation of multiple ball bearings, less so by lever insertions, and very little, if at all, by multiple lights.

Results are shown in Fig. 5.10. Following the 1-CS phase in which all stimuli showed significant levels of contact in the paired group, the introduction of 7 or 20 CSs resulted in significant increases in contact in the paired condition for all CS types. For the bar and light the increase was primarily (although not exclusively) before the presentation of food. For the ball bearing high levels of contact again occurred across the entire session. The unpaired group for the ball bearing, and to a lesser extent in the 7-CS phase for the bar, showed higher levels of contact than the baseline group, although it was differential before and after the CS.

Several points are raised by these data. First, regular, repeated presentations of a probe stimulus at regular intervals preceding and following the presentation of a single pairing between that stimulus and food elicits behavior despite the fact that none of the extra presentations are ever followed by food. Second, the probe stimulus showed both excitatory and suppressive effects of number. In the multiple CS (probe) phases, the average contacts were greatest in the 20-CS phase for the lever, roughly the same in the 7- and 20-CS conditions for the lever, and higher in the 7-CS phase for the light. In short, number of probes was most excitatory for the ball bearing, next for the lever, and least (but still present) for the light.

Third, the light and lever stimuli showed increased contact predominantly, although by no means exclusively, in the 10 min preceding the food. In contrast, the ball bearing showed increased contact with their CS throughout the 20-min session. However, in the unpaired ball bearing group the contact was greater before than after the presentation of the food. Fourth, the ball bearing group, and to a lesser extent the lever group, showed strong excitatory effects of presenting the probes on responding in the unpaired condition. The ball bearing particularly showed striking effects in the 20-CS condition. It is important to note that this effect is particular to this paradigm; it is not characteristic of a random relation between ball bearings and food (Timberlake et al., 1982) or of responding in random interfood clock intervals during an IFI of 48 sec (K. M. Silva & Timberlake, 1998a), or in using ball bearing probes in tests with no food present. It might be that a 1-min interval balances the excitatory effects of the bearing presentation against the consummatory aspects of interacting with it, with food adding to the excitatory qualities. This might also account for the unusually high baseline of contacting ball bearings in the CS-only group.
These data appear to be a puzzle for theories emphasizing an associative view. It is not clear how to explain why, given that the animals appear to know the reward is in the middle of the interval (based on both a tendency to scalp in responding to the prefood CSs for the lever and light and on the peak in head-in-feeder data—not shown), they continue to respond to the CS probes before and even after the single pairing.

The behavior systems approach receives support from the relative amounts of contact frequency to the different CSs and the enhancement effects of multiple CS presentations on CS contact. The data also provide good evidence for postfood search states that produce interaction with CSs that are never followed by food. The data also point out the unique qualities of the ball bearing to sustain interest and contact despite multiple presentations and even when there is not a forward pairing with food. This sort of sensitivity and persistence would be expected for behavior related to an unconditioned general search mode important in a species' niche. One last thing worth noting is that the bearing contacts in the unpaired group, despite being nearly as high as in the paired group, differed considerably in intensity. A measure of carrying the bearing showed a significant difference between the paired and unpaired groups, and the unpaired group did not differ from the baseline group.

**CONDITIONED MODES AND TRADITIONAL PAVLOVIAN PHENOMENA**

This section briefly examines the preliminary relevance of search modes to a number of traditional Pavlovian phenomena: backward conditioning, context blocking, and conditioned inhibition. I do not argue that these phenomena are completely explained by the conditioning of search modes and modules. I do argue that focusing on the potential contribution of search modes provides a number of novel predictions and considerations that appear to be important in a complete theory of Pavlovian conditioning.

**Backward Conditioning: Conditioning Modes Versus Responses**

The behavior systems framework posits that postfood focal search modes follow the delivery and consumption of food and can be conditioned to postfood stimuli reliably present (see Fig. 5.2 and picture a CS presented following food). F. J. Silva et al. (1996) provided evidence for a two-part hypothesis: Backward pairing of a CS and US at short intervals will condition a focal search mode on the basis of proximity, but will not condition focal perceptual-motor units because the latter requires the prediction of proximate food. Postfood focal responses, though, will likely appear, evoked by the presentation of food, the stimulus support present, and the presence of the postfood focal search mode.

