

1 Lessons From Animal Learning for the Study of Cognitive Development

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*The epigenesis of
Mind: Essays on
Biology & Cognition*

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Why open a book on cognitive development with a chapter on animal learning? It is not to argue that an account of cognitive development should use animal models of learning. Rather, it is to take advantage of developments in this area that provide insight into the question of how to characterize cognitive development. We argue that any account of cognitive development is incomplete if it attempts to explain both the what and how of learning solely in terms of general processes—be they associations, prototype abstraction, hypothesis testing, induction, analogical reasoning, assimilation, generalization, or differentiation. We argue that there are reasons for also postulating domain-specific determinants of the nature of cognitive structures. These determinants guide learning, creating structures with their own rules of organization. These ideas about cognitive development have been in the air for sometime; what we offer here is a fleshing out of them. We are emboldened

to do so in part because of what we have learned from considering cases of learning in species other than the human. The message of this chapter is that much learning in animals is best thought of as the product of behavioral mechanisms with elaborated internal structure that have evolved to guide learning of species-relevant features of the environment.

Specification of the conditions under which learning occurs has been a central goal of experimental psychology since its inception as a natural science. A major research agenda from this tradition has been to delineate general laws of learning that hold across species and problems (domains). It was this fundamental commitment to general laws that led major learning theorists (e.g., Thorndike, Hull, Skinner, and Watson) to the behavior of man with laws derived from animal models. Indeed, it has been argued that the main agenda of experimental animal learning was not to explain animal learning but to understand human learning (Schwartz, 1981). From this position, animal-specific solutions are not only irrelevant, they are a positive nuisance in the march towards understanding the general laws of learning that explain human behavior. Animal models, if they are to elucidate human behavior, must assume commonality.

A quite separate intellectual tradition determined the research agenda of the ethologists. Biologists by training or tradition, they sought to uncover the diversity of animal solutions to varying (or identical) environmental pressures. They recognized not only diversity of organisms but also diversity of mechanisms within organisms.

Far from seeking general laws of learning, the main tenet of this creed is innately directed, or preferential, learning (Tinbergen, 1951), which reflects the selective adaptive pressure of a particular environmental niche. This perspective emphasizes the structural integrity of an adaptive complex. Learning, like other adaptive solutions, is embedded within the structure of coherent contexts, and the particular properties of a learning mechanism make sense only with reference to this system. It is the business of ethologists to map the fit of the animal's behavior to its environmental niche and to describe the diversity of such adaptive solutions.

In the latter part of the 1960s, a movement arose within psychology that was heralded as a rapprochement of these two views. Seligman and Hager (1972) called it a "reunion of thought between the psychology of learning and behavioral biology after almost a half-century of separate development" (p. 1). This movement introduced the notion of constraint to deal with the fact that some associations in classical and instrumental conditioning are much easier to form than others. Even here, in the natural territory of general process learning theory, the notion of selectivity was seen as operating pervasively. Animals can form some associations easily, others with some difficulty, and others not at all. Seligman, among others, argued for biological

preparedness for certain forms of learning, stating that "preparedness of organisms reflects the selective pressure that their species has faced" (Seligman & Hager, 1972, p. 464).

As we make clear in this chapter, we prefer the phrase "privileged relationship" to "constraint" or "boundary." A problem with the phrase "constraints on learning" was noted in both of the seminal books that heralded this rapprochement (Hinde & Hinde, 1973; Seligman & Hager, 1972). The phrase suggests that there is a general process mechanism that is somehow too powerful or generative. Uneasiness with this potential interpretation goes back to the beginning of this literature. The terms "boundaries" and "constraints on learning" were called "unfortunate" even in the original Hinde and Hinde (1973) book with that title. The term *predisposition* was added as a subtitle because of a fear that the term *constraint* would lead to the inference that the position could rest "comfortably in the framework of existing learning theories." At the Hinde and Hinde symposium, there was considerable discussion of whether it would still "prove profitable to think in terms of general laws hedged about by constraints, or whether some quite new formulation would seem more profitable" (Hinde & Hinde, 1973, p. 470).

This dissatisfaction with the connotations of the word "constraints" appears repeatedly in the discussion of general process theories, biological constraints positions, and ethological approaches in the issue of *The Behavioral and Brain Sciences* devoted to this question (1981, Vol. 4). Garcia (1981) argued that the notion of biological boundaries suggests that the constraints are "subservient to the general process tradition" (pp. 143-144), and Malone (1981) wrote "in stressing exceptions to the laws of GPLT [General Process Learning Theory], this approach . . . almost gives the laws themselves an added legitimacy" (pp. 151-152). According to Petrinovich (1981), the notion of "... constraints involves a tacit acceptance of a uniformity view that holds that there is a general associative mechanism that typifies learning processes, and that this general law is abridged, or amended, by special factors" (pp. 153-154). Furthermore, Shettleworth (1981) asserted that "Biological boundaries to learning have been threatening to become mere adjustments to parameter values of GPLT, while theorists ignore their implicit message that learning is best understood as part of an animal's adaptation to its natural environment" (pp. 159-160).

