An animal-centered, causal-system approach to the understanding and control of behavior

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Abstract

In a world of increasing demands and diminishing resources, the understanding and control of behavior is likely to be a key to successful relations between human and nonhuman animals. The traditional laboratory study of animal behavior, centered on systematic manipulation of single variables, has provided powerful causal laws connecting manipulations to effects, but these laws have proved surprisingly difficult to transport to field and applied settings. The recent increase in anthropomorphic interpretations of behavior has the advantage of emphasizing the contribution of the animal rather than the experimenter, but by itself anthropomorphism holds little possibility of improved understanding and prediction. I argue for development of a causal-system approach that captures an animal's point-of-view without unnecessary assumptions of a human-like mental life. By realizing this approach within the structural framework and regulatory processes of behavior systems, it should be possible to develop a model of animal behavior that integrates and expands data from laboratory, field, and applied settings, and may contribute to successful relations between human and nonhuman animals. © 1997 Elsevier Science B.V.

1. The practical problem

The understanding and control of behavior has become of critical importance as the 20th century draws to a close. The remarkable rise in human populations and the even more remarkable increase in their demand for land, food, natural resources, and pets has led to enormous changes in the use, numbers, and distribution of nonhuman animals (e.g., Wilson and Peter, 1988; Wilson, 1992). In the last 25 years millions of species of forest insects have vanished, populations of whale species have sunk to new lows, numbers of amphibians have markedly decreased, and many species of song bird have declined by more than 50%. At the same time many other species have increased to well above the usual carrying capacity of the environment. In the USA, for example, horse...
cats, opossums, rabbits, commensal rodents, and even deer, roam at will around new housing and commercial developments, each extracting their own costs from the environment and, inevitably, from other species.

On the positive side, we know a good deal more about animals and their behavior than we did 100 years ago. At the level of both behavior and neurophysiology, laboratory scientists have made great advances in studying the mechanisms of learning, metabolism, reproduction, development, and genetics (Alcock, 1993; Mackintosh, 1994; Hogan and Bolhuis, 1994; Slater and Halliday, 1994; Drickamer et al., 1996). Although the concept of motivation has received a drubbing over the past 30 years, research related to the regulation and structure of behavior still has made advances (Colgan, 1989; Fentress, 1991; Berridge, 1994). Further, as amply demonstrated in this journal and many others, increasing numbers of scientists work in applied settings, bringing to bear rigorous techniques of study on practical problems related to human interaction with domestic animals.

On the less positive side, transporting laboratory knowledge to ‘real world’ situations has been a slow and surprisingly difficult process. Well-intentioned pet owners may purchase a second dog to keep company with their first, only to find that the dogs treat each other badly, competing over scraps and places. Cat-lovers fondly harbor multiple free-ranging individuals and still wonder where the local birds have gone. Farmers may redesign housing facilities and feeding regimes for their chickens in order to increase cleanliness and efficiency, only to find that egg production drops or animals damage themselves or each other through increased pecking (e.g. Lindberg and Nicul, 1994).

Even when presumably well-informed and highly motivated humans have extensive control over an animal’s physical and social environment, there is no guarantee of success in controlling behavior. We have built new and larger zoos to help preserve and study animals and not infrequently have found that we cannot ensure successful mating or prevent the development of bothersome stereotypies (Mason, 1991). Laboratory science has been compelled to spend large sums on new housing facilities for animals with stainless-steel caging and 15 air returns per hour only to discover that many primate species much prefer dirt floors, while rodents prefer their own urine-caked cages, and cats prefer wooden sleeping shelves.

The problem of transportability of laboratory knowledge has been compounded by a decrease in first-hand practical knowledge of animals, and the accompanying rise in anthropomorphic projections of human needs, desires, and feelings onto animals. The cumulative experience of practitioners such as live-in farmers, shepherds, life-long observers, and subsistence hunters has increasingly gone missing (e.g. Nahman and St. Antoine, 1993). The great majority of first-hand experience with animals in Western culture is based on interactions with personal pets, a situation in which animals are treated primarily as children. Although many owners believe they know their pets intimately, their understanding is filtered through cognitions and behavioral interactions closely tied to the relations between human parents and children. One only has to see an owner’s shocked realization of the killing prowess of a pack of pet dogs to realize that anthropomorphic intuitions can be of little use in predicting behavior.

In short, applied field work is potentially hampered by problems of transportability of laboratory results and a tendency toward anthropomorphism. I believe the situation can be helped by the development of an animal-centered approach to behavior that helps summarize current knowledge and provides effective guidance for gaining more. In the first section, I focus on the disadvantages of the traditional causal approach of laboratory research as applied to the study of learning, and point out the relative advantages of a more complete causal systems approach. In the next section, I consider some of the negative qualities of anthropomorphism and suggest an alternative animal-centered approach. In the final section, I discuss the organizational and regulatory qualities of a behavior-systems approach that can serve as an animal-centered framework for summarizing and integrating work from laboratory, field, and applied settings.

2. Simple causal relations versus causal systems

Historically, the critical contribution of laboratory research was to raise the study of behavior from anecdote to science (Warden et al., 1935). This was achieved by working out procedures that reliably produced a behavior of interest, establishing a simple index of that behavior, and systematically exploring the effects of manipulating single independent variables. The results of this simple causal approach were captured in the form of abstract general laws relating the experimenter’s manipulations to the index of behavior. This approach has been applied successfully to topics ranging from feeding to sexual behavior, but it has especially dominated the study of learning. For example, over 60 years ago Skinner (1938, 1956) worked out procedures and apparatus for studying learning in the form of lever pressing in hungry rats. Subsequent experimenters have shown that the rate of lever pressing is lawfully related to the proximity, frequency, and certainty with which lever pressing is followed by reward, given other variables are held constant (Mackintosh, 1974, 1983).