F. J. Silva et al. (1996) obtained evidence for this hypothesis by training different groups of rats with either forward or backward pairings of food with a three-equal-element serial light CS (a total of 24 sec in duration). (Superimpose a three-element CS either preceding or following
food on the modes shown in Fig. 5.2). Following initial conditioning, different groups of animals were tested under forward pairings between a compound CS and food. For each group the compound was formed by combining one of the 8-sec elements of the previous serial light CS with a new lever stimulus. Thus, there were three compound groups that first received backward serial training and three compound groups that first received forward training.

The purpose of using the lever was to see whether previous training with the serial CS had conditioned focal perceptual-motor units that interfered with conditioning of approach to the lever or focal search modes that facilitated contact with the lever. Thus, in both the backward and forward conditioning of the three-element serial CS, the 8-sec element most proximal to food should have differentially conditioned a focal search mode, but in addition the forward near element should have strongly conditioned focal search responses to the light (approaching and nosing in the food tray), whereas the backward near element may have facilitated the expression of, but should not have conditioned, specific focal search responses. The most distant CS element in both backward and forward should have differentially conditioned a general search mode, with slightly better conditioning of general search responses in the forward group. The intermediate CS element should fall between the near and distant elements.

On these grounds we can predict that for the backward groups, responding to the lever should be highest in the compound with the near element because the near element should have most strongly conditioned a focal search mode but without potentially interfering perceptual-motor units. In contrast, in the forward group the near element should show lowest initial responding to the lever because in addition to the presence of a conditioned focal search mode there should be conditioned focal responses that interfere with attention to the lever. Figure 5.11 (top) supports both of these predictions. In the backward conditioned groups, responding to the lever in compound with either the near or intermediate elements is far higher than in the far element backward compound group or the near element forward group. Considering the forward groups only, responding to the lever in the near element group is somewhat lower than in the intermediate element group and considerably lower than the far element group. The bottom of Fig. 5.11 shows approximately inverse effects for the groups in terms of entries to the food tray.

In short, the data support the hypothesis that CSs proximal to a food US condition a focal search mode whether presented before or after the US. In addition, however, forward CSs condition focal perceptual-motor units, whereas backward CSs, although they evoke focal perceptual-motor units, do not appear to condition them. Follow-up experiments support this view as well (e.g., F. J. Silva & Timberlake, 2000; F. Silva, Timberlake, & Cevik, 1998). These results show some promise in making sense out of the complex results of backward conditioning (e.g., Tait & Saladin, 1986).

Conditioned Inhibition
As previously noted, in the behavior systems view the time between regular presentations of food is presumed to be divided among postfood focal search, general search, and prefood focal search. At a
conceptual level this appears to leave no place for conditioned inhibition, (the accrual of negative associative strength between CS and US that is presumed to occur when backward or unpaired CSs are presented along with food (Rescorla, 1967). It is possible that the current behavior systems approach is simply incomplete in this area by not subscribing to an inhibitory associative relation that applies to the strength of particular types of learning. Another possibility, though, is that at least sometimes the phenomenon of conditioned inhibition reflects the results of conditioning a general search mode to the CS, the expression of which is not indexed by a measure of focal search like nosing in the food tray, and may, in fact, initially interfere with that response.

To test the possibility that a negative CS (CS−) may condition a general search mode, Tinsley and I first conditioned a discrimination between paired and unpaired CSs on a Fixed-Time (FT) schedule in which every 90 sec food was presented following a 4-sec positive CS (CS+). At the 45-sec midpoint of each interval a 4-sec CS− was presented. One set of animals receiving this training was then exposed to tests of conditioned inhibition: The summation test compared responding to a compound of CS+ and CS− with that to a compound of CS+ and novel CS (CSN). The retardation test compared the effects of presenting the CS− and food with the presentation of a CSN with food. As would be expected from both the traditional conditioned inhibition view and the conditioned general search view, the CS− significantly reduced acquisition of nosing in the food tray in the retardation test, and decreased (although not quite significantly) the expression of nosing in the feeder in the summation test.