In this book, we advance the thesis that domain-specific learning mechanisms make learning possible. The focus is on how these mechanisms make learning possible, not on how they constrain a general mechanism from achieving faulty generalizations; hence, our view that it is better to talk about *privileged as opposed to constrained acquisitions*.

We begin with a discussion of biologically specified privileged pairings in what is commonly called associative learning, using as our prime example

conditioned food aversion in rats under laboratory conditions. We then consider examples in which a specific representation-forming learning mechanism makes it possible to acquire crucial information at specific stages in animal development. The argument that complex representation-forming systems are a foundation of development is elaborated by considering the acquisition of bird song, prey recognition in vervet monkeys, and spatial learning in rats.

ASSOCIATIVE LEARNING

General Process Learning Theory

The theoretical framework for the traditional study of animal learning shares much in common with the theory of association as developed by the British empiricists. The fundamental assumption is that knowledge about the world and how to respond to it is based on the capacity to form associations in a lawful way. The empiricists formulated two laws of association: (a) the more exposures to a particular association opportunity, the stronger the association (the law of frequency), and (b) the more proximate in time and space the occurrence of the component members of the association, the more likely the association will be formed (the law of contiguity).

There is nothing in the laws of association about the nature of stimuli or responses that can be associated with each other, nor anything that varies with the ontogenetic stage of the individual. The original theory treated all effective sensory inputs and all observable responses as equipotential vis-à-vis the associative process. Learning about language and number should be traceable to the same fundamental laws of association that explain the rat's learning to avoid poisonous food or the pigeon's ability to learn the temporal parameters of a schedule of reinforcement.

Modern animal learning theory and some views of cognitive development retain the general process assumption, though not necessarily the equipotentiality assumption. The position is that all learning is based on the capacity to form associations; there are general laws of learning that apply equally to all domains of stimuli, responses, and reinforcers; the more frequent the pairings between the elements to be associated, the stronger the associative strength; and the more proximate the members of an association pair, the more likely the learning.

The general process theory of learning has been developed around the study of classical and instrumental conditioning and extended in a variety of ways to deal with phenomena of generalization, discrimination, and inhibition and to take into account the central role that reinforcement can often play in whether an association is formed. It has also been significantly revised

in response to experiments on classical conditioning showing that it is not the pairings per se between a conditioned stimulus (CS) and unconditioned stimulus (UCS) but predictiveness that determines whether or not an association forms. If the CS and UCS are independently distributed in time, so that the occurrence of the CS does not predict the occurrence of the UCS, then no conditioning occurs despite numerous fortuitous pairings of the CS and US (Rescorla, 1968). Also, if a new CS predicts what is already predicted by an old CS, no association forms between the new CS and the US, no matter how frequently or closely they are paired (Kamin, 1969). Finally, if another CS accounts for more of the variance in US occurrence than the CS in question, then associations between the CS in question and the US do not form despite frequent pairing (Wagner, Logan, Haberlandt, & Price, 1968).

The idea that associations build as a function of frequency is neutral with respect to the size of increments that occur as a function of trials. The Rescorla-Wagner law (Rescorla & Wagner, 1972), sometimes called the "delta" rule in the literature on learning in parallel distributed systems, gives the function for the change in the strength of the n th association (ΔV_n) as a function of various parameters and of the sum of the pretrial strengths of the other associations:

$$\Delta V_i = K(\lambda - \Sigma V_i)$$

In this equation, K , the associability parameter, reflects the readiness with which the CS and UCS can be associated. The introduction of this associability parameter was motivated by the evidence against the equipotentiality assumption. λ is the asymptotic associative strength parameter. The closer ΣV_i is to λ , the less the increment in associative strength (ΔV) on a conditioning trial. ΣV_i is the sum of the strengths of the associative bonds linking the CSs present on a trial to the US. Roughly speaking, the equation captures the idea that the more strongly something (the US) is expected on a given trial, the less its occurrence alters one's expectations.

The parameters K and λ are CS-UCS pair-specific and are determined empirically. There is no theory of why K is large for some CS-US pairs and not for others. The Rescorla-Wagner law also says nothing about the time frame over which the associative process operates. General process theorists make pair-specific assumptions about the degree of temporal contiguity that there must be between the CS and UCS for learning to occur. A similar conclusion holds for stimulus sampling models of human concept learning; they either build in factors like selection or use parameter variations to capture stimulus-specific effects (see Atkinson, Bower, & Crothers, 1966, for a review of these models).