All this is, of course, familiar territory to the reader. But I believe there has been an important side-effect of the simple causal approach to behavior, namely, the often surprising difficulties in applying laboratory laws in more practical and/or field-like settings (e.g. Collier, 1983; Timberlake and Farmer-Dougan, 1991; Timberlake, 1995). It could be argued that application problems arise because practitioners have less control of the subjects and environment than do experimenters. However, major problems in applying simple laws arise even in well-controlled environments like zoos. It might also be argued that practitioners lack adequate knowledge and experience in working with experimental paradigms, but Breland and Breland (1961) had a good deal of experience when their training efforts were confounded by the sudden emergence of misbehavior.

2.1. Causal systems

I believe that difficulties with transporting simple causal laws from the laboratory to applied settings arise in part because these laws are based on incomplete documentation and analysis of the complex causal relations that are present. There is a strong tendency to treat simple causal laws as though they were the entire solution to the puzzle of
behavior rather than an artificially isolated piece. Not only do laboratory laws fail to deal with the complex causal relations typically present in applied settings, they also fail to consider directly many of the important relations present in the laboratory (see discussion of tuning in the next section). In terms of an analogy, the simple causal model treats the presentation of a response-contingent reinforcer as similar to the straightforward physics of applying a simple force to a body at rest. In practice, presenting a reinforcer seems more akin to adding a powerful reagent to a set of ongoing chemical reactions involved in a complex and potentially fragile equilibrium.

A simple causal model of reinforcement focuses only on the relation between the experimenter’s manipulation and the result, failing to consider directly the contribution of the structure and processes of the causal system involving the animal and the environment. When the apparatus and procedures fail to organize the results of the experimenter’s manipulations in a simple causal way, we speak of constraints on learning (e.g. Sevosten, 1973), or behavior (Breland and Breland, 1961), or superstition (Skinner, 1948). But closer examination suggests these phenomena are simply particularly clear examples of the contribution of species and individual structure and processes to the results of the experimenter’s manipulations. At base, learning is not organized by experimental paradigms but by organismic function and mechanism.

The importance and complexity of the contribution of species-typical causal organization to learning can be revealed particularly clearly in the effects of presenting food at regular intervals. When the foodinter interval is short, pigeons and rats show stereotyped ‘superstitious’ responses focused around the feeder (Staddon and Simmelhag, 1971; Timberlake and Lucas, 1985). As the interfood interval is increased, complex postfood responses appear, followed by behavior related to more general search of the environment (Staddon, 1977; Timberlake and Lucas, 1991). When the interfood interval reaches 24 h or longer, a different timing system appears to be engaged (Mishelberger, 1994).

Rats show one-trial anticipation that food will be presented 24 h after an active circadian feeding (White et al., 1995).

At a regulatory level, the experimenter’s schedule for presenting the reinforcer contingent on a response, in addition to potentiating a variety of response classes, imposes a set of complex relations between the preferred rates of instrumental and contingent responding. For example, Timberlake and Allison (1974), following the lead of Premack (1965), showed that the reinforcement effect produced by making access to water for a thirsty rat contingent on wheel running could be eliminated or reversed (turned into a punishment effect) simply by altering the terms of the schedule. The key determinant was not overall deprivation or the use of known reinforcers, but the presence of a conflict between the terms of the contingency schedule and the preferred baseline levels of responding in the same situation (Timberlake and Allison, 1974; Timberlake, 1995).

Researchers have defended their concentration on the simple causal approach on the grounds that they are trying to characterize ‘pure’ learning, not the embodiment of learning in behavior. But practical requirements in applied settings permit no such distinction, and, even in highly controlled laboratory conditions, learning and performance can be difficult to separate (Shettleworth, 1994). At the least, learning does not appear restricted to simple associations or individual strengthened responses.

2.2. Tuning

A critical contributor to the apparent usefulness of the simple causal model, and a telling argument against its sufficiency, is the pervasive but rarely mentioned use of the technique of tuning (Timberlake, 1990, 1995). Tuning refers to the selection of variables, the development of procedures and apparatus, and the identification of measures that facilitate straightforward testing of simple functional laws. Arguably, every effective experimental procedure and laboratory apparatus has been carefully tuned by previous experimenters to facilitate manipulations of independent variables and to simplify and clarify their effects.

An unusually well-documented example of the contribution of tuning was provided by Skinner (1938, 1959) in discussing development of the lever press as an operant response. Skinner’s conceptual focus in his account was on the shaping of lever pressing by the presentation of reward contingent on successively closer approximations to the desired response. Thus, he reported that the rat was rewarded first for orienting toward the lever, then for approaching, then contacting, and then pressing it. However, underlying and supporting Skinner’s conceptual focus is his account of carefully tuning the position, size, shape, and extent of the lever to facilitate the emergence of lever pressing.

The importance of Skinner’s extensive work in tuning his apparatus can be attested to by anyone who has attempted to build a lever from ‘scratch’. It is disconcertingly easy to build levers that rats will more likely gnaw than press, nose up rather than press down, or tug so hard they will prevent retraction (see also Boakes, 1979). As to the procedures for shaping lever pressing, most experimenters combine Skinner’s basic approach with further ‘tuning’ of their own. For example, some trainers are careful to deliver reinforcement while a rat is looking up over the bar (as opposed to under it) as this promotes faster acquisition by encouraging rearing and promoting accidentally coming down on the bar.

It is not my intention to criticize tuning as a process. Tuning uses empirically derived information about the animal to help make contact with any general laws being tested. What is problematic from an applied point of view is the failure to incorporate information contained in tuning into the laws established in the laboratory. As a result, the transportability of the laws from one laboratory situation to another, or from the laboratory to the field, depends as much on an appreciation of the tuning process as on understanding the laws. To better comprehend the mechanisms underlying laboratory laws and to improve their transportability, it is necessary to clarify the causal system that tuning helps coordinate with the experimenter’s manipulations.