The second set of animals receiving CS+/CS− discrimination training was then exposed to the combination of stimuli used in the summation and retardation tests (with the addition of the CS+ alone), but instead of being followed by nothing or by food, each CS or CS compound was followed only by a ball bearing probe stimulus overlapping the CS, beginning 2 sec after CS onset. In this way the ball bearing served as an unconditioned probe for a general search mode (see K. M. Silva & Timberlake, 1997), predicting an increase in contact with the bearing following a CS−, and no increase or a decrease in the case of the other CSs. In contrast, the conditioned inhibition view should predict either no effect or a suppression of contact of the bearing following the CS−.

Figure 5.12 shows that only presentation of the CS− significantly enhanced ball bearing contact relative to baseline, thereby supporting the argument that the CS− should control a general search mode. Presentation of the CSN and CS+/CS− had no effect on baseline ball bearing contact, and presentation of the CS+ alone and the CS+/CSN decreased contact with the bearing, presumably because of the conditioned mode and modules related to focal search.

Context Blocking

Context blocking refers to the effect of multiple presentations of the US prior to conditioning in markedly reducing acquisition of responding to the CS (Balsam, 1985). The typical explanation of this phenomenon is that multiple presentations of the US condition the context stimuli, which then block subsequent conditioning of a predictive CS. The behavior systems view argues that at least some aspects of the blocking effects may be based on a combination of competition between modes and their potential repertoires.

For example, Timberlake (1986) showed that multiple presentations of a food US prior to conditioning interfered with subsequent conditioning of approach to a ball bearing CS only when the animal received
the US presentations while nosing in the feeder; that is, only when a focal search mode was strongly conditioned. The same number of presentations occurring when the animal was away from the feeder had little or no suppressive effect on subsequent conditioning. These results suggest that context blocking can relate not only to interference at the level of the perceptual-motor unit, but at the level of modes at well, a possibility suggesting blocking is more complicated than suggested by traditional models.

Higher Order Conditioning

In this section, I report no data but provide further examples of how a behavior systems approach can generate predictions related to complex Pavlovian phenomena. Higher order conditioning is a procedure in which animals are first trained with a CS1 paired with food and then receive pairings of a CS2 with CS1; these higher order pairings are frequently interspersed with continued pairings of the CS1 and food. We suspect that the surprisingly mixed success of this procedure has been due in part to a lack of relation between the modes conditioned and the responses measured.

In our view, if the initial conditioning trials produce a focal search mode controlled by CS1 (as would be the case if a 4-sec light CS1 preceded food), then following a CS2 (such as a 4-sec tone) with the CS1 should produce little transfer of the focal search mode and behavior to the CS2 because it precedes the focal search mode. However, the CS2-CS1 sequence should differentially condition a general search mode and response to CS2 based on predicting the focal search mode related to the CS1. However, if the experimenter measures only focal search responses to CS2, there should be little or no apparent effect.

This procedure could be changed to test the behavior systems analysis a variety of ways. For example, the original CS1 training could be simultaneous rather than delayed, thus differentially conditioning a handling and consuming mode to CS1. Subsequently, when CS2 is presented 4 sec before CS1, CS2 is in the temporal and sequential relation to the handling and consuming mode evoked by CS1 that is appropriate to condition a focal search mode to CS2. In this case, measuring a focal search behavior to CS2 like nosing in the feeder should reveal conditioning.

A second example of procedure to reveal mode conditioning would be to keep the original CS1 interval to the US at 4 sec and the subsequent CS2 interval to CS1 at another 4 sec, but use a CS2 and a conditioning measure more related to general search (such as a ball bearing CS2 and a measure of contacting the bearing). One would predict conditioning of a general search mode to the CS2 ball bearing revealed by increased contact.

These examples should make clear that a variety of combinations of training and testing could easily be proposed to test the contribution of modes to higher order conditioning. In many of these tests I find myself in agreement with the recent analysis of R. R. Miller and Barnet (1993) and Barnet, Cole, and Miller (1997) based on the assumption that animals learn the timing of the CS-US interval as well as characteristics of the CS and US. I simply assume that the timing information is encoded primarily by the conditioning of different search modes. The behavior systems approach adds to the timing hypothesis the importance of measuring appropriate response repertoires, and that CS-US relations other than timing may be important also, including spatial, correlational, and evolutionary dimensions.