The idea that there are structural determinants of learning that go beyond those set by the nature of an organism's sensory and motor endowments has

influenced the study of classical and instrumental conditioning in animals. Where it was once almost universally assumed that research would yield up general laws of learning—ones that would apply to all species, at all ages, in all environments, and to all stimuli and response pairings—there is now much debate. Even those who defend the idea that there are general laws of learning have formulated their theories in such a way as to take account of a pervasive fact: Animals behave as if they treat many stimulus–reward, stimulus–response and/or stimulus–stimulus pairings as privileged. What these privileged relationships are can vary from species to species. These privileged relationships cannot always be explained by an animal's conditioning history; instead, they often make sense only when considered in terms of the evolutionary-functional role they play in the animal's life. The privileged relationships betray the presence of a system that leads the animal to notice and respond selectively to one kind of stimulus as opposed to another under certain conditions. In this sense, they serve as the fundamental evidence for an argument that there are high-level (or nonsensorimotor) determinants of what is learned and how.

Some Examples of Privilege

Avoidance Learning. The equipotentiality assumption that prevailed in learning theory from Pavlov to Skinner asserted that any perceptible stimulus could be associated with any other perceptible stimulus or with any response in the animal's repertoire with equal ease. There are now many and diverse demonstrations that equipotentiality does not obtain. Whereas pigeons readily learn to peck a key in order to obtain food, they have difficulty learning to peck a key to avoid shock (Hineline & Rachlin, 1969). In contrast, they readily learn to flap their wings to avoid shock.

The effect of the reinforcer or US on which responses may be learned can be explained if one assumes that pigeon learning is expressed through response systems tailored to serve specific biological functions in specific contexts, so that the animal does not choose its responses independently of the context. When a bird perceives the threat of shock to its feet, it flies or attempts to fly; it does not peck. The same complex structures that preordain the appropriateness or inappropriateness of certain responses in certain contexts preordain what is likely to predict what. An experiment by Lolordo, Jacobs, and Foree (1982) supports this conjecture, as does Bolles' (1970) account of avoidance learning. Lolordo et al. presented pigeons with a redundant CS made up of a light and tone. Reasoning that pigeons treat sound stimuli as danger signals and visual stimuli as food-related stimuli, they proposed that control of a pecking-for-food operant would be selectively established to the visual component of the CS and that control of avoidance

behavior would be selectively conditioned to the sound stimulus. This was exactly what happened; different components of the CS controlled the target behaviors during transfer tests. Such cross-over effects provide compelling evidence against the view that all stimuli, responses, and reinforcers are equipotential in the creation and maintenance of learned behavior. To account for the privileged treatment accorded certain pairings, it often helps to adopt a biological perspective. Consider Bolles' theory of avoidance learning—one that places such learning in the context of the animal's problems in nature.

The general process theory account of avoidance learning has the animal gradually learning to perform a targeted behavior in response to the presentation of a CS. If he does, he avoids shock. For the CS to become effective, it obviously has to be paired with the UCS. Over trials, the conditioned response in question occurs when the CS occurs and thus the animal avoids shock. Bolles pointed out that this account of avoidance learning makes little sense if we consider an animal in the state of nature rather than a laboratory. It will not do to have the animal go through a series of encounters with a predator in order to learn to escape or avoid it. Instead, it seems plausible to take the position that animals are endowed with species-specific defense reactions, such as fleeing, freezing, and fighting—reactions that occur immediately to predators, threats, and the sudden appearance of innocuous stimuli. As Bolles (1970) put it, "no real-life predator is going to present cues just before it attacks. No owl hoots or whistles 5 seconds before pouncing on a mouse. And no owl terminates his hoots or whistles just as the mouse gets away so as to reinforce the avoidance response. Nor will the owl give the mouse enough trials for the necessary learning to occur" (pp. 32–33).

The implications of Bolles' position for the laboratory study of avoidance learning are clear: One should expect differences in the ease with which different classes of stimuli come to control different classes of responses. The case of the differential rate at which a pigeon learns to fly as opposed to peck a key to avoid shock fits this view. So do the experiments done by Bolles that show, for example, that rats learn rapidly to run to avoid shock but learn very slowly, if at all, to rear to avoid shock. Running is a component of a flight response. Rearing is not; it is an exploratory behavior.

