Chapter 7

APPETITIVE BEHAVIOR IN ETHOLOGY, PSYCHOLOGY, AND BEHAVIOR SYSTEMS

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ABSTRACT

Appetitive behavior can be viewed as variable but nonrandom strings of responses that increase the probability of a functional outcome. Ethologists have focused on the organization and control of naturally-occurring appetitive behavior that leads to a releasing stimulus and a stereotyped consummatory response. In contrast psychologists have focused on learned appetitive behavior featuring novel strings of arbitrary responses followed by a reinforcer. We outline a behavior systems approach to appetitive behavior that combines aspects of both ethological and psychological models. We show how learning procedures can be used to analyze the contribution of behavior system structures and processes to the form and patterning of appetitive behavior.

INTRODUCTION

Appetitive behavior can be characterized as variable but nonrandom strings of responses that converge on a functional outcome. Examples of func-
tional outcomes include performance of a stereotyped response, reception of a critical stimulus, reduction of motivation (quiescence), and optimization of the benefit per unit of response cost. Thus, the appetitive behavior of a hungry cat includes searching the environment for prey stimuli, waiting quietly as the prey approaches, and springing on it. The sequence often ends with a stereotyped killing-bite and ingestion (Lorenz & Leyhausen, 1973; Turner & Bateson, 1988).

The appetitive behavior of a Canada goose migrating in the spring involves flying north until it reaches the critical stimulus conditions signifying its summer breeding grounds. A small adult female moose in a nonreproductive state engages in a variety of search and ingestive behaviors during the day, becoming quiescent after consuming around 10,000 kilocalories. Closer analysis of the moose reveals optimal timing and distribution of effort among temperature regulating behaviors, browsing, and eating aquatic plants (Belovsky, 1978).

Although behavioral scientists agree on the importance of appetitive behavior, they disagree on how it should be studied. Ethologists have focused on naturally occurring strings of responses, especially those terminating in stereotyped actions triggered by a releasing stimulus (Barlow, 1977). An example of such a string of responses is a cat hunting for and killing a rodent. On the other hand, psychologists have focused on learned appetitive behavior, illustrating and analyzing the principles of learning necessary to shape novel strings of arbitrary behaviors. An example of such a novel string is provided by the case of a laboratory rat trained to climb a spiral staircase, lower and walk across a drawbridge, climb a ladder, retrieve a car and pedal it through a tunnel, climb another staircase, run through a tube to an elevator, lower the elevator, and press a bar for food (Pierrel & Sherman, 1963).

The initial goal of this paper is to examine similarities and differences between ethological and psychological views of appetitive behavior. The second goal is to present and provide evidence for a behavior systems approach to appetitive behavior that combines an ethological focus on the evolutionary and ecological bases of naturally occurring appetitive behavior with a laboratory emphasis on the importance of learning and its analytic possibilities. We hope that by calling attention to the possibility of integrating these different views we may gain perspective on issues that currently impede progress in understanding appetitive behavior.

ETHOLOGICAL AND LABORATORY LEARNING APPROACHES TO APPETITIVE BEHAVIOR

The ethological view of appetitive behavior was founded on extensive observation of naturally occurring strings of behavior in a variety of species (Baerends, 1988; Hinde, 1953; Lorenz, 1981; Tinbergen, 1951). Though field observation was common, many ethologists also raised animals at home. Isolating an animal from its selection environment often highlighted stereotyped aspects of responding, while accidental disruptions of behavior provided insight into underlying causal mechanisms (Heinroth, 1910; Lorenz, 1935, 1937). Ethology was well launched when observation was followed by the development and testing of causal constructs, such as releasers, taxes, and fixed action patterns (Lorenz, 1950; Tinbergen, 1951).

In contrast, the laboratory psychologist's view of appetitive behavior was based on the use of standard experimental manipulations and apparatus to construct novel sequences of arbitrary responses in a few species, primarily rats and pigeons. For psychologists the critical aspect of appetitive behavior was that it reflected the result of acquired associations among stimuli and responses. The goal was to establish general, cross-species laws and mechanisms by which appetitive behavior was learned.

Despite contrasting goals and techniques, psychologists and ethologists have shown some remarkably similar concerns in analyzing appetitive behavior. We will briefly compare their views on five such concerns: the appetitive-consummatory distinction, stimulus-response chains, hierarchies of control and motivation, system interactions, and the role of learning in appetitive behavior.

The Distinction between Appetitive and Consummatory Behavior

Early ethological researchers studied eye-catching stereotyped motor acts, such as displays of water fowl (Huxley, 1914; Lorenz, 1935) and doves (Craig, 1918). Craig (1918) termed these stereotyped responses "consummatory actions" and argued that they served as end points for restless, searching behavior. This variable appetitive behavior persisted until the animal reached the "appeted stimulus," which released the consummatory behavior and produced quiescence. Repetition of an appetitive-consummatory sequence was governed by an underlying cycle of appetite. Motivation built up until the animal was goaded into restless movements which continued until the release of consummatory behavior depleted the motivation. The animal then remained in quiescence until the motivation recovered to a point where the cycle began again.

Lorenz (1935, 1950) further developed the notion of consummatory actions in his concept of instinct. An instinct included a genetically-based consummatory act (a fixed-action pattern), its action-specific energy, an innate releasing mechanism sensitive to a particular releasing stimulus, and a taxis element controlling the orientation of the fixed action pattern. Appetitive behavior still consisted of undirected persistent restlessness that brought the animal into contact with the appropriate releasing stimulus.
Learning psychologists also distinguished between appetitive and consummatory responses, but in a different way and to a different end. Their inspiration came from Sherrington (1906) rather than Craig (1918). Based on his physiological and anatomical work, Sherrington (1906) distinguished consummatory reactions from anticipatory reactions. Consummatory reactions were simple localized reflexes controlled by the autonomic nervous system and sensory receptors tuned to proximate (body) stimuli. Anticipatory (precurrent) reactions were whole animal movements controlled by the skeletal nervous system and sensory receptors tuned to the external environment.

Largely unaware of parallels between the work of Craig (1918) and Sherrington (1906), psychologists used Sherrington’s work to distinguish between two forms of learning. Pavlovian conditioning dealt with learned transfer of the control of a simple consummatory reflex from its natural eliciting stimulus to an arbitrary one. This transfer was achieved by close temporal pairings of a predictive arbitrary stimulus with the natural eliciting stimulus. Thus, repeatedly presenting a light prior to the delivery of meat powder to a hungry dog gradually produced (anticipatory) salivation to the light as well as continuing salivation to the meat powder.

In contrast to Pavlovian conditioning, instrumental (operant) conditioning dealt with learning an arbitrary skeletal response by means of presenting a reinforcing stimulus following its performance. For instance, in the case of a hungry rat, presenting food following the response of pressing a lever soon increased the rate of lever pressing. In this fashion two different learning procedures were established, one concerned with the transfer of stimulus control of consummatory responses, and the other with the acquisition of specific appetitive responses.

To isolate the study of learning processes from potential interference by instinctive responses, psychologists trained novel appetitive behavior based on artificial stimuli and arbitrary operant responses. For instance, Thorndike (1911) placed his cats in a puzzle box where they had to perform an arbitrary response to escape and obtain food. With the exception of rubbing against a vertical stick (Moore & Stuttard, 1979), the instrumental response required to escape was not part of the animal’s initial reactions to the situation. In fact, Thorndike noted that it was not until the cat stopped attempting to escape using its immediately available repertoire that the required response slowly emerged.

Skinner took the flexibility of instrumental conditioning one step further by showing that animals could be shaped to perform almost any response by rewarding them for successively closer approximations to the required response. Using the technique of shaping, it was possible to produce startling results, such as training pigeons to play a game of ping pong (e.g., Skinner, 1962), or guide a missile to its destination (e.g., Skinner, 1960). Skinner (1938) also explicitly pointed out the possibilities of using arbitrary stimuli to set the occasion for the reinforcement of an operant response. Thus, a rat could be trained to leverpress for food when a small light beside the lever was illuminated, and refrain from leverpressing when the light was not illuminated.

In short, ethologists distinguished appetitive and consummatory behavior on the basis of variability versus stereotypy of response form, whereas psychologists distinguished them on the basis of skeletal versus autonomic control and the possibility of operant versus Pavlovian conditioning. Ethologists emphasized the natural stereotypy of consummatory behaviors as evidence of the importance of evolution and genes in determining behavior. Psychologists emphasized the learned stereotypy of arbitrary appetitive behavior as evidence of the critical role of learning.