DISCUSSION

The data reviewed in this chapter provide considerable support for the hypothesis that a sequence of several motivational modes underlies predatory foraging behavior in rats. Modes appear to consist of repertoires of perceptual-motor organization involving stimulus sensitivities and related response components. This organization arises from unlearned and learned sources in combination with the particular environmental circumstances in effect. Perhaps most important, modes can be conditioned to environmental cues, including the passage of time (K. M. Silva & Timberlake, 1998a, 1998b).

Data from both ethological analyses of naturally occurring appetitive behavior and laboratory construction and analysis of strings of instrumental behavior support the conclusions that appetitive and instrumental behavior is more than an invariant string of stimuli and response units, and that multiple modes (and their repertoires) support multiple transitions within a repertoire and less frequent transitions between repertoires. In addition, the data support the existence of more differentiated repertoires than suggested by the traditional contrast between appetitive and consummatory behavior. In fact the majority of data suggest a minimum of four modes—general search, prefood focal search, handling and consuming, and postfood focal search. Of the four, pre- and postfood focal search are most similar in repertoire, differing primarily in the absence of conditioned postfood modules and the different temporal characteristics in periodic schedules (scalar timing for prefood focal search and a relatively fixed time for postfood focal search; K. M. Silva & Timberlake, 1998b).

Data from many laboratory studies by F. Silva and K. Silva and myself reviewed earlier support the hypothesis that motivational modes can be conditioned to predictive stimuli on the basis of the temporal,
spatial, and correlational separation of the CS and the US. Even for the same CS, a small temporal, spatial, or correlational separation between the CS and the US tends to condition a focal search mode and related behavior. A larger temporal, spatial, or correlational separation between CS and US tends to condition a general search mode and related behavior. No separation between the CS and US should produce conditioning of handling and consuming mode and related behaviors. In addition, it appears possible to make predictions based on the observed ecological (and presumed evolutionarily based) correlation between some stimuli and food (e.g., Timberlake & Washburne, 1989).

An increasing amount of laboratory data argues that the conditioning of motivational modes plays an important part in many of the phenomena of Pavlovian conditioning. The most striking contribution of the mode concept is the notion of mode-related repertoires of stimulus sensitivities and response components. This is of critical relevance to the choice of a conditioned response measure. Choosing a single measure can mislead the experimenter as to what is occurring (see also Holland, 1980, 1984). In conjunction with the idea of separate conditioning of the response mode and the responses, the mode concept has obvious potential relevance to phenomena such as backward conditioning, blocking, higher order conditioning, and perhaps occasion setting. Data briefly summarized earlier suggest the importance of both mode and perceptual-motor unit conditioning.

In sum, the phenomena discussed in this chapter are simplest to predict and integrate using the behavior systems concept of conditionable sequential search modes. Any single example undoubtedly can be explained on the basis of specific linked stimulus–response units in combination with others of the many concepts developed within associative theory. However, I think we are at the point where the array of specific assumptions and hypothesized associative and nonassociative processes has become, if not too plentiful, then too disorganized and unpredictable in application. The framework of a behavior system seems to provide a consistent heuristic organization of mechanisms of learning and behavior that can be built on in subsequent work. There are compelling reasons not to abandon all forms of acquired associations among stimuli and responses, but there are compelling reasons to stop trying to explain everything by these links. An advantage of embedding the study of learning within a behavior systems framework is that the framework calls attention to a grammar of modes in which to realize and clarify behavioral results. Such a framework can be modified and built on rather than discarded as particular interpretations and procedures fall from favor (Timberlake, 1993). Once you begin looking at appetitive behavior in general, and Pavlovian conditioning procedures in particular, within the framework of a behavior system, many anoma-

lous findings (ranging from adjunctive behavior and misbehavior to backward and higher order conditioning) become more understandable and predictable. Perhaps most important, many of the predictions that arise from considering how a behavior systems framework should interact with learning procedures have not evolved from traditional learning models.