Appetitive Instrumental Conditioning. It is not just avoidance learning that presents cases of privileged relationships between certain stimuli and certain responses. Shettleworth (1975) reported a similar result in her study of food-rewarded instrumental conditioning of six different golden hamster behaviors. The hamsters learned quickly to dig, scurgle, or rear for a food reward. They learned slowly or not at all when required to wash their face, scratch, or scent mark. At first, the rationale for these differences is not

apparent; however, if one considers the way hamsters respond in a natural environment, the differences make sense. Shettleworth observed the way hamsters behave under several conditions including the anticipated presentation of food when they are hungry. The behaviors of digging, scrabbling, and rearing become prevalent under these circumstances, whereas those of face washing, scratching, and scent marking tend to disappear. The former are all exploratory behaviors, the latter are not. The motivational state of hunger recruits those behaviors that might lead the hamster to find food and suppresses other components of the hamsters repertoire (Gallistel, 1980). Given that the exploratory behaviors can aid the animal's search for food, it is no longer surprising that hamsters learn rapidly to perform these responses and have more difficulty learning to perform those that are not hunger related. The preferred relationships betray the presence of a motivational mechanism that organizes the animal's behavior and its learning.

It might be argued that the differential ability to reinforce the two classes of behavior reflects a conditioning history of the hamster (Mackintosh, 1974), rather than a biologically organized motivational-response system that causes the animal to be selective. The problem with this position is that laboratory hamsters are unlikely to have had the opportunity to perform the exploratory behaviors—especially digging—in the presence of food. In fact, when reared in laboratory cages, hamsters spend a great deal of time grooming and little time digging in the wire floor. Despite the presence of food, they apparently do not relate grooming to it. Otherwise, Shettleworth should have had an easy time reinforcing grooming with the presentation of food.

Learned Food Aversions. The work by Garcia and his colleagues continues the theme that neural mechanisms that have evolved to serve a particular function determine what can be associated with what. Garcia and Koelling (1966) had rats drink water of a distinct flavor from a licking tube. Via a lickometer connected to the spout, their drinking also activated a flashing light and a noise. When the animals readily drank this funny tasting water from the spout that triggered noise and light, they were punished for doing so either by electric shock delivered through the spout at various latencies after the onset of drinking or by the administration of a poison that made them sick after a latency of about 20 minutes. Both punishments reduced their consumption. In associative terms, one would say that some or all of the stimuli (funny taste, flashing light, noise) had become associated with the punishing US. However, the poisoning was effective even at long delays between drinking and the onset of punishment, whereas the shock was effective only when the punishment was in close temporal contiguity with the drinking. The rats were then tested with water that had the same taste but came from a spout that did not produce the noise and light and with a spout

that produced the noise and light but gave water without the distinctive taste. The animals that had been punished by poisoning avoided the flavored water but drank readily from the spout that caused light flashes and noise, while the animals that had been punished by shock through the spout readily drank the flavored water but avoided the bright, noisy spout.

The Garcia and Koelling experiment reveals the presence of two distinct learning processes operating in accord with different principles about what goes with what and over what temporal intervals. One process treats the noise and flashes that result from touching tongue to spout as much more likely predictors of the shock than is the distinctive flavor of the water, but it recognizes this predictive relation only when the temporal link is tight. The other process treats the distinctive flavor of the water as a much more likely predictor of the subsequently experienced illness than are the noise and light that accompany drinking, and it picks out this predictive relation between a particular taste and illness even when the two experiences are separated by intervals measured in hours rather than seconds (Revusky & Garcia, 1970).

The differences between these associative mechanisms are treated as parameter differences in the values of the constants in the Rescorla-Wagner model. We have trouble with this, not because it is wrong to say that there are parameter differences; there obviously are, but the question remains "Why?". What is it about the relation between taste and illness that makes them readily associable over long delays? What is it about taste and illness that allows for what is essentially a violation of the law of temporal contiguity?

The principles by which these learning mechanisms operate reflect fundamental facts about the world in which these animals have evolved. Both taste and toxicity derive from the chemical composition of substances and tend, therefore, to covary, the more so in that many of the poisons an omnivore is apt to ingest have evolved in forage plants and prey animals as defenses, making it of adaptive value to the poison source to have a marked and distinctive taste. On the other hand, nothing in the structure of the everyday world makes the toxicity of a food covary with lights and sounds that accompany ingestion but do not emanate from the substance itself. Also, toxins generally take some while to make their effects felt. A learning mechanism sensitive only to tight temporal contiguity would never associate the distinctive tastes of most toxins with their delayed but potentially fatal effects. On the other hand, a mechanism for detecting predictive relations among external variables like lights, sounds, and shocks cannot readily be tuned to pick out predictive relations operating with temporal lags of hours, because in any one hour there are too many potentially predictive experiences of changes in these kinds of variables. It must require close temporal linkage to solve the problem of what predicts what. Thus, the characteristics that are optimal for one mechanism are precisely the wrong characteristics for the

other mechanism. The domain-specific tuning of the distinct learning mechanisms revealed by the Garcia experiments makes adaptive learning possible.