**Stimulus-Response Chains**

Despite their differences, ethologists and psychologists have had quite similar concepts of stimulus-response chains. A chain is an organized sequence of behavior in which each response serves to bring the animal into contact with a stimulus that evokes the next response. This process is repeated until the terminal stimulus is received. In ethology, reaction chains are identified by careful observation of a naturally occurring sequence of responses combined with inferences of the stimuli that control each transition. This is typically followed by manipulations of the presumed controlling stimuli to confirm their role (Baerends, 1941; Tinbergen, 1951; von Uexküll, 1934). For example, the foraging behavior of honey bees consists of a chain of three responses (1) approach to a flower, (2) landing on the flower and searching for nectar, and (3) insertion of the mouth parts into the flower and sucking the nectar. Each reaction is controlled by a different releasing stimulus. Approach is released by a visual stimulus, typically the color of the flower. Landing and searching is released by the odor of the flower, and insertion of the mouth parts is released by a combination of visual, tactile, and chemical stimuli (Tinbergen, 1951).

In psychology, artificial chains were constructed by rewarding the animal first for performing one response in the presence of an appropriate stimulus, and then continuing to add new response requirements until the entire chain had to be performed to obtain reward. One of the first chains to receive extensive attention was learning the sequence of choices in a multiple choice maze. Theorists, such as Hull (1930), postulated that these choice sequences were built up by the rat first receiving reward for making the appropriate final choice before the goal box, then the penultimate choice would be rewarded by environmental and internal cues associated with the final choice. The choice before that was then rewarded by environmental and internal cues associated with the penultimate choice, and so on. According to Hull each choice came to be controlled by
a combination of movement-produced stimuli, unique choice-point stimuli, and stimuli related to anticipation of the goal.

Although the chaining explanation for maze behavior was largely based on inference, operant psychologists using Skinner's (1938) shaping techniques and the backward chaining procedure developed by Hull (1930) have produced remarkable sequences of responding. For example, Skinner (1937) trained a rat named Pliny to press a lever to obtain a marble which it then carried to a small chimney to deposit for food. Similarly Breland and Breeland (1966) trained a duck to play a piano, and a chicken to bat a baseball and run to "first base." Subsequent work has shown that chains can be constructed forward from a first response as well as backward from a last response (Mazur, 1993).

An important unresolved question is the extent to which elements in a chain are independent. Is a reaction chain such as bee hunting by wasps (Tinbergen, 1951) a linked series of individual releasers and fixed action patterns, each with its own flexible appetitive behavior and specific motivation? Or are its components simply part of an environmentally organized string of responses that share a common motivation, lead to a common releasing stimulus, and result in a single consummatory behavior?

One way to answer the questions of independence is to observe the degree of naturally occurring variability in a chain. Such variation is clearly present in the chain of behaviors involved in stickleback courtship and egg fertilization. Morris (1958) documented repetitions of some elements, skipping of others, and terminations while the male engaged in other behaviors such as swimming through the nest, and termination of the chain at different points. Some of this variation may be due to differences in motivational thresholds among individual components of the chain (e.g., Tugendhat, 1960), but some effects imply a fair degree of independence for each component.

There is also evidence that the performance of a chain can be related to overall motivation that is reduced by reaching a terminal stimulus and a typical consummatory behavior (Tinbergen, 1951). Thus, a bee after sucking the nectar from a particular flower often returns to the hive rather than displaying other elements of the foraging chain. A male stickleback after showing its nest to a female, quivering, and fertilizing the eggs shows a reduced probability of immediately beginning a new sequence of courtship. Similar effects exist in learning situations. Pigeons pecking on long fixed-ratio schedules do not immediately restart the chain following feeding (Ferster & Skinner, 1957).

A second way to determine the relative independence of individual components of the chain is by using experimental manipulations, such as extending a link of the chain by preventing access to the next component, or shortening the chain by providing access to the final link before the behavior of the animal ordinarily would have produced it. For example, Baerends (1941) artificially extended the provisioning chain of a digger wasp by preventing its receipt of the next stimulus. Ordinarily a digger wasp inspects a nest, hunts for and captures a relevant host (caterpillar), carries it to the nest, and places it next to the nest opening. After a brief inspection of the nest the wasp returns to the surface to take the prey into the appropriate chamber. In his experiment Baerends waited until the wasp put down the caterpillar and entered the nest. He then moved the caterpillar a short distance away to see if the wasp could take the caterpillar directly down the hole, skipping a repeat of the inspection phase. Apparently it could not do so. Instead it repeatedly carried the caterpillar to the hole, re-inspected the nest, carried the caterpillar to the hole, re-inspected the nest, etc.

In terms of experiments attempting to short-circuit a chain by presenting a stimulus out of order, the data are mixed. Learning researchers have shown that well-trained rats will run past food placed in the alley to get to the goal box, or will run into walls that are moved (Olton, 1979). Both effects suggest a lack of independence of elements in a chain, with the responses set to run off in a particular order that is difficult to disrupt. On the other hand the outcome of giving a predator its prey without the requirement of a hunt supports the notion of independent motivation for the components of the chain. For example, Leyhausen (reported by Lorenz, 1981) provided a cat with a room-full of mice. After killing many mice, the cat then began only to capture and release the mice without killing. Finally it simply lay still in an alert watching posture, tracking particular mice with its eyes while ignoring others running over its paws. Lorenz (1981) argued that the greater persistence of the chasing and tracking behaviors showed the tendency of behaviors to have their own motivation in proportion to the amount typically required to obtain prey in natural settings (see also Bell, 1991). Supporting evidence for this notion also comes from work with carnivores at zoos. At the Brookfield Zoo in Chicago, stereotyped pacing behavior in mountain lions was reduced by providing the animals an opportunity to "hunt" an artificial moving object.

In sum, ethologists focused on naturally occurring chains of behavior. They confirmed the importance of stimulus-response linkages by manipulating the stimuli presumably controlling each response. Psychologists attempted to ensure their understanding of chains by using artificial components, training each component before adding another. Ambiguities exist in both natural and artificial circumstances concerning the independence of components of a chain. Some data suggest that the entire sequence forms a coherent whole that is difficult to interrupt, while other data indicate the existence of considerable independence among the different components of a chain. The similarity of the issues raised in the study of naturally occurring and artificial chains suggests the possibility they share a number of underlying mechanisms.
Hierarchical Models

Perhaps nowhere is the difference between ethology and learning psychology more striking than in the role of hierarchical structures in explaining behavior. The focus in psychology on establishing basic conditioning principles in simple circumstances delayed the consideration of complex behavior. Some central-motive state models (e.g., Beach, 1942; Bindra, 1961) introduced greater complexity in dealing with motivational phenomena, but they had little effect on the study of learning. Hierarchical models were restricted to analyses of motor control (Kelso, 1982; Lashley, 1951) and analyses of language (Chomsky, 1972).

The close observation of a species in free-behavior situations typically reveals overall organization not captured by the appetitive-consummatory dichotomy or the concept of reaction chains. For example, reproductive behavior in the stickleback is sustained over a period of weeks and consists of many appetitive-consummatory combinations and multiple reaction chains organized into larger functions, such as territorial defense, courtship, and parental behavior. To capture the underlying organization of this potpourri of stimuli and responses, ethologists developed the concept of a hierarchical system of behavior.

In Tinbergen's (1951) representation, a reproductive behavior system in the stickleback linked responding to motivational centers at higher levels and fine-grained motor and neural control at lower levels (see Figure 1a, which omits the lower level neurophysiological hierarchy). The highest level of the model is a superordinate center for reproductive motivation and control that is energized by changes in day length and produces the appetitive behavior of migrating into shallow and warmer water. These latter stimulus conditions allow motivation to flow into a variety of subcenters related to fighting, courtship, nest building, and parental behavior. Each of these subcenters in turn has its own appetitive behavior and an innate releasing mechanism, the release of which energizes all the behaviors below that subcenter while inhibiting motivation flow from the other subcenters at that level. Each action pattern under a subcenter also has its own appetitive behavior, innate releasing mechanism, and appropriate releaser. Thus, the reaction chain comprising stickleback courtship will begin once the courtship subcenter has received the releasing stimulus.

