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Constructing Animal Cognition

William Timberlake

Cognition refers to a subset of processes that define and operate on the relations between environment and behavior. The current study of animal cognition varies from emphasis on the specialized to the general. Scientists interested in a particular species often focus on complex cognition particular to that species. Thus, students of temperate zone songbirds are interested in song learning and migration. Other scientists are primarily interested in how closely the cognition of nonhuman animals approaches that of humans, as in the case of language (Savage-Rumbaugh et al. 1998). Still others are interested in cognition that is characteristic of a wide range of species, as in the case of scalar timing and conditioning (Gallistel and Gibbon 2000). This essay considers an approach to animal cognition that is compatible with this range of interests, an approach based on constructing the mechanisms, function, and evolution of cognition in one species at a time.

Constructing cognition in this way requires tools and information from a variety of sources. Three sources have roots in the nineteenth century: ethology, learning psychology, and the physiology of perceptual-motor relations. A fourth contributor is a modern version of the art of creating artificial animals, now based in computers and robots (Taylor, chapter 21 in this volume). The final contributor is the ancient human practice of using experience-based knowledge to view the world as though one were, in fact, a particular animal. I will call this practice "theromorphism" (taking the animal's view) to distinguish it from the more common anthropomorphic practice of presuming that the cognition processes of human and nonhuman animals are fundamentally the same, and from the even more common emautomorphic practice of presuming that the cognition processes of other beings, regardless of species, are identical to one's own. In the following discussion I briefly outline what each source potentially contributes to the study of animal cognition.

Ethology

Ethologists grounded animal cognition in careful observation of the development, control, and vigor of naturally occurring behavior. Influenced by naturalists like von Uexküll, they were also concerned with the animal's view of the world. In an influential paper on the "Umwelt" of an animal, von Uexküll (1934/1957) combined his personal observations with information on the physiology of receptors to create pictures of the sensory world of animals ranging from mollusks to flies and dogs. Ethologists like Tinbergen (1951) created more dynamic scenes by carefully observing naturally occurring sequences of behavior, dividing them into interlocking sets of perceptual-motor units (critical releasing stimuli and species-typical responses). By manipulating characteristics of the releasing stimuli, they explored mechanisms controlling the occurrence and intensity of responses. For example, after carefully illuminating the courtship dance of male and female sticklebacks (a small temperate zone fish), Tinbergen (1951) performed experiments using artificial "models" of males and females to clarify the mechanisms underlying perceptual-motor organization.

Based on both observations and experiments, Tinbergen (1951) summarized the reproductive behavior of male sticklebacks in a hierarchical, motivational model. This model divided the perceptual-motor units into repertoires associated with different motivational states (feeding, migrating, territory defense, courtship, and parental behavior), which were determined by the current stimulus conditions and the previous state. Although he did not extend his modeling efforts beyond this example, other investigators developed motivational systems of fear, aggression, parental behavior, and feeding (see Eibl-Eibesfeldt 1975).

In short, ethology established the importance of careful observation of naturally occurring behavior and showed the value of experimental manipulation of critical stimuli in clarifying the control of perceptual-motor units. Based on observation and experiment, ethologists developed functional models relating stereotyped responses, stimulus filters, and motivational states. Finally, ethologists showed how classical evolutionary comparisons designed to trace phylogenetic descent or environmentally based convergence of morphological characters could also be applied to perceptual-motor units (Lorenz 1950; Tinbergen 1959).

Learning Psychology

Learning psychology defined cognition by using artificial tasks created by experimenters. In reaction to widespread anthropomorphic speculation about the motivations and feelings of animals (e.g., Romanes 1884), early learning researchers aggressively tested and argued for the sufficiency of simple learning explanations for complex tasks. For example, Thorndike (1911) tested the ability of hungry cats to solve latch puzzles to gain access to food. He found that their performance improved trial by trial, based on rewarded repetition, rather than with the suddenness expected from reasoning, observational learning, or general cleverness. He subsequently showed that monkeys solving similar problems also used trial and error. No shrinking violet, Thorndike set an influential precedent by very early summarizing his data in the form of general laws of the effects of reward and punishment in generating efficient new behavior, laws that were presumed to apply to all organisms.