Rozin and Kalat (1971) and Rozin and Schull (1988) point out that the special tuning of the learning mechanism that mediates bait shyness is but one aspect of a behavioral complex that shows many special adaptations that promote healthy food selection in the rat. For example, rats have an innate bias for things that are sweet, which tend to be high energy compounds, and an innate aversion for things that are bitter, which tend to be alkaloid poisons. These biases alone will not guarantee success. Not all bitter things are toxic, and not all sweet things are nutritious. What helps the rat sort out his food environment are three feeding habits. The first is to eat familiar foods and avoid novel foods. The second is, when eating a novel food for the first time, to eat only small amounts. If the novel food contains a toxic substance, the rat is not likely to eat enough of the food to die but it eats enough to experience the ill effects. The third is to wait a long time between meals involving novel foods, allowing time for illness to develop without producing confusion over the source of illness.

Recently, Galef and his associates (1987; Galef, McQuoid, & Whiskin, 1990) have shown another aspect of this adaptive specialization. Part of what contributes to a rat's sense of familiarity with a food is smelling it on the breath of fellow rats. In Galef's experiments, an "observer" rat is exposed to a "demonstrator" rat that has recently eaten one of two novel diets. Seven or 8 days later, the observer ingests both novel diets and subsequently becomes ill. When next tested with the two diets, the observer avoids the novel diet that it did not smell on the breath of another rat a week earlier. Smelling a substance on the breath of a conspecific tends to prevent that substance's being perceived as the source of illness, even when the experience of ingestion and illness occurs long after the experience with the demonstrator rat. It does not matter whether the "demonstrator" was or was not ill during the demonstration. This aspect of the poison-avoidance mechanism operates on the implicit principle that other rats know what they are eating. Noting that a demonstrator ate something gives that something the seal of safety no matter what the condition of the demonstrator rat.

The storing of memories of the food odors it has detected on the breath of conspecifics for use—often much later—in deducing which foods have caused it to become ill is analogous to the young song bird's storing memories of the songs of conspecifics for later use in developing its own song (see Marler, this volume). It is another example of Marler's "instinct to learn," that is, of the innate foundations that determine what is stored and how that information is employed to direct subsequent learning and behavior.

In summary, a complex of special adaptations, including adaptations of the learning mechanism, make it possible for a rat to learn to avoid foods that are bad for it. Specialized learning mechanisms with implicit commitments to the

nature of the world they must adapt to also make it possible for young birds to adjust the parameters of the circuitry that extracts from sounds the angular position of their sources, and they make it possible for migratory birds to learn as nestlings the facts about the night sky they will need to know to maintain their orientation during the migratory flight they will first make months later as young adults.

NON-ASSOCIATIVE LEARNING

The preceding section gave examples of relationships whose learning is privileged. These examples were developed within the conceptual framework provided by the associative analysis of learning. Gallistel (1990) has questioned whether this conceptual framework is the correct one for understanding the nature of the learning that occurs in these and other examples of classical and instrumental conditioning. He gives a simple but powerful analytic model of classical conditioning in which the notion of an association plays no role. He shows that this model, which has no free parameters and is computationally simpler than the Rescorla-Wagner model, gives a more adequate account of the salient findings from the last 20 years of classical conditioning experiments. In the Gallistel model, classical conditioning experiments do not study a general learning process; rather, they study a learning mechanism that is specifically dedicated to computing a representation of the temporal dependence of variation in one variable on variation in one or more predictor variables—multivariate time series analysis.

Whether or not the associative framework is the appropriate framework in which to view the examples in the previous section, there are many examples of animal learning that do not fit this conceptual framework. These examples make it very clear that for most kinds of animal learning to occur there must be a specific learning mechanism that makes that particular kind of learning possible. All of these learning mechanisms have been shaped over evolutionary time so that the structure of the learning mechanism—what information it processes and how—reflects the structure of the problem that has shaped its evolution.

How the Barn Owl Learns Where Sounds Come From

Localizing the source of sounds accurately is important to the adult barn owl, who relies on the sounds rodents make to orient its predatory attacks. It can pluck a scurrying mouse off the forest floor in total darkness, guided only by the rustle the mouse makes as it moves through the litter. Sound localization is based on frequency-specific binaural differences in the intensities and arrival times (phases) of sound waves. The owl is born with circuitry that

processes these differences in order to extract the angular direction of the sound source, but the innately given parameters of this specialized circuitry are necessarily only approximately correct, because the interaural differences in intensity and phase for a sound of a given frequency from a given direction depend on the idiosyncrasies of the animal's head shape. They vary from individual to individual, and, of course, they change as the head of an individual grows larger during maturation.