Based on his observations and experiments with the digger wasp provisioning its offspring, Baerends (1956) proposed a similar hierarchical model that allows multiple connections between lower level and higher level units (see Figure 1b). Baerends' use of this lattice hierarchy makes explicit that a given action can be motivated and controlled by different higher order centers. Baerends also showed that the animal's "place" in the hierarchy could be strongly controlled by the external stimulus conditions. For example, when provisioning multiple nests, the behavior of the wasp switched instantly to the type of

Fig. 1. (a) The Hierarchical Instinct Model proposed by Tinbergen (1951) and redrawn in Eibl-Eibesfeldt (1975). (b) Baerends' (1956) hierarchical model redrawn in Eibl-Eibesfeldt (1975). Note that the lower centers are controlled by several higher centers. The dotted lines represent inhibitory relations among elements at the same levels.
provisioning appropriate to the local nest, and even to beginning to dig an entirely new nest when the stimulus conditions were appropriate.

In summary, data from the observation of animals in relatively free-behavior circumstances not only shows variable and stereotyped behavior, and local reaction chains, but strongly suggests that behavior is organized in a control hierarchy related to a particular function. The hierarchical system can be invoked by particular sets of cues (e.g., changes in day length, food deprivation) and contributes to the organization of subsequent behavior. Among psychologists, the notion of hierarchical control has been an important contributor to the study of skilled motor behavior and, to an extent, the study of motivation, but has been of little concern in the traditional laboratory study of learning.

System Interactions

In free-behavior situations it was immediately clear that even the complexities of a hierarchical model were insufficient to deal with the interruptions, variability, and out-of-context (displacement) behavior that were frequently observed during appetitive behavior. For example, in a courtship situation, why would a male stickleback break off in the middle of a zig-zag dance with a female to go fan the nest, swim through it, or dig in the substrate (Sevenster, 1961)? Such behavior seemed to imply the existence of multiple hierarchical subcenters that were competing for access to the final common path controlling behavior (McFarland & Sibley, 1975).

Researchers such as Wiepkema (1961) and Baerends, Brouwer, and Waterbol (1955) provided evidence for multiple motivations underlying courtship behavior in fish by combining extensive recording of behavior sequences with the use of multivariate statistics designed to identify "clumps" of action patterns that resembled each other in terms of their sequential dependencies. Each "clump" of activities was typically identified with a particular motivational state, and the actual sequences of behavior were seen as a product of competition and interaction among these states. For example, Wiepkema (1961) produced a factor analysis of courtship behavior in bitterslings supporting the existence of systems related to fear, territoriality, and courtship.

Other evidence for system interactions grew from research on displacement activities, responses that appeared irrelevant to the dominant motivations of the animal but emerged when expression of these motivations was thwarted by conflict or the absence of proper stimulus support (e.g., nest fanning in sticklebacks; Tinbergen, 1951). Subsequent research has favored the notion that displacement activities are not irrelevant, but reflect the emergence of behavior normally blocked from expression and which may serve an instrumental function in changing motivation (e.g., Wilz, 1970).

In the laboratory, Falk (1977) argued that excessive or irrelevant (adjunctive) behavior produced by the intermittent delivery of food was actually a form of displacement behavior. It occurred when the feeding drive of the animals was thwarted by delivery of the widely temporally-spaced food pellets. For example, hungry rats drink very large quantities of water during a session in which 45 mg food pellets are presented each 120 sec (Falk, 1961). Similar increases have been shown for other apparently irrelevant behaviors such as aggression, gnawing, and running (Staddon, 1977; although see Roper, 1981).

Other evidence from laboratory learning indicates that some types of learning are specific to characteristics of the deprivation state and reward. Early studies of the role of motivation in learning summarized by Kimble (1961) indicated that maze learning was independent of whether the initial drive-state involved food or water deprivation. The intensity of deprivation, though, is apparently coded more permanently. Differences in the drive level in acquisition were capable of affecting later behavior under a common level of motivation (e.g., Timberlake, 1967). Finally, a number of studies have shown that different combinations of motivation and incentive can affect the form of the conditioned response (Davey, 1989; Timberlake, 1986).

Neurophysiological work also supports the importance of systems interactions in determining behavior. The pioneering work of von Holst and von St. Paul (1963) showed that stimulating the brain of chickens using large electrodes produced combinations and alternations of behavior apparently belonging to different systems. For example, under brain stimulation a chicken could increase both its feeding and alarm behaviors. More recent investigators, such as Davis (1984), have begun to show the specific neural basis of system interactions in relatively simple organisms such as pleurbranchia.

In summary, using extensive observation, multivariate statistical analysis, astute experimentation, and neurophysiology manipulations, ethologists and some psychologists have converged on the notion that interacting systems underlie behavior. Such systems contain individual stereotyped behaviors and levels of motivation that link together the level of activation of a group of behaviors related to common goals. Ethologists have shown that accounting for complex naturally occurring strings of behavior leads rapidly to a concern with interacting motivational states. Psychologists have shown that even in tightly controlled circumstances, motivational states appear to make important contributions to behavior.

The Role of Learning in Appetitive Behavior

Our presentation to this point may have suggested a caricature of ethologists as impervious to the possibility that learning has contributed in important
ways to naturally occurring appetitive behavior, and a caricature of learning researchers as guarding against any contamination of their work by naturally occurring behavior so they may carefully define the contributions of simple conditioning mechanisms. Although there are important differences between ethologist’s and psychologist’s approaches to learning, we do not feel this oversimplified picture captures the important points.

Ethologists have long been concerned with learning, but within the context of ongoing appetitive behavior. When ethological researchers deal with learning, they are interested in how it contributes to known appetitive behavior relevant to a particular function. For example, Tinbergen’s (1951) work on learning in digger wasps focused on their ability to learn landmarks around the burrows they were provisioning. Hailman’s (1967) work clarified how learning contributed to the control of the begging response in young gulls. These wonderful analyses of learning must be contrasted with specific instances treatment of the general topic of learning. Ethological textbooks appear to have no more idea of what to do with the requisite chapter on learning than learning textbooks know where to put the chapter on instincts.

Psychologists began this century with an interest in how learning related to ecological questions (e.g., Timberlake, 1983b), and recently have begun to consider these issues again. Despite the focus on the analysis of learning using experimental paradigms, data arose within traditional paradigms indicating that animals entered the experimental situation with stimulus sensitivities, response priorities, and motives that appear related to naturally occurring strings of appetitive behavior (Rozin & Schull, 1988; Timberlake & Lucas, 1989). The best known examples are found in the constraints-on-learning literature in which some combinations of stimuli, responses, and rewards are easier to learn than others (Bolles, 1970; Hinde & Stevenson-Hinde, 1973, Shettleworth, 1972). For example, Sevenster (1973) showed that male sticklebacks bit a glass rod to obtain visual access to another male more readily than they swam through a ring for the same reward. The reverse was true when the reward was visual access to a female. These differences argue for the influence of naturally occurring behavior chains related to the functions of territorial aggression against other males and courtship behavior directed at females.

Careful study of the phenomena of “misbehavior” supports similar conclusions. Misbehavior refers to the emergence of disruptive behavior in the latter stages of training an operant response (Breland & Breland, 1961, 1966). A classic example is that of the pig trained to deposit a token to obtain a small food reward. The pig was shaped first to pick up the token, then to deposit it, then to carry it to the “bank” from increasing distances. Training went well until a certain distance was reached and then the pig began to drop the token and push it along the ground with its nose, displaying what appeared to be rooting behavior typically used by this species to find food.

The phenomenon of “autoshaping,” basically the application of Pavlovian conditioning procedures to skeletal responses in unconstrained animals, also showed that naturally occurring appetitive behavior can emerge within learning paradigms. For example, Jenkins, Barrera, Ireland, and Woodside (1978) used a light on top of a short pole to predict the imminent delivery of food for a hungry dog. The dogs soon went to the light when it was switched on rather than to the feeder, nosed it, played bowed, and barked at it, all behaviors related to food begging from conspecifics. Jenkins et al. (1978) suggested that Pavlovian signals could be thought of as conditioning naturally occurring episodes of behavior. Hollis (1990) used visual stimuli presented to male blue jays to predict imminent access to a second male. The males receiving the signal would swim to a partition and prepare their aggressive displays for the male about to arrive.

Finally, work on adaptive specializations in learning has continued to thrive (Rozin & Schull, 1988). Garcia’s classic work on aversions developed to novel taste cues followed by sickness showed extremely long temporal gaps between a taste signal and the subsequent unconditioned response of nausea (Garcia & Koelling, 1966). Further work indicated large differences in the neurophysiological substrates related to taste avoidance learning and similar learning to external cues. The work on bird song learning also has revealed the existence of an entire specialized neurophysiological system concerned with processing, learning, and storing auditory information (Marler, 1991; Nottebohm, 1991).