In addition to an abiding interest in general causal laws, learning psychology contributed a set of experimental paradigms (combinations of apparatus, procedure, measures, and species) that provided a “test bench” for establishing functional relations among dependent and independent variables. In some cases these paradigms were used to test predictions of general laws and models, with a strong emphasis on using control groups to isolate the effects of interest. In other cases (notably in Skinnerian and applied psychology) paradigms were used primarily to shape behavior and establish reliable response patterns and relations to stimuli.

In still other cases, tasks were developed to establish the ability of different species to solve complex cognition problems, such as matching one stimulus with another, forming learning sets, discriminating the odd stimulus among three, counting, or reasoning. Initially, the point of this research was to establish a protoevolutionary ranking of species’ abilities (Timberlake and Hoffman 1998); however, more recent experimenters, following an analysis of the component skills involved in unique human behaviors, have tested animals separately for each skill (e.g., Pepperberg 1999; Povinelli et al. 1997; Premack 1988; Savage-Rumbaugh et al. 1998).

Physiology of Perceptual-Motor Relations

A good portion of the study of animal cognition during the first half of the twentieth century involved investigation of the anatomy and operating characteristics of the sensory receptors of particular species. When combined with the enumeration of reflexes and the development of learning tasks, considerable knowledge was added about the sensory windows of specific species, including the physical range, sensitivity, and discriminative capabilities of different senses. Based on the study of insects, biologists led by Loeb (1918) proposed a set of simple models of how specific sensorimotor mechanisms controlled orientation and movement. Unfortunately, psychologists studying the sensorimotor control of the orientation and movement of rats in mazes found remarkable interchangeability among different senses in controlling behavior (see Munn 1950). This contrast between simple general models and subsequent causal complexity set a pattern in this area that was repeated several times over the century.

Much of the subsequent data clarifying the sensory and motor worlds of animals has come from combining neurophysiology, mechanics, and the circuitry of sensory receptors with a fine-grained analysis of the behavior controlled by these receptors. Thus the navigational path integration system of desert ants has been shown to be a product of specialized receptors for polarized light and the calculation of optical flow (Wehner and Wehner 1990). Classic work by von Frisch (1965) on communication among foraging bees related characteristics of their dance behavior to the path and energy necessary to find the food source; subsequent work established more of the sensorimotor mechanisms responsible (Dyer 1998; Gould 1998).

The past two decades have witnessed the discovery of remarkable connections between sensory processing of prey cues by predators and their related search and capture behavior. For example, careful work on the visual system of the European toad reveals a clear relation between the firing rate of a class of cell in the optic tectum and the behavioral response of the toad to worms (Ewert 1987). For an extensive summary of other specific examples of the complex and intimate ties between the neurophysiology of the sensorimotor world and behavior, see Carew (2000).

Uttal (1998) recently argued compellingly that it is not possible in principle to reduce cognition processes defined by environmental stimuli and responses to brain circuitry because of the degrees of freedom created by the complexity of brain elements and function. This problem increases in severity the more complex and abstract the cognition under study. The most progress has been made in relating simpler perceptual-motor cognition to physiological mechanisms, especially given the many points of linkage between the environment and behavior that occur in predation (Carew 2000).

Because evolutionary success is not based on a top-down design, we should not expect the nervous system to contain the clear circuitry of a well-designed television set or central processing chip. Instead, we might expect echoes of previous designs and sensorimotor circuits based on unexpected relations involving the environment and activity of the brain. Our increasing technical capacity to peer into brain activity, abetted ultimately (but probably more slowly than hoped) by artful gene knockouts, should facilitate analyses. This knowledge should help rule out implausible assumptions about cognition and its relation to neurophysiology, and suggest more plausible ones, especially in combination with modeling and the multiple ties between environment and behavior.