The barn owl has a specialized learning mechanism that recalibrates its sound localization circuitry during development (Knudsen, 1983; Knudsen & Knudsen, 1990). Like the other specialized mechanisms we have been considering, this mechanism is dedicated to constructing a particular kind of representation—in this case, a representation of the angular direction of a stimulus source. And again, some principles about the relevant aspects of the world are implicit in the innately given structure and functioning of the learning mechanism. In this case, one may recognize two such principles:

1. The angular position of the source for auditory and visual inputs originating from one object is a unique location in one and the same space. A mouse does not reflect light from one location in space while simultaneously causing rustles from a different location. Thus, the location assigned to the origin of the auditory input from a source should be the same as the location assigned to the origin of the visual input from that source.
2. Vision is inerrant; the location assigned to a source by the visual system can be used to calibrate the circuitry that computes a location from auditory input.

The eyelids and the auditory canals of baby barn owls open when they are about two weeks old. If the correspondence between the location assigned to a source by the auditory system and the location assigned to the same source by the visual system is altered at this age, either by putting a plug in one ear canal or by fixing displacing prisms in front of the eyes, the birds adjust the direction in which they orient their head in response to a sound by as much as 20°. Thus, the orientation of the head in response to a sound from a given direction matches the orientation of the head in response to a flash from that direction. If the alteration has been produced by an ear plug, this adjustment means that the resulting orientations to sound have been corrected so that the head is now oriented toward the source, but if the alteration has been produced by prisms, this adjustment means that the resulting orientations to sound are now in error by the same amount as the visual orientations. The visual orientations are off by nearly the amount by which the prisms deviate the visual input. The barn owl visuo-motor systems cannot learn to correct for the effects of deviating prisms (unlike the human visuo-motor systems),

and the auditory system treats the locations determined by visual input as the standard against which to calibrate the auditory localization circuitry. One result is that prism-reared barn owls miss stimulus sources—both audio and visual—when they try to approach them, because the body follows the “aim” of the head, which is systematically in error.

If the canal plug or the prisms are installed when the bird is 21 days old or older, the adjustment to the experimentally induced audiovisual discrepancy is incomplete, no matter how long the discrepancy is experienced. Thus, a bird that at 50 days of age has prisms installed that deviate the visual field 23° to the right learns to orient to about 10° to the right of a sound source, which is 13° to the left of where it would orient in response to a flash from the same source (a residual audiovisual orientation discrepancy of 13°). This discrepancy persists indefinitely. When the prisms or plugs are eventually removed, the bird initially shows an orientation error that was approximately equal in magnitude to the correction it has learned to make, but opposite in direction. Thus, when the 23° rightward prisms are removed, the bird that has learned a 10° rightward correction now orients 10° to the left of the source. If the prisms are removed at an early enough age, the bird learns the correct correspondence over a period of about 25 days, so that it comes in time to orient toward the sound source with normal accuracy and precision. If, however, the prisms are removed after sexual maturity, the bird never learns the correct orientation. It persists indefinitely in the reversed misorientation that it shows upon prism removal.

The older the bird at the time the prisms or plug are first installed, the less the birds adjust; hence, the larger the residual audiovisual orientation discrepancy and the smaller the reverse misorientation after prism or plug removal. When the age at installation is somewhat more than 100 days, the birds only adjust by about 3° , which is the amount by which adult birds will adjust. Thus, 100 days marks the end of the *sensitive period*, the period during which the developing bird can learn an audiovisual correspondence that is substantially different from the normal one. The *critical period*, by contrast, is the period during which exposure to the normal audiovisual correspondence permits the bird to learn normal sound localization precision and accuracy, after the experimental discrepancy is removed. The critical period is much longer than the sensitive period. It comes to an end abruptly at about 200 days of age, which is approximately the age of sexual maturity. Whereas the magnitude of the adjustment that the bird can make to an abnormal audiovisual correspondence declines steadily during the sensitive period, the magnitude of the restorative correction it can make when prisms are removed does not appear to change during the critical period. It can make a large restorative correction anytime during the critical period, provided the correction is completed before the end of the period. If, however, the return to

normal audiovisual alignment is not complete when the critical period abruptly ends, then the remaining misalignment remains indefinitely. In summary, the mechanism for learning to localize auditory sources by reference to the visual world is dedicated to the construction of a particular kind of representation, it comes with some innate machinery in place to get the process going, and it only operates during a certain phase of development.