With the help of field observations, it is possible to infer a considerable amount about the underlying causal system by deciphering the information present in successful combinations of laboratory apparatus and procedures (Timberlake and Silva, 1994). Perhaps the most rapid headway can be made by observing closely the results of successive bouts of tuning apparatus and procedures. Examining Skinner’s account of successive changes in the lever pressing apparatus and procedures suggests that rats readily feed in enclosed areas, that high illumination can interfere with behavior, and that rats direct investigation and manipulation responses to projecting invaginated
and/or moving stimuli proximate to a known food location. His data also indicate that a hungry rat is more active than a sated rat, and that a very small amount of intermittently discovered food will sustain active manipulative search for relatively long periods of time. Combining these observations in a model should be helpful in predicting behavior both in the laboratory (e.g. Silva et al., 1996; Timberlake and Lucas, 1989) and in applied settings (e.g. Timberlake, 1995).

3. Anthropomorphic versus animal-centered approaches

At this point in history, there seems little question that the complex learning abilities of animals exceed what would be expected from an extreme behaviorist approach (e.g. Mackintosh, 1994). So it is not surprising that recent researchers have added cognitive concepts such as attention and representation to the basic behavioral account. Cognitive concepts provide a layer of complex and flexible relations between the stimulus input and the motor output, a layer that can be tested in the same way that any intervening variables can be tested (Toates, this volume). What is surprising, though, is the number of recent experimenters who appear to advocate a return to the anthropomorphism of the late 19th century (see Kennedy, 1992). In this section, I will examine some reasons for anthropomorphism and consider an alternative approach, theriomorphism, which appears to have many of the advantages of anthropomorphism and fewer disadvantages.

Anthropomorphism—human-centered approach

The study of animal behavior during the 19th century and the beginning of the 20th consisted in large part of using observation-based inferences of the mental and emotional processes of individual animals (see Boakes, 1984). The theory of evolution posited continuity between other animals and humans in terms of their mental and emotional life, as well as their morphology. Darwin (1871) and philosophers such as Romanes (1884) provided evidence for this continuity in terms of anecdotes that could be interpreted as showing the existence of intelligence and moral character in animals.

The rule of inference was simple: the observer was to assume that the animal thought and felt whatever the observer would have in the same situation. This type of inference in which animals are treated as humans dressed in fur or feathers was termed anthropomorphism—treatment of nonhuman animals as possessing the intelligence, emotions, and consciousness of humans. The overly easy attribution of mental life to animals was strongly questioned by Morgan (1896) and rejected vehemently by the behaviorists (e.g. Watson, 1919) as unrelated and even counter to the emerging experimental science.

Despite this resounding historical defeat, interest in anthropomorphic interpretations of animal behavior recently has risen again in parallel with re-emergent interest in human consciousness and concerns of animal welfare (Griffin, 1981; Dawkins, 1990; Bekoff and Jamison, 1991). Why? One reason appears to be the seemingly omnipresent proclivity of human to infer human mental life in entities with which they interact. For example, not only do humans apparently believe their pets have a mental life like their own, they also act as though inanimate objects have a similar mental life as well. Thus, computers may be out to get them, airplanes can be persuaded to keep flying by speaking to them nicely, and cars like to be clean and run better for it.

Beer (1992) hypothesized that the tendency to attribute mental life to other entities is based on an evolved tool-kit for coping with the cognitive and social aspects of human life. Presumably this attributional tool-kit has proved adaptive overall in dealing with other humans, and apparently there has been little direct selection against its use with other animate and inanimate entities. In the absence of a compelling evidence against it, anthropomorphism appears to be a default method of interacting with the world (Kennedy, 1992). Extensive knowledge about other entities can circumscribe what we are willing to attribute to their mental life, but even so, if Beer is right, the tendency to anthropomorphize seems unlikely to disappear (Kennedy, 1992).

Another reason for increased interest in anthropomorphism has to do with the loosening of the behaviorist focus on extreme peripheral mechanisms of motor movement and stimulus reception. As interest in cognitive issues has increased, some researchers have viewed anthropomorphism as a useful way of moving beyond the ‘fixation’ of behaviorism on motor movements and peripheral stimuli to deal with more central determinants of behavior, such as representations and attention. Similarly, the focus in behaviorist ecology on life history strategies and optimal behavior tuned attention away from peripheral mechanisms toward a more abstract functional form of analysis. Anthropomorphism fits with these trends in positing complex cognitive processes and strategies such as deception and intention (e.g. Ristau, 1991).

A third reason for increased interest has to do with the perceived advantages and even necessity of anthropomorphism in analyzing the behavior of social species. Specifically, inferring the goals of an animal is thought to be an important contributor to good observation and research. For example, Dunbar (1984) argued that, “to be able to study…social systems the observer has to second-guess what his animals are up to…not only what it does, but what it is trying to do”. Other scientist-observers have argued more generally that anthropomorphism can be a highly useful technique for predicting the behavior of an animal (e.g. Cheney and Seyfarth, 1990).

In my opinion, what is being espoused in these last instances is scarcely the anthropomorphism of doting pet owners or the instant empathy of first-time observers. Instead, these scientists are arguing for the use of descriptions and predictions based on a fairly precise causal-system model of the animal being observed, a model built up over continued experience with a species or individual. If these observers were simply attributing causal intentions and emotions based on their experience as humans, then any human (at least from the same culture) who observed the same behavior should make similar predictions. However, I am quite confident that if Cheney and Seyfarth and I watched the same set of monkeys, they would be remarkably more refined in their observations and accurate in their predictions.