Computational and Robotic Models

The construction of model animals that move by wind or muscle power is an ancient art. Even model animals based on gears and levers powered by gravity, water, steam, or springs have been around for at least half a millennium. In the last half of the twentieth century, though, scientists began to focus on computers as mimics of the actions of brains. Initially researchers focused on general-purpose artificial intelligence programs designed to solve abstract problems (e.g., Newell and Simon 1958). More recently, researchers have worked on connectionist software models that use layers of neurons and simple learning rules to model sensory processing, categorization, spatial learning, and even language parsing and production (e.g., McClelland and Rumelhart 1986). A limitation of these models is that they are not unlike a brain slice in a dish in their dependence on someone to embed them in an environment.

A second form of model consists of simple, autonomous robots designed with bottom-up (subsumption) rather than top-down architecture (Brooks 1999). A major advantage of working with bottom-up robots is that they typically are designed to function (i.e., survive) in a real environment (such as the Martian landscape or the bottom of the ocean). Thus the builder is forced to include all the processes necessary for survival. There can be no promissory notes that in the future the robot will be made energy efficient or receive sensory organs or motor effectors. As a result, the robot comes closer to mimicking the embodied and situated realities of a living organism in three important ways.

First, there are constraints and tradeoffs involving efficiency and capacity, for example, fineness of discrimination versus speed of reporting, speed of movement versus endurance. Second, because the robot functions in a particular environment, the qualities of that environment can be assumed and used in the robot's cognition. Thus, a functional memory for food locations in an open, flat environment might be achieved by marking the substrate rather than by building a general memory capacity capable of storing the results of triangulating food locations using multiple landmarks. Third, there are potentially powerful advantages to requiring hardware and software to perform multiple functions. The result is that cognition is embedded in the interaction of parts of the robot with each other as well as with the environment. Like real animals, the robot cannot be understood as an isolated brain or slice; its behavior needs to be analyzed within its "selection" environment.

Finally, the bottom-up approach can be combined with genetic algorithms to produce a third form of modeling in which genetic algorithms are applied to either software animals or combinations of software and hardware animals (Beer 1990; Nolfi and Floreano 2001; Yamauchi and Beer 1994). These models provide an important component that has been missing in the study of animal cognition—the possibility of getting at the process of cognitive evolution more directly. These animals may or may not resemble actual organisms, but it is possible to implement "experiments" to determine environmental and organismic prerequisites for the evolution of communication, or the circumstances conducive to the evolution of more, or of less, dependence on learning. Obviously as we come closer to modeling actual animals, the results of our evolutionary experiments become more relevant to animal cognition.

Constructing Animal Cognition

To this point I have briefly reviewed the kinds of contributions and tools provided by ethology, learning psychology, the physiology of perceptual-motor relations, and computational and robotic models. The next step, combining this information to construct the function and evolution of cognition, raises important questions about the sheer amount of data, its potential incompatibility, and the best way to organize and summarize the data.

Amount of Data

An underappreciated lesson from the successful genome projects of the past several years is that each project focused on laying out the genetic structure of a single species at a time, but the whole species, not just the head genes, or the muscle genes, or the genes on the first two chromosomes. I propose following a similar approach by trying to construct cognition in projects concerned with a single species at a time not just vision, or categorization, or motor capacity, but a functional animal. Once we get the hang of it, the construction of the cognition of different species should go much faster.

Incompatibility of Data

The problem of integrating data from different disciplines may be more apparent than real. The past 20 years of research on the physiology of perceptual-motor relations have focused on naturally occurring behavior that fits well with or was borrowed directly from ethology [see Carew (2000) for classic examples ranging from cricket calls to hunting in toads and barn owls]. Functional motivational systems and perceptual-motor units gleaned from observation and experimentation provide an immediate context to help analyze how the receptor characteristics and neurophysiological pathways relate environmental stimuli to behavior. In turn, neurophysiological analysis has clarified the mechanisms that control both stereotyped and more variable appetitive behavior. Analysis of the mechanisms of perceptual-motor relations also has profited from use of the experimental paradigms provided by learning psychology, while the results provide data about sensory processing that might promote the use of more effective combinations of stimuli, responses, and rewards.