Related Views

The behavior systems approach is by no means the first to hypothesize the existence of motivational states or substates. In the first part of this century Sherrington (1906) and Craig (1918) proposed a distinction between appetitive and consummatory behavior, a distinction built on by Tinbergen and Lorenz. Within the learning tradition Rescorla and Solomon (1967) highlighted two-factor theory, and Konorski argued for a distinction between a preparatory (drive) state and a consummatory (goal) state. The preparatory state supported the conditioning of diffuse excitatory responses at relatively long CS–US intervals, whereas the consummatory state supported the conditioning of precise focused responses at short CS–US intervals. Wagner developed Solomon and Corbit’s (1974) opponent process idea within the context of Pavlovian conditioning, separating motivation into two processes: an anticipatory process before presentation of the US and an opposing process following presentation of the US (e.g., Wagner & Brandon, 1989). Holland and his co-workers (1980, 1984) pointed out transitions among different components of conditioning. More recently Killeen (1998) applied the concept of increasing arousal underlying the development of an appetitive string of behavior.

A careful analysis of the similarities and differences among these theories and a contrast with behavior systems is beyond the scope of this chapter. There are many similarities and each theory has its own strengths. The behavior systems approach differs from any one of these theories largely in completeness and specificity. It argues for more than two classes of motivational modes: general, focal, handling/consum-
ing, and postfood focal search. Most previous approaches appear to fail to discriminate these modes or do not consider their influence in deciding on CS presentations and response measures to test their theories. The behavior systems approach also attempts to specify the large repertoire of stimulus sensitivities and response components available to the animal in each mode.

A second difference is that most previous approaches treat appetitive behavior as consisting only of variable and diffuse excitatory responses, most often controlled by relatively contextual stimuli. The behavior
The systems approach is more empirical. For example, for many predators, forms of specific general search appear evoked by moving cues of a certain size; consider the actions of the rat with respect to moving stimuli of around ¾-in. diameter (Timberlake et al., 1982), and the reactions of several species of rodents to smaller bearings (Timberlake & Washburne, 1989). Further, the general search behavior of many predatory birds, such as kestrels, consists of systematically searching general areas of potential prey (Daan, 1981).

Third, in contrast with the ethological approach, behavior systems make clear how laboratory learning circumstances interact with the system framework and can be used to explore it. In contrast to laboratory approaches, behavior systems theory assumes a good deal of specific perceptual-motor and motivational preorganization that the animal brings to the circumstances. Although the physiology of the body and the physics of gravity and momentum set limits and windows on the functioning of sensory apparatus and motor output, there is no theory that as yet predicts precise response form or stimulus sensitivities a priori. At present these data must be entered for each species, system, mode, and module on the basis of observation and structural, neural, and chemical analysis. However, when such a theory arises, it should be possible to incorporate it into a behavior system framework that probably already contains aspects of its predictions (see Domjan, 1994; Fanselow, 1994; Hogan, 1994).

Characteristics of Motivational Modes

It should be apparent that the concept of modes and repertoires is sufficiently clear to make predictions and account for a considerable amount of data. However, it should be equally obvious that the behavior system approach, and especially the concept of motivational modes, is neither settled nor complete. There are several issues of importance that need further development and resolution.

One issue is the number of modes. As previously indicated, I think it is evident that there are more than two modes in the case of feeding: a general search mode, prefood focal search, and handling/consuming modes. There are also several reasons to believe that postfood focal search differs sufficiently from prefood focal search to make a total of four modes (e.g., F. J. Silva et al., 1986; K. M. Silva & Timberlake, 1999b). My intuitive reaction is that three to four modes is sufficient, particularly if, as Fig. 5.2 indicates, modes overlap along the dimensions of CS-US relatedness, including time, space, correlation, and evolutionary function. Exactly how these dimensions relate to each will require a model of some complexity, but the implied flexibility allows a given CS the potential to condition and evoke more than one mode and more than one behavior.

However, it is worth considering an alternative model in which there are no discrete modes or separate dimensions of relatedness to the US. Instead there simply are modules arranged on a continuum of arousal that can be conditioned in relatively discrete segments (F. Silva has argued this case in several presentations). It is clear, however, that such a continuum would still effectively locate modules in clumps of increased interchangeability within a range of arousal values that can be conditioned, a not dissimilar picture. Also, it may be difficult to argue that arousal will do all the work of the dimensions of temporal, spatial, correlational, and evolutionary relatedness to the US. The choice of a model may well come down to factors of flexibility and ease of representation.