It might be argued that Cheney and Seyfarth are generally better at the practice of anthropomorphism than I am, but I don’t think that is the issue. I could practice my anthropomorphism daily on computers, cars, leaves, insects, or even humans and have no effect on my ability to predict the behavior of vervet monkeys. The best way to improve my ability to understand and predict the behavior of vervets is to watch them...
while intentionally (or inadvertently) observing correlations between particular stimuli, expressions, and movements and subsequent behaviors. Almost inevitably I will assemble these correlations with other knowledge of the animal into some form of animal-centered causal-system model, a model summarizing current knowledge, generating hypotheses, and integrating the results of new knowledge and tests. I don’t think it is appropriate to call this process anthropomorphism. I suggest calling it theromorphism (Timberlake, 1993a)—that is, considering the world from the standpoint of the animal rather than the standpoint of the human observer, and including multiple determinants rather than only simple laws.

But what of the times that traditional anthropomorphic inference appears to facilitate the understanding and prediction of behavior? Indeed, why not encourage the use of anthropomorphism as a beginning point, as a heuristic generator of hypotheses that can be subsequently tested and refined? Although this seems a good idea in many respects, there are reasons to be cautious. First, if Beer (1992) is correct about the existence of a tool-kit for attribution of emotions and purpose, there is no need to encourage anthropomorphism, it is inevitable. If anything, we need to be clearer about its problems. Second, it should give us pause that anthropomorphism makes little or no distinction between anthropomorphism directed at a familiar species and that directed at less familiar species, which may have markedly different sensory windows on the world (e.g. moths or bees), or entirely different body plans and muscle programs (e.g. echinoderms and marine molluscs). A lack of consideration of the species involved tends to make anthropomorphism a simple causal model of the most extreme sort, a model in which causation is inferred from an imagined relation between an outcome and a single emotion or goal (e.g. my dog chewed on the bed frame because it was angry).

Finally, there is a simple pragmatic reason not to be caught up in a general anthropomorphic approach—it has a very slyly track record as a predictor of behavior even when applied to humans. At a personal level, consider that each of us misattributes the intentions and feelings of other humans on a daily basis. In fact, it is not uncommon to misinterpret or mispredict the relation between our own mental state and our subsequent behavior. We get better at predicting the behavior of humans as we take either a statistical view, or we acquire experience with humans. In essence, we become better at how we acquire information that we can incorporate into a model of human behavior. This model is in many ways similar to a traditional scientific model. Any inferences of thoughts or emotions are delimited and constrained, based on our past experience. These limitations and constraints are a specific function of the species and individuals we are observing. Thus, even though an observer may be using aspects of his or her own mental life as cues to predict behavior, they are no longer modeling the animal as a human, but as the appropriate species and individual.

2. An animal-centered (theromorphic) approach

I believe there is much to be gained and little to be lost by rejecting an anthropomorphic approach in favor of the development of an animal-centered approach. For experimenters working with social vertebrates, especially primates, an anthropomorphic approach undoubtedly seems to be more portable to semi-naturalistic conditions and easier to relate to the animal than a simple causal approach. But I believe all of these advantages are contained within an animal-centered approach without the contradictions and liabilities of anthropomorphism (Timberlake, 1993a).

As argued above, instead of an anthropomorphic attempt to make the animal into a human, scientists should engage in a theromorphic attempt to place themselves in the position of the animal. There is bound to be some confusion here, because the tendency is overwhelming to ask how you as a human would feel as a lioness, skulking through the tall grass of the veldt, keeping track of your compatriots, and looking for a likely meal in a nearby herd of zebras. But this inference of motivation and feelings by itself is not likely to be any more revealing of lion behavior than imagining how a blade of grass feels when trampled by a passing lioness would explain how it sprang back up. Because it is centered on the animal, anthropomorphism may trigger questions of relevance to predicting behavior (Martin and Bateson, 1993). However, at best, the assumption that the lion has the same feelings and desires that we do only suggests variables to examine. At worst, it provides a woefully incomplete, if not rudely false, sense of understanding.

What should work more efficiently is to be unabashedly theromorphic. For example, what can a lioness see at eye height in a field of waving grass stalks? What do we know about the sensitivity of the visual system of cats to movement and its ability to accurately resolve adjacent edges? What sort of edges produce the greatest attention? Which way is the wind blowing and how sensitive is the olfactory system to relevant types of molecules? What are a lion’s reactions to moving stimuli? What is its top speed relative to that of the prey? What is the lion’s experience in this location? What is its body state? What changes in behavior occur as a function of the presence of other members of the pride? In other words, don’t ask what you would see if you were a lion, ask what the lion sees, what sort of motor and strategic alternatives are present, what social context and experience.

How does one develop a reasonable animal-centered model? I think the ethologists were far ahead of most other researchers in this regard. They combined extensive observation of particular species and individuals with the use of experimental techniques to test and further analyze their models. One of the first things they identified was ‘units’ of perceptual motor organization that linked the animal to the world. Beginning with Von Uexkull (1934), they established unique aspects of stimuli that led to particular responses (Land, 1983). Longer strings of behavior could be generated if a particular response in turn placed the animal in position to receive other stimuli related in turn to another type of response, and so on. Another animal-centered contribution of the ethologists was the concept of complex motivational systems that encompassed sets of perceptual–motor units within a hierarchy. Activating a particular motivational state led the animal to particular stimulus conditions and sensitized a set of reactions (Dawkins, 1983).

It is important to point out that, as scientists began to carefully test the general ethological approach to behavior, they found important errors in specific predictions (e.g. Hinde, 1970; Dawkins, 1983; Halliday and Slater, 1983). For example, some perceptual–motor units were less fixed in both repetition and sequential expression than had been assumed (e.g. Morris, 1958; Barlow, 1977). Perhaps most importantly, the
general motivational approach appeared overly simplistic and in some cases mistaken (Hinde, 1970). Although these criticisms could have been viewed as setting the stage for a revision of the ethological approach, they most often have been treated as reasons to abandon it. In the next section I will consider some advantages of attempting to develop further a general organizational framework with ties to ethology.