In the face of these demonstrations of the relevance of the species to learning, most learning researchers focused on the issue of whether the resultant behavior could be accounted for by the accepted mechanisms of conditioning. Many concluded that constraints data could be incorporated rather handily into traditional theory by noting that ease of conditioning was basically a question of parameter values in the general laws of learning (Domjan & Galef, 1983; Logue, 1979; although see Gardner & Gardner, 1988). Unfortunately, the most unsettling issue was lost in the scuffle. The existence of unexpected phenomena such as long-delay taste-aversion learning and misbehavior implied the necessity of a different framework of analysis, a framework of naturally occurring appetitive behavior rather than a framework of conditioning principles. The artificial environments, standardized paradigms, and arbitrary stimuli and responses were not sufficient to preclude contributions of the animal's naturally-occurring appetitive behavior.

Summary

There are marked similarities between the psychological and ethological approaches to the conceptualization of appetitive behavior. Both established a
basic stimulus-response unit of analysis, distinguished between appetitive and consummatory responding, studied chains of stimulus-response units, and dealt at least peripherally with system interactions. Differences, of course, are equally obvious. Many stem from the psychologist's focus on learned behavior and their concern with separating the phenomena of learning from the study of motivation and instinct. While ethologists developed a hierarchical model of the motivation and control of naturally occurring response strings, psychologists developed effective experimental paradigms—procedures, apparatus, and measures—that produced arbitrary strings of responding. Their learning principles were presumed to apply to all species, responses, and stimuli.

Because psychologists were fascinated by the effects of learning in organizing a disorganized organism, their behavioral units were units of learning rather than naturally occurring behavior. Nonetheless, as the data above indicate, animals bring species-typical processes and organization to psychologists' experiments (e.g., Breland & Breland, 1961). Although the experimental procedures of laboratory learning can be used to create novel strings of responses, these response strings are not extracted from the blank slate of a randomly acting organism.

**Towards an Integration of Ethology and Psychology: A Behavior Systems Approach to Appetitive Behavior**

The case for integration of ecological and psychological approaches has been made with great persuasiveness by many researchers, including Tinbergen (1951), Miller (1977), and Kamil (1988). In the last section we noted many parallels but also several important differences in how psychology and ethology have treated appetitive behavior. A straightforward path toward integration is to combine the ethologist's functional, system-centered approach to naturally occurring appetitive behavior with the psychologist's skills in constructing behavior through learning procedures. This integration would provide an evolutionary and ecologically grounded background for the study of learning, while allowing us to take advantage of learning procedures as tools to analyze the operation of an evolved system of behavior. This approach has been implicit in recent research on foraging combining simple response units, standardized apparatus, and clever experimental procedures to manipulate and analyze the acquisition and control of semi-natural behavioral sequences leading to food (e.g., Balda & Kamil, 1989; Brodbeck, 1994; Cassini, Kacelnik, & Segura, 1990; Collier, 1983; Krebs, Healy, & Shettleworth, 1990).

The integration of ethological and learning approaches has been made more explicit and general in work on behavior systems (Davey, 1989; Fanselow & Lester, 1988; Tinbergen, 1983ab, 1990, 1993; Tinbergen & Lucas, 1989). The basic premise of the behavior systems approach is that the structures and processes underlying behavior have been organized by evolutionary selection pressures into a functional system (Baerreis, 1988; Davey, 1989; Fanselow & Lester, 1988; Tinbergen & Lucas, 1989). A behavior system consists of stimulus filtering and processing, timing and memory functions, motor programs, motivational states and processes, and their interrelations (Tinbergen, 1993). Typical learning manipulations have their effect by interacting with the structure and processes of a system. The approach can be most clearly stated by considering a specific example.

**The Structure and Processes of a Feeding System**

Based on the observation and research of a number of investigators, including Barnett (1975), Calhoun (1962), Ewer (1971), Galef (1990), Steiniger (1950), and Telle (1966). Figure 2 shows a schematic of part of the feeding system of a rat. The feeding system consists of a hierarchy of four levels of organization and control: system, subsystem, mode, and perceptual-motor mod-
The individual components of a system are functional units that represent characteristic combinations of determinants and classes of outcome. Together, these four levels and their components select and coordinate individual responses, termed action patterns.

The system level (not shown) accounts for the tendency of behavior to be organized around important functions, in this case feeding. Subsystems refer to a coherent subset of stimulus sensitivities and response components for meeting the needs of a particular system. In this case, the predatory subsystem in the rat involves sensitivity to moving stimuli and increased likelihood of chase and capture responses.

Modes are motivational substates that relate to the sequential and temporal organization of action patterns. Modes control responses ranging from general search behavior to specific consummatory responses. For example, a feeding sequence typically begins in a general search mode, characterized by attention to novelty and a search for cues that might predict the location of food. When cues highly predictive of food occur, the animal moves to a focal search mode in which action patterns are more focused and related to the immediate procurement of food. When food is present, the animal enters a handling/consuming mode, in which action patterns are focused directly on the food item. This sequence of modes is also reversible. As the certainty of obtaining food declines, the animal first reenters a form of focal search mode (area-restricted search). If food is discovered, the animal re-enters the handling/consuming mode, and repeats the following focal search mode. If food is not discovered, the animal returns to a more general search mode, then either repeats the cycle or stops foraging.

Perceptual-motor modules reflect the importance of preorganization to respond to particular stimuli with particular response components (see Hogan, 1988). The perceptual aspects include sensory filters that gate or sharpen particular stimulus dimensions or configurations as well as rules for organizing and combining different stimuli (e.g., Baerends & Kruijt, 1973). The motor organization in a module results from motor “programs” or rules for their assembly related to particular stimuli and other motor programs (Bingham 1988; Fentress, 1976; Kelso, 1982). Finally, the action patterns represent the expression of the system in behavior. Note that this is an incomplete representation of a behavior system. Missing from this characterization are representations of positive and negative feedback from responding, internal stimuli, relations among components of different systems and subsystems, and rules for combinations of and competition for expression among action patterns.

Relation to Ethological Models

On first glance the hierarchical system in Figure 2 resembles a truncated version of Tinbergen’s hierarchy turned on its side and missing the hierarchy of motor control borrowed from Weiss (1941). However, the apparently simple act of turning the model sideways calls attention to several important distinctions concerning the motivation and control of responding. In Tinbergen’s model the sequence of types of behavior in a system is isomorphic to the order with which motivation is presumed to reach each successive center. Thus, motivation is present initially only in the highest center producing restless activity and migration. Arriving at a suitable territory releases motivation to centers for courtship, territory defense, and parental care. The subsequent receipt of specific releasers for these subcenters allows motivation to “flow” down to the consummatory acts, etc. It follows that presenting a releaser for a lower center out of the usual order should produce little behavior until motivation has been released to that level.

In our version of a behavior system hierarchy, motivation and the sequence of behavior are less interdependent. A general “flow” of motivation does not necessarily correlate with the course of behavior. Systemwide motivation is usually present at all modes and modules any time a system is engaged. Motivation available for a particular module is affected also by critical stimuli and by the strength of underlying motivational modes. Behavior relevant to a system typically begins (at the top of Figure 2) with responses related to general search. It then moves to responses that are successively more closely related to finding, handling, and consuming food items.

An advantage of separating motivational “flow” from the sequence of behavior is the increased opportunities for environmental control, such as short-circuiting a string of behavior. For example, under some circumstances we should be able to present a hungry rat with food, and have it eat promptly rather than go through a sequence of general search and predatory behaviors to allow motivation to reach the ingestion module and produce eating. We hasten to add that there are circumstances in which presenting a cue out of order will not short-circuit a string of responses. We previously mentioned that well-practiced rats will run by food in a maze on their way to the goal box. In other cases the motivation for behaviors at the end of a string will be highly dependent on stimulus input at points earlier in the string. For example, a nest bowl is not very effective in encouraging a female ring dove to build a nest and lay eggs unless she has been courted by a male. The situation may be similar for stickleback courtship and reproduction.