A second issue about modes is their distribution in time, especially relative to USs and CSs. It appears from free response data that, other things equal, the temporal extent of the prefocal modes is scalar relative to the IPI and the temporal extent of the postfood focal search is fixed for a particular reward amount. However, it makes sense that the temporal extent should be flexible and should vary with the presence of the CSs and the CS-US relations. The data of K. M. Silva and Timberlake (1999) indicate both a tendency toward a particular temporal distribution of modes across an interval and a temporal flexibility in tying modes to stimuli. Data from the multiple CS “envelope” study suggest a temporal range of effects from a single US far beyond what might be expected from typical Pavlovian results.

Further, data from serial CS studies (e.g., F. J. Silva, Timberlake, & Cevik, 1998; F. J. Silva, Timberlake, & Gont, 1998; F. J. Silva et al., 1996) suggest that the temporal extent of a mode can be quite flexible. Apparently, at least some aspects of the timing of modes can be conditioned to different elements of fixed-length serial CSs, and short elements at that. An interesting consideration is that time judgments may differ within different modes. The underlying “clock” may run faster in focal search mode than in general search modes. Similarly, because the postfood focal search mode has the unique quality of following rather than preceding food, there is no particular reason to assume that the animal is judging an interval as it might be in anticipating food. The question of timing is far from resolved.

A third question relates to what determines the strengths of modes, and, in fact, whether we should think of modes as having a coherent strength that affects their repertoire of modules equally. For simplicity, I assume that modes have a basic strength reflecting system variable that may be affected directly by specific neurophysiological conditions and by CS and US that activate perceptual-motor structures. A related issue...
concerns the mechanisms of learning that operate for modes. For example, to what extent can modes be associated with each other and with the environment, the US, and components of perceptual-motor organization, and are these possible associations similar for all modes (see Hilliard et al., 1998)?

A final set of issues revolves around the contributions of system and species differences to the influence of motivational modes. The great majority of research on behavior systems has focused on the feeding system of rats. Evidence from fear systems suggests that the equivalent of a focal search mode (seeking to remain unseen in the presence of a predator) may be considerably longer in duration than a food-related focal search mode (Fanselow, 1994). Similar differences appear to be present in the courtship system in quail (Domjan, 1994).

Even the operation of the feeding system of a particular species may differ according to the density of prey, its location, and the potential difficulty in acquiring it. Clearly the probability of different repertoire components of focal search may differ with the type of prey and its potential resistance. It is equally reasonable that the length and relative extent of general and focal search and even their potential differentiation into a larger number of modes should vary with the ecological niche of the animal. Bell (1991) and Roche and Timberlake (1999) suggested that the physical food niches in an environment can affect the number and form of available repertoires. Pecoraro, Timberlake, and Tinsley (1999) suggested how a behavior system might serve as a framework for combining changes in foraging repertoires and the psychological concept of frustration in dealing with downshifts in food availability. A key to using a behavior system well is to carefully ground it in the repertoires and environments available for each system and species.

SUMMARY

The behavior systems approach brings together and extends historical ideas about the sequence of motivational states underlying appetitive strings of behavior. In practice search modes appear to encompass differing repertoires based on both US and CS sensitivities and response components. The strength of a search mode as well as the individual stimulus sensitivities and response components expressing it reflect both the overall system motivation and specific contributions of stimulus environment. Data supporting the importance of motivational modes come from the analysis of appetitive strings of behavior in both the field and the laboratory; research investigating the effects of temporal, spatial, correlational, and evolutionary relations between CS and US on conditioned behavior; temporal characteristics of modes; and several tradi-

tional phenomena of Pavlovian conditioning, including backward conditioning. Modes should provide a long-term basis for the study of purposive behavior in general and should facilitate the understanding and control of behavior in both laboratory and field settings.

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TIMBERLAKE


5. MOTIVATIONAL MODES IN BEHAVIOR SYSTEMS


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