4. Behavior systems

Despite the initial popularity of motivational explanations of behavior in the first half of this century, interest waned in the 1960s and 1970s because it became clear that motivational concepts were overused and underconceptualized. The positing of a general deficit-driven energization doesn’t account for the varied effects of deprivation on different behaviors (Miller, 1956; Hinde, 1970), or add very much to the careful analysis of the mechanisms involved in regulatory behavior (e.g. Dethier, 1976). The easy positing of drives, such as exploration, sleep, play, specific nutrients, and stimulation seeking, had elements of the classic error of explaining by naming. Further, behavior is not terminated only by its expression, as hypothesized by early ethologists, but also by the receipt of particular stimuli (Hinde, 1970).

Finally, the appeal of motivational concepts was often buttressed by the questionable assumption that behavior is directly determined by goals (Kennedy, 1992), a belief that often seems based more on assumption than on careful overall assessment. As an everyday counterexample, consider that a stated goal of most humans is to be happy. Because many humans are consistently not happy, it would follow that they are either desperately incompetent, unable to recognize happiness, or somehow singled out for individual frustration by poorly documented powers of the universe. The alternative, of course, is that much of human behavior is not determined very directly by its explicit alleged goals.

Despite these problems, I believe there are advantages to viewing the structures and processes underlying behavior within a general motivational framework similar to that of Tinbergen’s hierarchical model (Tinbergen, 1951; see also Baerends, 1988). Motivational concepts call attention to the organization of behavior by focusing on the different repertoires related to particular functions, and on the sequences of varied and stereotyped behavior that precede and follow the reception of critical stimuli. Regulatory concepts also remain a potentially useful way to deal with intermediate term variation in the amount of responding. In general, a motivational framework can facilitate the integration of laboratory, field, and applied work by providing an animal-centered common model for summarizing what we know about the organizational and regulatory underpinnings of behavior.

4.1. Organizational aspects of behavior systems

An important contribution of Tinbergen’s hierarchical model of motivation (Tinbergen, 1951; see Fig. 1) was that it provided a framework for combining relatively peripheral perceptual–motor units (combinations of fixed-action patterns and releasers) with a hierarchical motivational control structure. The result improved on previous models by showing links between different perceptual–motor units and by clarifying the overall sequential and hierarchical organization of stimulus and response events that make up complex behaviors such as reproduction. A second advantage of Tinbergen’s model is its concreteness (it dealt with the specific responses and stimuli involved in the courtship behavior of male sticklebacks). Thus, it is a causal–system model, complexly mapped to the stimulus environment and to natural behavior, as opposed to a simple causal model mapped to a single stimulus and an arbitrary index of behavioral change.

From a traditional laboratory view, the concreteness of Tinbergen’s model can be a nuisance. It requires that the user have access to extensive knowledge about the subject in order to apply the model. But requiring and using knowledge of the animal actually is a major strength of this approach to knowledge. Because of its specificity, Tinbergen’s model serves both as a summary of what is known about sticklebacks and courtship, and as a predictor of complex behavior based on this knowledge. The combination of a general framework for understanding naturally occurring behavior with the requirement of a specific realization makes this framework transportable between laboratory and applied settings.

4.1.1. Considerations

As with any model, Tinbergen’s model has a number of aspects that could be improved. First, the overall sequence of behavior is assumed to parallel the hierarchy of
the ‘flow’ of motivation through the model. Only as an adequate releaser for each successive behavior is received, is the appropriate behavioral center ‘energized’. One of the things this suggests is that there can be no out-of-sequence behavior. Although I am sure that this state of affairs accurately represents some aspects of a system of behavior (e.g. Baerends, 1988), it is not true of others. For example, providing a farrowing (birthing) sow with shelter will prevent her from engaging in the extensive locomotor behavior that typically separates her from her social group, yet she is still able to move to the next behavior of nest building (Jensen and Tontes, 1993; Jensen, personal communication, 1994). Migrating birds do not necessarily migrate if they are placed in the appropriate location. Thus, the confounding of motivational ‘flow’ and the typical sequence of behavior in Tinbergen’s model appears unnecessarily restrictive.

Second, in the most common representation of Tinbergen’s model (Tinbergen, 1951), no relation is specified between the subsystems or organomotor acts appropriate to each level. It is clear from Tinbergen’s own work that sequences of responding readily occur, but they are based only on peripheral chains of stimuli and responses. For example, in stickleback courtship, each response to a stimulus is presumed to place the animal in position to receive the next stimulus, leading to the next response, and so on. Yet inspection of real data (e.g. Morris, 1958) suggests that behavior has a direction whether a specific sequence of responses is followed or not, and interruptibility of a sequence of responses varies as a function of proximity to the end point (Timberlake and Silva, 1995).

Third, the focus of the model is on stereotyped consummatory behavior. Variable appetitive behavior is considered important in the early stages of the action chain, but as the animal gets closer to the end of the chain, responding presumably becomes more stereotyped. In fact, the distinction between appetitive and consummatory responding and the relation of stereotypy to the point in the response chain is not always so clear (Nelson, 1964; Hindè and Stevenson, 1970; Barlow, 1977). Thus, in the initial phases of hunting can perform quite stereotyped search and marking patterns, whereas aspects of administering the killing bite can be quite variable depending upon the stoutness of the prey’s resistance and its physical characteristics.

Fourth, the role of learning is not directly discussed in Tinbergen’s model. It seems likely that Tinbergen would have had no problem with conceptualizing learning as modifying properties of the ‘filters’ representing particular releasers, but there does not seem an adequate possibility for learning arbitrary responses and strings of behavior. How should we represent the activities of Skinner’s trained rat, Pliny, as he climbed a ladder, walked a tight rope, let himself down an elevator and raised a flag before obtaining food? At the least, there should be the possibility of representing learned stereotyped behaviors in the model.