In contrast, there is a history of conflict between ethology and laboratory learning, in part because the former concentrated on naturally occurring behavior and the latter on experimenter-defined behavior in artificial environments. However, three recent developments argue that this separation may be reconcilable. First, more researchers have drawn on the control and hypothesis testing traditions of laboratory learning to clarify the basis of niche-related behaviors, such as the distribution of foraging effort and the mechanisms of food storage and retrieval in birds (see Shettleworth 1998). Second, there is evidence that the presumably artificial paradigms of laboratory learning are based on niche-related mechanisms. In the process of tuning their experimental paradigms to produce reliable, vigorous, and interpretable behavior, it appears that psychologists have inductively made contact with mechanisms of niche-related learning (see Timberlake 2001a). An example is the apparent similarity between laboratory maze paradigms and the observed tendencies of rats to establish and follow trails in natural environments.

A last support for reconciliation lies in the use of motivational systems models similar to that of Tinbergen (1951) to describe and predict behavior in both natural settings and laboratory paradigms (Timberlake and Lucas 1989; Timberlake and Silva 1995; Timberlake 2001b). A behavior systems model, such as the predatory subsystem of feeding in rats shown in figure 14.1, is based on the combination of observational data from free behavior circumstances and experimental data from laboratory paradigms. Behavioral observations provide the initial basis for the organization and components of the system. Reading across columns under each heading in the figure, the rightmost column represents actions, such as track (visual tracking at a distance). The next column to the left relates these actions to modules (learned or unlearned perceptual-motor units), such as chase (small moving objects). The next column to the left organizes modules in repertoires within modes (such as general search). In the leftmost column, modes are related to functional subsystems, such as predatory (behavior), and systems, such as feeding (level not shown).

Naturally occurring sequences of behavior can be generated by tracing actions (and related modules and modes) from top to bottom of the diagram, with oscillation and retracing when the behavior of the animal locates stimulus support for alternative modules or is unsuccessful in locating stimuli that maintain the present mode or lead to the next. The animal begins by expressing general search mode actions controlled by learned and unlearned perceptual-motor modules. In typical environments, these actions lead to circumstances that produce a shift to actions characteristic of the repertoire of perceptual-motor modules related to the focal search mode, which in turn leads to handling and consuming actions related to still another repertoire of perceptual motor modules.

It is important to note that laboratory procedures such as Pavlovian conditioning can be very useful in testing and clarifying such a model Timberlake (1994, 2001b). For example, the procedure of presenting an artificial moving prey stimulus that predicts food to different rodent