The present model follows Baerends (1956) and Bell (1991) in proposing a more differentiated view of appetitive behavior, one that contains at least three motivational substates (modes) instead of the typical single distinction between appetitive and consummatory responding. In fact, appetitive and consummatory behavior need not designate distinct forms of behavior that inevitably differ in degree of stereotypy. Appetitive and consummatory behavior are perhaps better seen as reflecting different search modes. Some behaviors related to a general search mode can be highly stereotyped, such as the systematic search of an area
by an aerial predator. On the other hand, some behaviors related to the handling-consuming mode may be surprisingly flexible. For example, Zweers (1982) documented how pigeons vary their swallowing actions and tongue and bill movements as a function of the size of the seed that is being ingested.

To clarify the complexities of control possible in a behavior system, Figure 3 shows a general template of potential stimulus inputs at each level of the system. An action pattern can both increase excitation (positive feedback) and decrease excitation (negative feedback) at each level. In addition to feedback from responding, each level may receive excitatory and inhibitory inputs (not separately drawn) from other levels, from internal sources specific to that level, from within the same level, and from the environment. Given the relations shown in Figures 2 and 3, a system can handle many types of effects, including general and specific motivation, and top-down and bottom-up control. The high degree of flexibility requires the specifics for a particular system to be "filled in" by observation and experimentation.

An element of control only suggested in Figure 3 is the possibility that a particular unit can be controlled by different "boss units" (Dawkins, 1976). This is the lattice hierarchy of Baerends (see also Gallistel, 1980). Figure 2 showed several action patterns that were controlled by different modules, and several modules that were controlled by more than one module. It is also possible that different boss units can be found in different systems. For example, the same locomotor behavior could be controlled by a superordinate unit related to provisioning or courting, or the same general search mode could be engaged in searching for food or for females.

In short the behavior systems approach resembles the system models outlined by Tinbergen (1951) and Baerends (1956), but with several changes. The present approach specifically allows for separation between motivation and the sequence of behavior and clarifies the multiple roles of stimuli in determining behavioral output. It also differentiates appetitive behavior into several search modes, and questions the basis for the sharp distinction between appetitive and consummatory responses.

Relation to Laboratory Learning

The behavior systems approach assumes that the basis of learning evolved and is expressed within the context of a functioning system, such as the present feeding system. A particular behavior system provides the raw materials for learning. It is a substrate the elements of which can be integrated, linked, and differentiated within and across levels by its fit with the environment. Thus, learning can be remarkably varied and complex. It also can be simple as when a particular stimulus readily fits filters that are closely coupled to highly integrated and differentiated response programs. This view that learning takes place within and involves the structure and processes of a functioning system not only clarifies why examples of ecological learning such as acquisition of bird song frequently do not mesh well with the paradigms of laboratory learning, it also provides the basis for an ecological analysis of laboratory learning. For example, a behavior systems approach readily provides the organization to account for phenomena such as constraints on learning and misbehavior (Timberlake, 1993; Timberlake & Lucas, 1989).

An important contributor to integrating a behavior systems approach and the laboratory study of learning is the recognition that the fundamental paradigms of learning, Pavlovian and operant conditioning, may be viewed as experimental procedures instead of processes, mechanisms, or models of learning. As procedures their effects must reflect their interaction with the underlying structure of the behavior system involved (see Suboski, 1990). It follows that conditioning procedures can be used as tools to explore and clarify the nature of a behavior system. At the same time, knowledge of a relevant behavior system can assist in understanding and predicting the nature of learning.

The procedure of Pavlovian conditioning has two major advantages in analyzing a behavior system and predicting responding. First, it does not specify the nature of the conditional response (CR). This allows us to use the form of the
response to reveal what modules are involved in the behavior that is produced. The second advantage is that characteristics of the conditional stimulus (CS) can be manipulated to engage different aspects of the system. Among these characteristics are its quality (perceptual characteristics), and its temporal and physical proximity to the unconditional stimulus (US). The quality of a CS refers to how readily a stimulus is passed by filters of specific perceptual-motor modules and thus makes contact with particular response components. For example, a small moving stimulus readily engages chase and capture modules in a predatory animal like the rat, provided the animal is not in a handling-consuming mode.

Before we illustrate how one integrates the study of learning with the study of a behavior system, we should address the concerns of those who believe that analysis of functional behavior is not possible in the laboratory. Some zoologists feel uncomfortable about the relevance of artificial environments to an evolution-based behavior system, particularly when that research is based on the laboratory rat in a laboratory box. Put succinctly, the criticism is that laboratory rats are not real animals and laboratory boxes are not real environments.

There are, though, problems with this stance. First, it appears based on the questionable premise that the changes produced by natural selection outside the laboratory are fundamentally different than those produced by artificial selection within it. More important, comparative psychologists have accumulated considerable data over the past 25 years demonstrating that laboratory rats show complex and natural behaviors given appropriate stimulus conditions (e.g., Blanchard & Blanchard, 1990; Boice, 1972; Galef, 1990). It appears that laboratory domestication, like other changes in selection environments, predominate alters response and stimulus thresholds, rather than eliminating old behavioral potentials or introducing entirely new ones. Laboratory rats are less aggressive, less timid, mature earlier and are more fecund than wild rats, but they still behave like rats if tested appropriately.

Finally, the argument that functional behavior systems cannot be studied in the laboratory seems to go against all we have learned from Tinbergen and others in their analyses of evolved mechanisms using artificial stimuli and environments. That animals have not been selected to deal with artificial environments argues that they have little choice but to filter the laboratory environment through the best-fitting sensory, motor, and motivational structures provided by evolution and experience. In most laboratory experiments these underlying structures and processes have to do with feeding.

Closer examination of actual laboratory research indicates that most laboratory circumstances are not as arbitrary or artificial as they appear. Clever experimenters have spent considerable time tuning them to particular species and problems. Tuning here refers to the iterative process of modifying the environment, the stimuli, and the procedures to produce more robust, orderly, and efficient responding. For a brief account of how Skinner developed the response of lever pressing, the reader is referred to Timberlake and Silva (1994). It does not seem an accident that the three basic instrumental responses used in animal learning, lever manipulation and maze running in rats, and key pecking in pigeons, all appear to be organized aspects of a feeding system that can be elicited nearly full blown either by simple exposure to the apparatus (Timberlake, 1983a), or by simple pairings of appropriate stimuli with food (Timberlake & Lucas, 1989). Thus, in the course of their development, laboratory apparatus has been accommodated more to the “nature” of the animal than critics of learning literature have supposed (Timberlake & Silva, 1994).

MODULATIONS, MODES, AND PAVLOVIAN CONDITIONING IN A BEHAVIOR SYSTEM

In this section we examine several instances of learning that illustrate the integration of learning procedures and ethological approaches. We combine the existing knowledge about feeding systems with the use of conditioning procedures to analyze modules and modes and predict the form and ease of learning. The result is a bootstrap procedure in which multiple sources of knowledge are used to develop a clearer picture of appetitive behavior. In the first section we examine the role of perceptual-motor modules in learning; in the second section we examine the contribution of modes to simple conditioning and chaining.

A Role for Modules in Laboratory Learning

Here we review two examples of using forms of Pavlovian conditioning to explore and analyze perceptual-motor modules in the feeding system of several species. The first example uses a social stimulus as a predictor of food in rats and hamsters. Here we focus on the perceptual quality of the CS, that is, on its ability to fit the filters for a particular module. The second example involves “superstitious” behavior in pigeons and focuses on the importance of environmental stimuli in supporting modules evoked by temporal conditioning (the presentation of reward predicted by the passage of a fixed time).

A Social Module in the Feeding System

There are many reasons to expect that social behaviors should be easily conditioned to social cues that predict food for rats. Rats follow each other to food, use odor cues from other rats to forage for specific foods, and as juveniles learn to eat what adult rats are eating while avoiding what adults are not eating.
(e.g., Galef, 1990). They also steal food from each other, and wrestle for its control. Thus, the feeding system of the rat probably contains a social module, one that is related to a motivational mode of searching for food. We should be able to engage it by presenting a rat as a CS predicting the imminent delivery of food. Indeed, approach, sniffing, and crawling over responses directed to a stimulus rat increase markedly when it predicts food (Timberlake & Grant, 1975). The presentation of a stimulus rat alone, or the random intermixing of food and a social stimulus are not effective in increasing attention to the stimulus rat over trials. A rat-sized block of wood predicting food was effective in increasing orientation at a distance, but not approach or any form of social behavior.