Fifth, it is not entirely clear how Tinbergen’s model should be integrated with laboratory manipulations, perhaps especially learning manipulations. For example, if the experimenter were to present a light predicting the presentation of a female stickleback in a tube, how would this be represented in Tinbergen’s model, and what result would be predicted. Similarly, what should happen if a female were presented periodically at regular intervals?

Sixth, although Tinbergen was well aware of the possibilities of interactions among different motivational systems, this awareness is not adequately conceptualized in his initial model. Tinbergen dealt extensively with displacement activities, seemingly irrelevant behavior that appeared to emerge in conflict and thwarting situations. For example, when a territorial male gull was in the midst of displaying to its neighbors, it might suddenly engage in a bout of ‘grass pulling’, a behavior at least partly involved in nest building. Von Holst and Von St. Paul (1963) summarized extensive interactions between different behaviors and systems based on their brain stimulation work with chickens. Finally, work such as that of McFarland (1977) and Houston and McNamara (1988), attempting to conceptualize the distribution of behavioral resources across alternatives, has no obvious representation in Tinbergen’s system.

4.1.2. A recent behavior-systems approach

These considerations are in no sense either exhaustive or dismissive of the worth of Tinbergen’s model. They are simply issues that can be raised in an attempt to further develop and improve his approach. Fig. 2 represents a recent attempt to apply elements of Tinbergen’s basic approach to the feeding system of rats. In this diagram, the motivational hierarchy is read from left to right, while the behavior sequence is read from top to bottom. Out of the picture on the left, the system level refers to common aspects of behavioral expression related to a particular function, feeding in this case. The subsystem level reflects a slightly lower level of organization that relates to strategies for particular types of food.

The perceptual–motor modules (the boxes on the right) represent the perceptual–motor organization present, while the motivational modes to their left capture the sequential

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**Fig. 2.** The structure of a behavior system includes four levels: system, subsystem, motivational mode, perceptual–motor module. This figure focuses on the motivational modes and perceptual–motor module, the predatory subsystem of the feeding system of the rat. The far right of the figure shows the action part controlled by the different modules.
aspects of behavior in the form of different sets of stimulus sensitivities and motor repertoire as a function of proximity to food. Hungry animals typically begin in a general search mode with attention to cues that control behavior related to locomotor search, general inspection of the environment, and sensitivity to cues that predict more proximal food. In the presence of cues more specifically predicting food, the focal search mode becomes stronger. Finally, in the presence of food, the handling/consuming mode is expressed (Timberlake and Lucas, 1989; Timberlake and Silva, 1995).

In essence, motivational modes capture the overall goal-seeking aspects of behavior by focusing on the conditions of transition between sets of stimulus sensitivities and related response repertoires. Mode transitions occur as a function of receiving stimuli related to the next mode. Thus goal-seeking behavior does not require a particular sequence of stimuli or responses, or even a fixed goal, though certainly all of those aspects of goal-directed behavior can occur with appropriate stimulus support and repetition. Further, modes place no requirements on how stereotyped or variable particular modules may be. There is a tendency for responding to be less variable and stimulus filtering more specific as one goes from general search to handling/consuming. However, there are stereotyped searching behaviors as well as variable consummatory responses. Again this is a product of the specifics of an animal, not the conceptual dictates of the system.

An advantage of picturing the hierarchy from left to right rather than from top to bottom is that the sequence of actual behavior (reading output from top to bottom) is separated from the motivational aspects (reading from left to right). In other words, the model doesn't require that behavior must be performed in a particular order because it is both motivated and released by performance of a previous behavior. Instead, motivation is present in the levels to the right when it is present at a higher level on the left or when particular stimuli impact lower states (see Timberlake and Silva, 1995). The sequence of actual behavior is determined by the interaction of environmental and animal-based stimuli with the perceptual–motor structures at the right. Whether a particular behavior can occur out of sequence or not is a function of the specific system under consideration and the particular stimulus support present. It is not a function of the general framework.

The 'real world' lies to the right in this diagram. Stimuli enter the system as input to specific perceptual–motor modules and, in a more general way, as input to particular modules and systems. In the laboratory, the stimulus typically has a particular relation to a response or a particular timing with respect to presentation of an unconditioned stimulus. Learning occurs at the level of changing stimulus filtering and refining and linking behavior within a perceptual–motor module. It is expected that old modules can be modified and new modules can arise as a function of learning and development. Their stereotypy of expression should be related to their evolutionary and local function, and not necessarily to their proximity to the end of the string of behavior or stimulus reception. Learning also involves the control of modes by external stimuli (Timberlake and Lucas, 1989; Timberlake, 1994).

The structural predispositions and constraints of a behavior system can help explain many of the anomalous effects that occur in laboratory learning. For example, Timberlake and Lucas (1989, 1991) suggested that polydipsic drinking in rats should be a likely outcome when the temporal spacing of small amounts of food creates a conflict between terminating a meal (no further eating for a time) and anticipating a following bite. Finishing a bite in the absence of immediate cues for further food creates part of the stimulus conditions for the end of a meal, thereby increasing the likelihood of postprandial drinking as the interval lengths. At the same time, anticipating the next bite within a few minutes creates the circumstances for continued search activity. The relative strength of these two tendencies may produce both the rising and falling sides of the inverted U function of intake over interfood interval (Falk, 1971). The falling side of the function may also relate to fewer discrete opportunities to drink at long intervals.