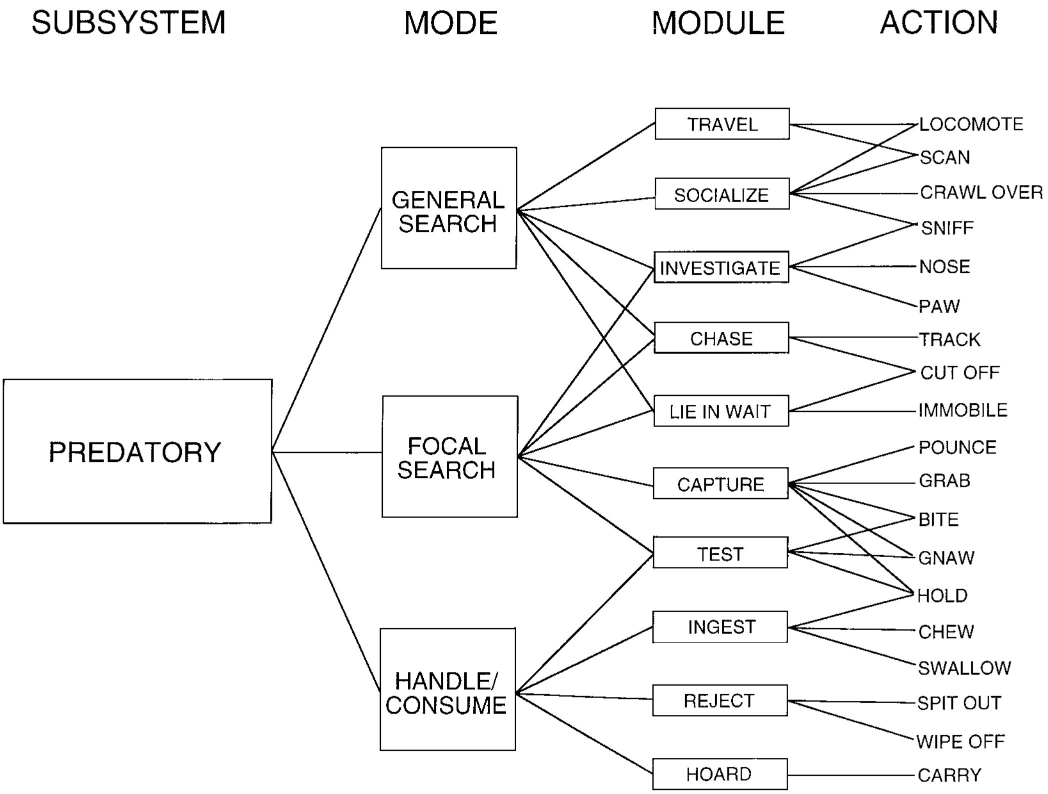

Figure 14.1
Proposed predatory subsystem of the feeding behavior system of the rat (*Rattus norvegicus*) consisting of modes, modules, and actions. The figure shows three search modes (general, focal, and handling/consummatory) and their overlapping repertories of learned and unlearned perceptual-motor modules. Actions controlled by system components in conjunction with the environment are shown on the far right. The environment can affect actions directly through local stimulus support and indirectly through effects at other levels of the system.

species with an appropriate delay reveals the organization of their general and focal search repertories related to predation (Timberlake et al. 1982; Timberlake and Washburne 1989). Finally, such a systems approach to modeling is general, not being limited to either feeding (Fanselow 1994; Domjan 1994) or rats (Domjan 1994; Hogan 1994).

Summarizing and Organizing Data

An efficient way to summarize and organize data is to construct a model representing the knowledge already assembled that can facilitate further thought and experiment, but this is not a trivial task. It appears, though, that humans have an attribute that can help in this process, namely, the ability to use their experience to integrate information about an animal's sensory physiology, behavioral organization, and learning to understand and predict its behavior, namely the theromorphism I mentioned in the introduction. Conversations with fishermen, hunters, and trackers reveal species and even individual specificity in their knowledge and predictions of animal behavior; this implies that they have a model of the animal developed from their experience. Listening to experienced observers of primates suggests that they develop similar models. Such implicit models appear to allow an observer to predict behavior by virtually placing him or herself in the position of a specific animal, not as a human, but as the animal. These models can be made more comprehensive and testable by giving them reality using computation and robotics. These models become more powerful as they include explicit knowledge of the animal's sensorimotor capacities and organization, motivational states, and learning possibilities.

Using Human Cognition as a Standard

This approach can be applied to any species, including humans. However, our tendency to use humans as a standard carries with it drawbacks, such as a tendency to focus on specialized processes that define us rather than cognition more likely to be shared broadly with other animals. There is also a tendency not to treat comparisons with humans using the same criteria as comparisons involving other species, namely, phylogenetic descent and environmentally based convergence and divergence. As in the case of any species, it would help to have carefully prepared motivational system models for humans that included relations with the behavioral physiology of sensorimotor relations. We could also use greater clarity about how human learning fits with niche-related mechanisms (e.g., Cosmides and Tooby 1987), and decrease our resistance to modeling humans in a bottom-up fashion.

Perhaps most important, using humans as a standard for studying other species makes it difficult not to invoke thoughts and feelings as direct causes of behavior, thereby stopping our inquiry short of the data needed to construct working models of cognition. In the approach described here, thoughts and feelings are phenomena to be explained, not the basis of explanation. To be sure, if there is no other information, anthropomorphic and emautomorphic inferences can be useful shortcuts to predicting human behavior. That is undoubtedly why these practices are a nearly ineradicable part of the human social toolkit (Beer 1992). But by continuing to invoke such human-centered explanations of the behavior of all nonhuman animals, we engage at best in a hopeful speciesism.

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