These results support the existence of a social feeding module in the rat, a perceptual-motor organization that is sensitive to rat-like cues and produces specific forms of interaction with the rat. The control of this module can be engaged by pairing a particular rat with the subsequent arrival of food. These results are not readily predicted by traditional learning concepts like stimulus substitution, nor do they support simple approach/withdrawal models such as sign-tracking (Hearst & Jenkins, 1974). Stimulus substitution arguments would predict some form of consumption related behavior directed to the stimulus rat or the food tray. A simple sign-tracking model would predict approach to the rat-sized block of wood. The hypothesis that the rat’s evolution-based feeding system contains a social module makes possible some interesting and potentially counter-intuitive predictions. For instance, such a model should be more readily activated by an adult than by a weanling rat because weanlings in the wild have no knowledge of where the food is located. On the other hand a weanling rat should show no such compunctions about using either a weanling or an adult as a predictor of food. These predictions were supported by the results of an experiment: on four groups of rats formed by crossing two types of predictor, weanling and adult rats, with two types of subject, weanling and adult rats (Timberlake, 1983). Social behavior to the stimulus rat increased in acquisition in all groups except for the one in which food for an adult was predicted by the appearance of a weanling rat (see Figure 4).

An interesting counterpoint to the case for rats involves hamsters. All field data we possess suggest that hamsters are not social feeders; after weaning they neither reliably feed with another hamster nor follow other hamsters to food. Thus, there should be no social module related to approach in the hamster feeding system. If anything a social stimulus should trigger competition and avoidance. However, on the basis of its proximal relation to food it should trigger an investigatory or test module producing manipulation and digging in the food tray. As predicted, pairing a hamster with food failed to generate approach and social behavior but did produce attention to the food tray (Timberlake, 1983b).

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**Appetitive Behavior**

![CONTACT](image)

**Figure 4.** The mean percent trials with a social contact for Pup-Adult, Pup-Pup, Adult-Adult, and Adult-Pup groups.

**Superstitious Behavior**

An important contributor to the belief that reinforcement operates to strengthen arbitrary responses was the phenomenon of “superstitious” behavior. In 1948 Skinner reported that if food were presented to a hungry pigeon once each 15 sec, the pigeon would soon come to display idiosyncratic responses. Skinner surmised that these responses had been shaped by the accidental juxtaposition of the food delivery and the behavior of the pigeon. If on a particular trial the pigeon happened to stretch its neck just before food was delivered, then the frequency of neck-stretching would go up thereby increasing the probability that the pigeon would stretch its neck prior to the next food delivery, and so on. Based on this excitatory cycle, neck-stretching soon would emerge as the pigeon’s idiosyncratic “superstitious” response to the conditioning situation.

Such an account makes perfect sense if one believes that behavior is a largely disorganized mass that is differentiated by the strengthening of particular responses that are followed by food. However, if one assumes that pigeons have
a feeding system organized something like that of the rat (shown in Figure 2), then there should be modules available that will generate a set of responses relevant to obtaining food. Admittedly there is no CS to help engage particular modules, but one would assume that particular stimulus circumstances present in the apparatus could combine with the timing aspects of food delivery to engage a restricted number of modules and their associated response components. The key to research in such a situation when the modules are unknown is to combine empirical exploration of the importance of particular environmental stimuli with testable hypotheses based on the presumed ecological function of the resultant behavior.

Armed with an inking of this argument and a bag of popcorn, one of us spent several noon hours on a park bench throwing kernels to pigeons at fixed 45-sec intervals. The 45 sec interval was chosen because with a shorter interval, it was too difficult to reward single birds, since many birds in the vicinity moved toward where the popcorn landed. Forty-five seconds was enough time for the pigeons to spread out again so that kernels could be thrown for one particular pigeon, and hopefully was enough time to allow the excitatory feedback loop to work. However, instead of engaging in a variety of unique superstitious behaviors, each pigeon engaged in perfectly respectable species-typical ground foraging behavior—bent over, eying the ground on either side as it walked in widening circles. This was interrupted sometimes by feather fluffing, “shivering” movements as the pigeon appeared to vacillate between staying in the same location, and moving on.

There were many reasons that we might not have gotten Skinner’s results in a park, so we attempted to replicate his results in the laboratory by presenting food from a hopper located in an end wall of a 30 x 30 inch chamber using an interfood interval of 15 sec. Contrary to Skinner’s reported results, the behavior produced by the periodic delivery of food was consistent across birds rather than predominantly idiosyncratic. The pigeons almost exclusively showed wall-directed behavior, including bumping, pressing, head bobbing, and stepping, often with wings half-drawn. Not only did our data contradict the hypothesis of idiosyncratic behavior, they also appeared to contradict the results reported by Staddon and Simmelhag (1971) that pigeons on short fixed-time food schedules predominately pecked the hopper wall.

By modifying the stimulus conditions of the apparatus in a series of over 20 experiments, we (Gary Lucas and Timberlake) were able to establish that the key to producing wall-directed behavior was the periodic delivery of food from within or near a wall. Even when food was delivered from a free-standing wall located in a nearby backyard, pigeons developed and continued to show extensive wall-directed behavior. These results argued strongly that behavior produced by periodic food delivery was part of a module in that it was relatively stereotyped, strongly influenced by particular environmental cues, and sensitive to the timing of the delivery of food (Innis, Simmelhag-Grant, & Staddon, 1983). However, we did not know the function of the module in an ecological sense.

A major hint of the function of wall-directed behavior came when we observed similar behavior forms in young squabs between the ages of 10 and 20 days begging from their parents (Mondloch & Timberlake, 1991) and in mature females begging from males in courtship. These observations, while not proving that wall-directed behavior in adult pigeons was related to a module controlling food-begging behavior, led directly to subsequent experiments that provided further evidence supporting this view.

In a series of unpublished experiments female pigeons engaged in more wall-directed nonpecking behavior than males, an effect expected if this behavior is related to a food-begging function because females show more begging as adults than males. Ring doves, a member of the same genus as pigeons, showed similar wall-directed behavior; but chickens, a different genus, showed only scratching and pecking. This was predicted from a consideration of differences in the feeding systems of the two species. Parent-young feeding in ring doves is similar to that of pigeons, but hatching chicks are precocial, almost immediately feeding on their own by pecking and scratching at food on the ground. A food-begging module is not part of their feeding system.

Chains and Modes in Laboratory Learning

An important question is what the behavior system approach has to say about the stereotypy, flexibility, and control of behavior chains. That response sequences are controlled by a combination of modules and search modes suggests that chains may show a great deal of flexibility. They should show clumps of perceptual-motor organization that will depend upon variables affecting the search mode, such as spatial and temporal proximity to food. We consider here the organization of chains of behavior leading to food and their relation to underlying search modes.

A Predatory Chain

Many predators, like cats, are very sensitive to moving stimuli as triggers of modules related to predation. Hunger plus a variety of stimuli produce systematic search followed eventually by chasing of moving prey, capture, killing, and eating. Based on previous field and laboratory work we anticipated that rats also should be predators. Figure 5 shows our conception of how a predatory chain can occur within the rat feeding system shown in Figure 2. Hunger and environmental stimuli engage the travel module producing systematic locomotor search behavior. Discovery of a distal moving stimulus (of
appropriate size) triggers behavior from the chase module. Proximate prey cues trigger behavior related to the capture module. Successful capture produces testing (killing), which produces taste and odor cues followed by ingestion.

Figure 6 shows how we tapped into this chain by using an artificial CS (a rolling ball bearing) paired with a food-US in a Pavlovian paradigm (Timberlake, Wahl, & King, 1982). The dark vertical line on the right side of the figure shows the environmental relation we imposed between the rolling ball bearing and a casein and grain-based food pellet. Most of the studies had an additional experimenter-imposed requirement that the bearing exit the chamber before food came, so the maximum but not the minimum interval between CS and US varied with the behavior of the animal to the bearing. Using this procedure Timberlake...
et al. (1982) appeared to engage a substantial portion of the appetitive chain related to predation. When the bearing was paired with food, rats reliably chased the bearing down, sometimes digging it out of the entry hole, seized it in their mouths, ran to a corner, and repeatedly gnawed the bearing while turning it in their paws. Eventually they would let the bearing go, perhaps retrieve it a time or two, and then bury their heads in the food tray.

These data are interesting on two grounds. First, pairing a small moving stimulus with food was sufficient to increase markedly the occurrence of a chain of predatory responses. That predatory behavior occurred despite the minimal resemblance of any known animal prey to a shiny bearing rolling down a track suggests that stimulus filtering for a chase module focuses primarily on size and simple movement as key stimuli. That pairing was important suggests the development of a connection between a search or chase module and a consummatory module. This connection could have been produced by creating a new module, one that incorporated the entire string of behaviors leading to food in a single chain of habits. On the other hand, the connection could have been supplied by the conditioning of motivational modes to the timing of the presentation of the ball bearing relative to food and/or to the sequence of stimuli typically encountered in the chain. The modes could then have controlled excitation of individual modules. We will return to this possibility in the next subsection.