Misbehavior (Breland and Breland, 1961) also appears to relate to an interaction of the environmental contingencies and the structure of a behavior system. For example, the Breland’s pig learned to carry and deposit a token in a ‘bank’ for food, its learned behavior began creating a pairing between the token and food, energizing a search module having to do with rooting. In more natural circumstances, rooting behavior in the presence of cues predicting imminent food would be effective in securing food, but in the circumstances imposed by the Breland’s, the behavior was counterproductive. Timberlake et al. (1982) explicitly examined the causal structure underlying similar misbehavior in rats (see also Boakes et al., 1978).

The present behavior systems representation is not in complete for example. It makes no explicit improvement in clarifying how interactions occurred between different systems. However, one can imagine the presence of facilitation and inhibition occurring within both the same and different systems. The resultant complexity can be used to understand and even predict the results of simultaneously activating different systems.

Finally, although perhaps not yet so apparent, the behavior-systems approach maintains Tinbergen’s commitment to facilitating connections to current physiology and neuroscience. As has long been recognized, the potential advantage of a behavior-level analysis is that it provides information about what to look for at a neurophysiological level. A difficulty is that most learning analyses have been so abstract that they have encouraged only the search for a centralized mechanism for all learning (Lashley, 1950; Hawkins and Kandel, 1984). An advantage of the behavior-systems approach is that it is tied to specific stimuli and responses that in many cases show relatively peripheral organization. Recent work has indicated that considerable learning can occur relatively close to the initial sensory synapses (Farley, 1988; Brennan et al., 1990). More specifically for a behavior-systems approach, Fanselow (1994) has shown that different portions of the periaqueductal gray in the midbrain are highly related to the pre-encounter and post-encounter modes of the fear system of rats.

4.2. Regulatory aspects of a behavior system

There seems little question that animals frequently behave as though deficient particular level of responding or intake, thereby lending credence to the usefulness of depletion/repletion model of behavior. For example, there is overwhelming evidence that under relatively constant conditions animals eat and drink a reliable amount, increasing their intake after enforced fasts, and decreasing their intake when food is available (Le Magnen, 1992). Responses such as breathing and tempera
regulation also show apparent defense of reliable levels, and even responses such as wheel running and exploration can show reliable amounts and temporal patterns (Kavanau, 1969).

4.2.1. Considerations

However, despite such evidence, there are at least three classic concerns with a simple depletion/repletion model of motivation. (1) Although some instances of behavior terminate after a certain amount of responding, others terminate after receipt of a particular stimulus; for example, a fasting sow apparently will stop locomotor behavior when she is presented with a shelter (a particular stimulus condition), but she will continue to express the behavior of nest building whether presented with an already completed nest or not (Jensen and Toates, 1993; Jensen, personal communication, 1994). (2) Different behavioral measures do not show identical functional relations with increases in motivation; for example, lever pressing and quinine tolerance for water show functional relations of different shapes over different amounts of deprivation (Miller, 1956). (3) Responding is apparently sensitive to numerous variables in addition to depletion (e.g. economic cost; Collier, 1983), and sometimes it is not sensitive to depletion at all (e.g. the meal size of free-feeding rats is not predictable from how long they have waited to eat. Le Magnen, 1992).

A control theory based on a physiological state often eliminates the problem of being forced to define the set-point in terms of either behavior or stimuli received (McFarland, 1971). For example, the set-point of feeding can be defined as a certain number of calories that can be achieved by any combination of ingestion and preloading of food into the stomach. A control theory with a physiological state as a set-point can also be shaped to handle differences in functional relations for different responses by including stimulus and response differences as part of the output and input mechanisms.

There are problems, though, in incorporating economic (cost) and incentive variables in a physiological set-point approach, and in explaining both unpredictable and predictable variation in behavior or its results. For example, although ingestion of food changes as a function of the size of the stomach load during the first half of the night, no such relation exists during the second half of the night (Strohbe et al., 1986). Also, although the concept of a physiological state set-point can be adapted to deal with activities such as wheel running, migration, singing, and exploration, it is certainly not as straightforward an application.

4.2.2. Alternatives

What follows are three examples of recent motivational approaches that deal with the above complexities with varying degrees of success. The first is an empirically grounded ‘multi-settling point’ approach (behavior regulation) based on the assumption that animals will act to preserve their levels and patterning of responding in a familiar environment if the conditions are held constant (Timberlake and Allison, 1974; Timberlake, 1993b). Although this approach has been implemented largely at the behavioral level, there is no reason why it could not be extended to physiological states. In the case of Collier’s procedure of imposing a cost on access to food (Collier, 1983), the results are predictable from a consideration of the simultaneous regulation of behavior with respect to set-points for total lever pressing, total eating, and, if needed, a set-point for typical meal length. The result is a compromise between the deviations from the different set-points in which the relative value of the deviations affects the final settling point (see Hanson and Timberlake, 1983; Timberlake, 1984).

A second alternative focuses on the optimality of behavior. Hanson and Timberlake (1983) were able to show analytically that an optimality approach can be considered a special case of a multiple set-point regulatory model. At least in a general sense, this appears reasonable. In optimality models, behavior is reduced to a single dimension such as cost/benefit. The optimal solution is that combination of benefit and cost that produces a global minimum. If choices can be reduced to a single cost/benefit dimension, the general optimality approach has the advantage, relative to the multi-set-point approach, that it can be transported readily from one situation to another. There is no need to empirically determine the levels and patterns of responding for each situation.

Further, the use of some optimizing approaches, such as dynamic programming, allows complex predicitions of both the timing and the amount of multiple behaviors. Thus, Houston and McNamara (1988) were able to predict the timing and amount of a dawn chorus in song birds based on their competing with conspecifics for food and with males for reproductive success. The difficulties with the general optimization approach include a tendency to oversimplify situations and lack of knowledge about mechanisms, constraints, and underlying assumptions (Stephens and Krebs, 1986; Dunning, 1990; Stephens, 1990).