Stellar Orientation in Migratory Songbirds: Nestling Astronomy

Migratory birds maintain their orientation at night in part by reference to the stars. The stars form a fixed pattern, which moves during the night with respect to an observer on earth. Within this moving pattern, there is a point that does not move, the celestial pole, the center of rotation of the night sky. To orient by the stars at night, one need only locate the celestial pole. The direction of the celestial pole relative to oneself may be estimated from a view of any recognizable portion of the star pattern (any constellation). For example, Polaris, the north star, lies on a line with the two stars that form the lip of the Big Dipper. If you look often at the sky at night, you come to know the approximate angular distance between the lip of the Big Dipper and Polaris, hence you can locate (approximately) the northern celestial pole from a view of the Big Dipper, even when Polaris is obscured by clouds.

Because of the very slow proper motions of the stars (their motions relative to one another), the shape of the night sky changes over what are short intervals from an evolutionary perspective. In 100,000 years, the Big Dipper will be unrecognizable as such. Because of the precession of the earth's axis of rotation, the location of the celestial pole changes even more rapidly. At the time of Homer, the northern celestial pole was somewhat off the lip of the Little Dipper, instead of at the tip of the handle, where it now is. If generation after generation of a given species is to orient the nighttime positions of their migratory flight by reference to the stars, each generation must learn for itself what the night sky looks like and where its center of rotation is.

Emlen (1967) put migratory indigo buntings in a planetarium in cages contrived so that he could measure the direction in which the birds attempted to take off. He blocked out different constellations one at a time and found that no one constellation was crucial. The birds attempted to take off in the direction that was appropriate to their autumnal migratory condition no matter which constellation was missing. But when he removed the entire circumpolar sky—everything within about 35° of the center of rotation—the buntings' orientation deteriorated. He also found that different individual buntings knew different constellations or combinations of constellations. Blocking out one combination would disorient some birds but not others.

When another combination was blocked, some of the previously disoriented birds regained their orientation, and others lost theirs.

The finding that the birds relied primarily on the stars within 35° of the stellar pole is not surprising in the light of other experiments showing that buntings learn the configuration of the night sky and its center of rotation in the spring of their natal year, while they are unfledged nestlings. The circumpolar stars do not pass beneath the horizon for an observer in temperate latitudes, hence they are seen on spring nights as well as in the fall. Stars farther from the stellar pole pass beneath the horizon. Most of the ones seen on a spring night will not be seen on an autumn night. If what one learns about the stars in the spring is for use in the fall, one should focus on the circumpolar stars.

Emlen (1969b, 1972) demonstrated that indigo buntings learn the constellations and the center of rotation of the night sky while nestlings—and only while nestlings. He raised some of them in a planetarium, where he made the night sky rotate around Betelgeuse, on Orion's shoulder. When the fall came, the now-mature birds were shown a stationary sky; they oriented as they would if they were trying to take off toward the south southeast (their normal fall migration direction) and Betelgeuse were the pole star. Other buntings were denied a view of the night sky while nestlings. Subsequently, these birds never oriented consistently with respect to the night sky, regardless of their migratory condition. By the time the knowledge of the stars was of use to them, they could no longer master it.

Learning the center of rotation of the night sky as a nestling makes it possible for the mature bird to orient with respect to the stars, but it does not determine what orientation the birds will adopt. That is determined by their motivational condition. Emlen (1969a) demonstrated the motivational dependence of the orientation adopted by manipulating the light-dark cycle in an indoor aviary so as to bring two groups of male indigo buntings into different migratory conditions simultaneously. One group was in the condition for a spring migration, while the other was in the condition for a fall migration. When he exposed both to the same stationary planetarium sky, the group in the spring condition oriented north northeast, whereas the group in the fall condition oriented south southeast. Martin and Meier (1973) reversed the polarity of the migratory orientation of caged sparrows by appropriate hormone treatment.

The learning of stellar configurations by migratory songbirds illustrates the assumption of domain-specific learning mechanisms that is central to the view of development underlying many of the chapters in this book. This learning is specific to a particular developmental stage, even though what is learned is fundamental to important adult behaviors. Similarly, in humans, the learning of the phonetics of one's language community and some aspects

of its grammar proceeds much more readily at a young age, even though what is then learned is used throughout adult life (Newport, this volume). Secondly, the learning involves the operation of specialized computational mechanisms, dedicated to constructing a particular representation for a particular use. The center of rotation of the sky cannot be derived from a single look. The nestling bird must store the image of the sky it perceives at one time and the orientation of this image with respect to local terrain. It must integrate the stored image with the image it gets when it looks again minutes, hours, or even days later. Thus, we have a domain-specific learning mechanism that determines what in the bird's environment will be attended to at a certain stage in its development, how that input will be processed, and the structure of the knowledge that is to be derived from that input. The learning of the location of the celestial pole is a striking instance of an instinct for learning (Marler, this volume).