The second interesting aspect of these data is that the response-chain was quite flexible in at least two respects: the initial systematic search phase was severely truncated, and the last few lengths were rather different than what would have happened had the bearing been an insect. Recall that the end of the chain involved the rat leaving the bearing and engaging a test module triggered by the stimulus of the food tray rather than its being able to dismember an insect or open a seed to obtain food. Further, the prey item obtained at the end of this sequence was a casein and grain-based pellet, not the animal protein that would be anticipated to terminate a naturally occurring predatory chain. In short, the response chain reflected flexibility in terms of the kinds of stimuli that controlled particular modules, the orientation and type of response produced, and the nature of the terminal stimulus. Yet these changes did not seem to pose any problem for acquiring a sequence of responding in the absence of any response requirement. The chain appeared to generate itself based only on a relation imposed between the presentation of the bearing and the delivery of food.

Timberlake and Washburne (1989) followed up these data by examining the effects on seven different rodent species of actually requiring contact with the moving bearing in order to receive food. Two aspects of these data are relevant here. The first is the use of an instrumental requirement of contact for gaining access to the food. In Figure 6 this would be represented by drawing a line connecting the response output of the capture module to the presentation of the food stimulus. From a behavior systems view, the addition of a this response requirement does not change the modules involved. Thus, the form the contact takes should reflect species-typical modules related to capture, chase, and/or the investigation and testing of food. The contact contingency, though, does add the possibility that food delivery will shorten the length of the contact by presenting the food stimulus immediately after contact instead of a fixed time after the bearing was presented or exited. Thus, we would expect to see animals moving to the food tray following contact rather than testing the bearing as they began to associate the noise of the feeder operation with food in the food tray. Previous work with rats supported this type of prediction (Timberlake et al., 1982).

The second relevant aspect of these data is that both the form of the contact and the ease with which contact was conditioned should have been related to the

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<th>Table 1. Comparison of Characteristic Sequences and Topographies of Responses to the Cricket and to the Ball Bearing for Seven Rodent Species</th>
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<tr>
<td><strong>Onychomys leucogaster</strong></td>
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<td><strong>Similarities:</strong></td>
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<td><strong>Differences:</strong></td>
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<td><strong>Peromyscus californicus</strong></td>
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<td><strong>Similarities:</strong></td>
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<td><strong>P. maniculatus and P. leucopus</strong></td>
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<td><strong>Similarities:</strong></td>
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<td><strong>Meriones unguiculatus</strong></td>
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<td><strong>Similarities:</strong></td>
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<td><strong>Acomys caurina</strong></td>
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<td><strong>Similarities:</strong></td>
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<td><strong>Sigmodon hispidus</strong></td>
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<td><strong>Similarities:</strong></td>
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feeding system of the rodents involved. As to the form of contact behavior, Table 1 shows that components of responding which a particular species showed to live crickets were also shown to the ball bearing, even though the animals receiving the ball bearings had never seen a live prey item of any kind. In terms of readily contacting and mouthing the bearing, we expected the best results for those species whose stomach contents and effectiveness in killing prey in laboratory tests suggested the existence of modules related to predation on moving insects. For those species who were shown to be less consistent predators, we expected significantly less contact and conditional mouthing of the bearing. These predictions were borne out.

**Conditioning of Modes**

As defined above, modes are motivational substates related to the imminence of food. The presentation of food is assumed to entrain a sequence of excitatory search states, beginning farthest from food with a general search state, continuing to a focal search state, then a handling/consuming state, followed by a return to the previous search states as food becomes more distant. Each of these states is differentially linked with particular modules. Thus, searching the environment for prey and distant chasing are related to general search. Terminal chase, digging, and manipulation are related to focal search. Seed shelling, testing, and the killing bite are related to handling/consuming. For the reader familiar with the theorizing of Konorski (1967), the present view adds more types of mode, and relates them explicitly to a variety of modules.

The relation of modes to learning occurs because the level of motivation of a particular mode influences the motivation level for those modules it is related to. The motivation of a particular mode is affected by (a) the perceptual quality of the CS presented (through its effect on particular modules which affect the excitation level in their associated modes), and (b) the temporal and physical distance between the CS and the US. For example, a long interval between a CS and a US should condition a general search state to any predictive stimuli (including the passage of time) and differentially support modules such as travel, investigate, and chase. In contrast, a short interval between the CS and the US would be more likely to condition a focal search or handling/consuming mode and thus support the expression of modules such as test and ingest.

It follows from these arguments that we could take the same stimulus and present it at different CS-US intervals and potentially condition different modules. Figure 6 illustrates what should happen if we presented a ball bearing at an 7.6-sec interstimulus interval, and Figure 7 illustrates what would happen with a 2.6-sec interstimulus interval. The 7.6-sec interval should condition an underlying search mode that supports tracking, chasing, and subsequent interaction with the bearing. The 2.6-sec interval should condition some combination of focal search and handling/consuming and would thus have a greater tendency to support chewing and gnawing and handling in the vicinity of food. The results in Experiment 2 of Timberlake et al. (1982) support these predictions by showing a much lower level of interaction with bearings that predict food with a short CS-US interval than those that predict food with a long CS-US interval. In the
case of the short CS-US interval, most rats used the bearing as a signal to go to the food tray.

The potential importance of modes in conditioning is also shown by recent data of Matthews and Lerer (1987) using a probe technique. These investigators presented a hopper of grain to hungry pigeons every 30 sec. During each interval they gradually increased the brightness of a keylight. Thus, during the first 10 sec of the interval the keylight was relatively dim, during the second 10 sec the keylight averaged a medium intensity, and during the last 10 sec, the keylight was very bright. Under this procedure the pigeons developed a reasonably consistent set of behaviors. They began by circling away from the hopper during the first 10-sec interval, followed by predominantly wall-directed behavior during the second 10 sec, and predominately pecking of the key during the last 10 sec. In a pigeons feeding system (see Timberlake & Lucas, 1985) this string of behaviors can be seen as a mixed chain, consisting first of a circling ground search related to a general search mode, then food begging related to a focal search mode, and finally beak manipulation behavior related to both focal search and food handling modes. A simple chaining explanation of the sequence, based on accidental reinforcement, would have difficulty accounting for the reliability of the behavior across the different pigeons.

After training the pigeons, Matthews and Lerer (1987) ran a series of probe sessions, the most interesting of which was to reverse the direction of keylight illumination so it went from bright to dim. In response, the pigeons simply reversed their sequence of responding. They began with keypecking of the bright keylight, showed wall-directed behavior during the medium keylight, and circled to the back of the cage just before the food was delivered. Other manipulations of the keylight showed similar control. These results are difficult for a chaining account of behavior to explain because the sequence of stimuli and responses in the chain was easily severed simply by reordering the amount of illumination present. However, these data readily support the notion that different motivational modes can be conditioned to different segments of a graded environmental stimulus as a function of time between the stimulus and the US. These motivational modes apparently gained more control of responding than did the preceding or following stimuli in the chain.

We recently adapted a probe technique of a different sort to test for the existence of different modes conditioned by the same quality of stimulus but presented at different CS-US intervals. Rats were first conditioned either to a long-duration tone CS of 16 sec or a short-duration tone CS of 4 sec predicting food. After extinction of the context and assessment of the baseline of responding to a rolling ball-bearing, test sessions were run in which ball-bearings were presented as probe stimuli 2 sec after onset of the CS. This test was based on the assumption that the ball-bearing was likely to activate the chase and capture modules controlled in part by the general search mode. If the long tone condi-

tioned more of a general search mode than the short tone, it should better help energize the modules controlling chase and thus produce more chase and capture of the bearing than the short tone. The results showed that bearing contact increased over baseline for the long-tone group, but not the short-tone group (Silva & Timberlake, 1993). These results suggest that long CSs do not produce worse conditioning, they simply condition different modes, and thus support different behaviors (see also Miller & Barnet, 1993).

The Generality of Modules and Modes and Systems

An important concern with any conception of behavior is its generality. Many theoretical distinctions depend on specific examples with only a little evidence for their assumed generality. The behavior systems approach certainly gains much of its predictive power from specific information about a particular species, but the general framework should at least provide a starting point for dealing with different species and different systems of behavior. As noted above Timberlake and Washburne (1989) showed the potential generality of a behavior systems approach to feeding in a variety of rodent species. As briefly noted below, other investigators have shown the behavior systems approach to courtship behavior in quail and predator avoidance in rats.