The last alternative here is a regulatory threshold model—a combination of conceptual, empirical, and optimization techniques. This approach begins with the basic depletion/repletion assumption—i.e. motivation grows in the absence of expression, and falls with expression—but adds to it three complications. The first is the assumption that there exist separate stochastic thresholds for beginning and ending the state associated with a particular behavior. Thresholds, particularly stochastic thresholds, provide basic regulatory swings characteristic of behavior without requiring that the animal achieve the same point every time. The average should be reliable, and may appear to be a set-point when the system is viewed over a long period of time, despite local variations.

A second complication is the assumption that thresholds are determined by regulatory effects with different time characteristics. Some regulatory effects are in the range of minutes, some are in the range of hours, and some are ultradian and even circadian in their effects. Such variations can be incorporated into thresholds as continuous functions, or (like light and dark portions of the cycle) may be conceived as contributing to a different set of thresholds for the day and the night. There is also every reason to assume that thresholds are not symmetric for the same behavior, or the same for different behaviors. Thus, changing the deprivation level may change the onset of feeding (the number of meals), but not the average meal length, and different behaviors may have remarkable different reactions to deprivation. The third complication is the use of statistical optimizing tools to fit the threshold values from a lengthy sample of data. Fitting stochastic thresholds allows simulation of behavior in real time. Not only can total frequency and duration of meals be computed, but also one can predict their distribution in time.
The threshold model is perhaps the most interesting of the three because it incorporates conceptual and empirical qualities with use of the powerful mathematics of optimality. Hogan (1997) reported a threshold model of feeding in jungle fowl that has many of the characteristics listed above, including a distinction between day and night thresholds. The model appeared to account for both the total amount eaten and its temporal distribution. If it proves possible to include thresholds for multiple behaviors, add a systematic way of representing the linkage that schedules provide between different behaviors, and provide evidence of the extent to which thresholds can be generalized across situations, this could be a profitable approach to pursue. When coupled with a hierarchical organization such as that in Fig. 2, a threshold regulatory model may provide a means of accounting for the differences in functional form of behavioral expression as a function of deprivation, as well as both goal-seeking and goal-directed behavior (McFarland and Bossert, 1993).

5. Conclusions

There is much to be concerned about in the current relations of human and nonhuman animals, yet there are also important opportunities. The information provided by behavioral and neurophysiological studies in the laboratory, the extensive observations and field experiments of ethologists, the continuing efforts to develop coherent approaches to the treatment of domestic animals (Hart, 1985; Appleby and Hughes, 1993), all speak to an unparalleled potential for sharing, integrating, and expanding our knowledge about animals. At the same time the sporadic nature of such integration speaks to its difficulty.

Three issues that contribute to this difficulty are: the dominance of a laboratory model of simple causation, the relatively unfettered use of anthropomorphism, and the absence of a transportable common framework for summarizing and integrating information. On the latter issue, I have argued that a behavior-systems approach, combining organizational and regulatory aspects of behavior, is a reasonable candidate for developing a transportable framework. Such a model has advantages over the simple causal laboratory approach in explicitly referring to the organization and functioning of the animal rather than relating behavior primarily in terms of simple causal relations, specific experimental paradigms, and abstract general laws. It is both general enough and sufficiently specific to combine the results of field observations, applied data, and laboratory manipulations in a common framework that should promote further testing and development of motivational structure and regulatory processes (Timberlake and Lucas, 1989).

A behavior-systems framework also provides a potential context for the simple causal laws that have characterized the laboratory study of learning and behavior. At the same time, it can interpret anomalous findings such as mishavvom and subjective behavior, and help extend our understanding of associative phenomena (e.g. CS-US interval effects—Timberlake, 1994; backward conditioning—Silva et al., 1996). It also helps clarify the role of tuning in laboratory research and the mechanisms and processes that must be considered in fitting a simple causal law to new circumstances (Timberlake, 1995).

Further, a behavior-systems framework supports an animal-centered approach that is not anthropomorphic. Viewing the world from the animal's standpoint is not the same as assuming an animal experiences the world as a human. Artists and children readily imagine how they would feel as a leaf in autumn—a dancer on the wind, slipping and spinning through the currents of fall. Such images delight our hearts, but they help very little in understanding the behavior of the leaf. We will make better progress in understanding leaf behavior as we reference our observations to a model that includes information about the leaf's shape, flexibility, strength, and stability, and the velocity and steadiness of the wind. Even if we could somehow take up temporary residence inside a leaf, we still would have to understand the behavior of the leaf in its own terms, not human ones. Human senses, feelings, and knowledge are likely to interfere with such a task unless directed and organized by a leaf-centered model.

I believe that the best and most interesting research adds an animal-centered quality to a complex causal analysis. An animal-centered causal-system model has advantages over an anthropomorphic approach because it is explicitly organized around the animal rather than around the feelings and intuitions of a particular human. This provides a more systematic and testable approach that has potential for combining the animal's view of things with laboratory manipulations. An animal-centered approach also allows the possibility that mental states are related to behavior without prejudging that human-like mental states are simple causes of behavior.

Finally, understanding and control of the behavior of individual nonhuman animals is only a portion of the causal matrix that determines the relations among human and nonhuman animals. The influence of other animals, in the form of conspecifics, resource competitors, predators, and prey, must be incorporated in any ultimately useful model. Further, because of human technology, numbers, and demands for resources, the behavior of humans is an increasingly important determinant of the relation of human and nonhuman animals. Understanding and controlling human behavior on a large scale is still very much at the level of anecdote, belief, social pressure, physical force, and intuitive manipulation. Any broadly useful causal model must apply to both human and nonhuman behavior, however difficult that my be to accomplish (e.g. Kellert and Wilson, 1993; Timberlake, 1995).

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References


Tourettes - data to be supplied.