Domjan (1994) has developed a Pavlovian conditioning procedure with male quail in which he uses a CS to predict access to a receptive female in a reproductive state. He and his associates have used this procedure extensively to examine learning in the reproductive system of the quail. Most recently, Akins, Domjan, and Gutierrez (1994) reported data strongly supporting the hypothesis we advanced above, that long duration CSs do not produce worse conditioning; they simply condition general search modes that support responses, such as restless activity, that are not usually measured. Using a 30 sec CS these researchers strongly conditioned approach and looking at a CS presented in the vicinity where the US was presented. Using a very long CS of 1200 sec they found no increase in approach to the vicinity of the CS, suggesting an absence of conditioning. However, when they measured amount of pacing and visiting of an adjacent chamber, they found a large increase as a function of presentations of the 1200 sec CS, just what would be expected if a general search mode were conditioned by the stimulus contingency. The results show that the behavior conditioned in a sexual behavior system also depends on the length of the CS-US interval.

Fanselow and his associates (Fanselow, 1991; Fanselow & Lester, 1988) have recently begun to analyze characteristics of the predator defense system in rats. Their central concept is a predatory imminence dimension that extends back from predation first to a strike mode, then to a post-encounter defensive
mode, and then to a pre-encounter defensive mode. In a pre-encounter defense mode, a foraging animal reorganizes its foraging behavior because of the threat of predation. In a post-encounter defense mode, the animal is likely to engage in freezing behavior when it detects the presence of a predator. In a circa-strike mode, the animal engages in activity bursts such as biting and jumping when the predator contacts the animal.

The conditioning of these modes and the behaviors associated with them can occur as a function of the CS-US interval, such that short CS-US intervals may elicit jumping and flinching, whereas longer CS-US intervals produce freezing, and still longer intervals may produce avoidance. Fanselow (1994) has gone much further than other researchers in relating the different modes to specific brain areas. He has shown that the lateral portion of the periaqueductal gray is involved in circa-strike behavior, while the ventral portion is involved in the post-encounter defense mode. Lesions in the ventral periaqueductal gray attenuate freezing, but do not affect activity bursts. Conversely, lesions in the dorsolateral periaqueductal gray reduced activity bursts to shock but do not affect freezing.

CONCLUSIONS

We have briefly described ethological and psychological approaches to the study of appetitive behavior in terms of their treatment of the appetitive-consummatory distinction, reaction chains, hierarchical organization, system interactions, and the role of learning. The ethological approach treated appetitive behavior as variable though purposive behavior leading to a stereotyped consummatory response, involving naturally occurring chains of stimuli and responses, hierarchical models of control, extensive system interactions, and a functional approach to the role of learning. The psychologist’s approach emphasized a difference between the types of learning occurring in the case of appetitive and consummatory responding (operant and Pavlovian), arbitrary chains of stimuli and responses, a lack of importance of hierarchical models of control, a modest account of system interaction, and a role for learning that encompassed rather than fitting within naturally occurring appetitive behavior.

We then considered a behavior systems approach to feeding behavior as a means of integrating the strengths of the ethological and psychological views of appetitive behavior. The behavior systems approach attempts to combine the interest in naturally occurring appetitive strings with the experimental possibilities of learning paradigms. In attempting this integration a behavior systems approach brings together an animal-centered approach and a manipulation-centered approach. The basic units of a behavior system are perceptual-motor modules. These may be either largely in place at birth or shortly thereafter (Hogan, 1988), or they may be acquired in large part through repeated practice. The behavior systems approach relates the behavior controlled by the modules to a series of motivational modes related to the imminence of reward. These modes are tied to specific stimulus qualities as well as to the anticipated time and distance to food; they affect responding by energizing a subset of modules appropriate to a particular distance to reward.

Advantages of a Behavior Systems Approach

The organizational and motivational structure of a behavior system has several advantages in dealing with persisting complexities of appetitive behavior. The existence of multiple alternative modules that vary in degree of integration and specificity provides for the diversity of variable and stereotyped appetitive behavior, yet the existence of relations between modes and specific modules limits this diversity and facilitates the generation of behavior chains under appropriate stimulus conditions. The motivational structure provides a framework for both bottom-up and top-down control as well as for both general and specific aspects of motivation. The distinction between appetitive and consummatory behavior is not sharp, and will depend considerable on the characteristics of the modules involved.

Finally, a behavior system provides an inclusive approach that readily combines the phenomena of learning and naturally occurring behavior within the same framework. Thus, it can be used to analyze the contribution of learning to naturally occurring behavior, and the contribution of the underpinnings of naturally occurring behavior to laboratory learning (see also Suboski, 1990). In the latter regard it can clarify the basis for tuning apparatus and procedures to produce vigorous and reliable behavior, an important contributor to the power of laboratory manipulations. Most importantly it provides a way for understanding in a functional and ecological way the effects of imposing Pavlovian and operant contingencies on behavior.

The behavior systems approach also has a number of general advantages for both ethological and psychological researchers. The focus of laboratory learning on manipulations and simple connections has meant that experimenters sometimes have tested theories to the detriment of finding out more about their subjects as functioning systems. Thus, when a particular theory is wrong, the theory and the data collected in testing it are left behind. The animal-centered specificity of the behavior systems approach provides a framework that potentially can be added to and corrected by further experimental results and observations. Rather than only proving or disproving theories about learning, research can contribute to and be affected by systematized knowledge about an organism’s
stimulus processing, motor behavior, motivational states, and their relations. Such concrete data concerning particular individuals and species are likely to be important in developmental, ecological, and neurophysiological analyses of learning (Fanselow, 1994; Hogan, 1994; Timberlake, 1994).

On the ethological side, the behavior systems approach also appears to escape some of the criticisms of adaptationist models because it provides a concrete framework that can be tested and modified in a cumulative way. The first tentative framework may be a type of just-so story, but with the power of learning paradigms to explore the presumed structure and tests of specific hypotheses, subsequent versions will have a much less story-like quality. The behavior systems approach also escapes the trap that behavior must be adaptive because a system evolved based only on relative success in particular circumstances. The extent of its success in a test environment will vary with the similarity of the test environment to the selection environment. Finally, a behavior systems approach avoids the problem of isolating learned and unlearned behavior by viewing learning as occurring within the context of an already functioning system.

Difficulties for a Behavior Systems Approach

Certainly the approach has shortcomings. The use of learning procedures and artificial environments as tools to investigate the structure of a functional system may appear rather foreign, though the use of artificial stimuli and environments has been prevalent in ethology (e.g., Haliman, 1967; Tinbergen, 1951). To an ethologist the behavior systems approach also may appear an unnecessary reiteration of Tinbergen's hierarchical model. We have, though, pointed out several important differences. The present model separates sequences of behavior and the hierarchy of motivation; it distinguishes a sequence of modes underlying appetitive behavior, and it questions the distinction between appetitive and consummatory behavior.

From the other side of the aisle in this tentative marriage, embedding traditional research within a behavior systems framework is not a trivial task. One difficulty is that laboratory learning has focused on arbitrary environmentally-defined responses and the processes and system structure of a US and a species (Timberlake & Lucas, 1989; Timberlake, 1990).

Another block to integration is that researchers in laboratory learning may be leery of the apparent complexity of the behavior systems approach. The sheer number of initial assumptions contrasts unfavorably with the apparent sleek economy of the idea that behavior is based on the reinforcement of simple connections. We believe, though, that the problem is not with the complexity of a behavior system, but with the failure of a traditional reinforcement approach to make clear the full set of requirements and assumptions necessary for its testing and application. Specification of a feeding system in rats simply makes explicit and tries to account for what experimenters ordinarily deal with by tuning their apparatus, procedures, and measures to allow them to ask apparently simple questions about causation (Timberlake 1993; Timberlake & Silva, 1994).

In sum, a behavior systems model is both a theory and a general approach that is capable of describing behavior and predicting the outcomes of experiments. It contains both bottom-up and top-down possibilities for control, provides for both stereotypy and variability in behavior, and for general and specific motivation. These issues must be resolved empirically for specific species and specific systems. Finally, a behavior systems model provides a framework for the analysis of learning, as well as the capability of using learning manipulations as tools for analyzing the structure and function of the system.

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REFERENCES


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