The Role of Special Learning Mechanisms in Optimizing Foraging

There is an extensive body of zoological literature on the strategies animals employ to optimize their foraging behavior. Some interesting examples, both theoretical and empirical, and covering diverse families of animals, are: Elner and Hughes (1978); Heinrich (1979); MacArthur and Pianka (1966); Pyke, Puliam, and Charnov (1977); and Schoener (1971). The predictions of optimality models have often been borne out by experimental tests and field studies. What is striking about these optimality models is that in spelling out the decision process underlying the optimization of foraging behavior they credit the animals with complex representational and computational abilities.

One often-confirmed prediction of an optimality model is the "ideal free distribution," derived by Fretwell and Lucas (1970; Fretwell, 1972) to explain the often-demonstrated tendency of animals with two or more foraging locations to match the time they spend foraging at each location to the relative abundance of the food encountered there. The relative abundance of the food at a location is the amount of food observed there expressed as a proportion of the total amount of food observed across all the foraging locations visited. This phenomenon was first discovered by experimental psychologists in the tendency of animals to "probability match," that is, to match the probability of their choosing to go first to a given maze location to the probability of finding food at that location (Graf, Bullock, & Bitterman, 1964). It rose to prominence in the Skinnerian literature with the formulation of Herrnstein's "matching law," which asserts that animals match the relative frequencies of their choices among response alternatives to the relative amounts of reinforcement obtained through each alternative (Herrnstein, 1961; Herrnstein & Loveland, 1975), rather than always choosing only the

more richly rewarded alternative. Similar findings arose in the foraging literature when, for example, Smith and Dawkins (1971) studied the hunting behavior of individual great tits allowed to feed in several different areas of different experimenter-determined food abundance in short bouts that did not last long enough for any appreciable depletion of the food in a patch. One might have expected the tits always to choose to feed in the patch in which the food was most abundant, but they did not; the relative frequency with which they chose a patch was roughly proportionate to the relative abundance of food in that patch.

The seeming irrationality of an animal's apportioning its foraging behavior among alternatives on the basis of their relative richness rather than always choosing the richest alternative puzzled both psychologists and zoologists. It was eventually realized that this behavior is not at all irrational when one considers the natural situation from a broad enough perspective. On the contrary, under natural circumstances, it may be the only evolutionarily stable strategy, the only pattern that does not tend to create conditions that select against that very behavioral pattern. Under the experimental conditions in which matching behavior is commonly observed, the observed animal is the only one attempting to exploit the resource that occurs at different rates in different places. This state of affairs is unlikely to persist for long under natural circumstances. Wherever there is food, other animals will gather. The more of them there are, the smaller is each one's share. The strategy of always choosing to forage in the area where previous experience suggests that food is to be found in greatest abundance is not evolutionarily stable. If such a pattern became the rule among animals, natural selection would favor those exceptional animals that went to the areas where food was less abundant but so were the competitors. It may be shown that under plausible assumptions, a strategy for choosing among patches of differing abundance that does not create a countervailing selection pressure is the strategy of matching the relative frequency of one's choices to the relative abundances in the options (Fretwell, 1972; Fretwell & Lucas, 1970).

The conditions under which animals might be expected to be selected on the basis of their ability to distribute their choices among options in accord with relative food densities are ones in which each animal has an approximately correct representation of the rate of food occurrence in each patch and is free to move from patch to patch. The distribution expected under these assumptions is called the ideal free distribution, because the animal's knowledge of the food densities is assumed to be "ideal" (that is, generally correct), and the animal is assumed to be free to go to any patch whenever it chooses.

Since the ideal free distribution was first derived, there have been many experimental demonstrations that animal foraging behavior in fact conforms to this distribution. For example, Godin and Keenleyside (1984) arranged for salmon eggs to drop into the two ends of a fish tank at different rates, ranging

from 10 per minute at one end to as few as 2 per minute at the other, and they recorded by means of a television camera how schools of six fish distributed themselves between the two ends. Within 30 seconds of the onset of the differential rate of provisioning, the fish distributed themselves between the two ends in approximate accord with the provisioning ratio: the end provisioned at twice the rate had twice as many fish swimming around snapping up the eggs. This apportionment was the result of individual choices, not competition. Each fish spent some time at both ends, but because each fish spent more time at the richer end, there were, on average, more fish at that end. When the "probability matching" experiment is run under these group conditions, what appeared to be irrational individual behavior suddenly appears rational, because it is obvious that it would be best to be at the poorer end if everyone else were at the richer end.

Harper (1982) did a similar experiment with a flock of ducks overwintering on a pond. Each day for several successive days, two experimenters, each carrying a sack of precut 2-gram bread morsels, positioned themselves about 20 meters apart along the lake shore and began throwing the bread out one morsel at a time at regular intervals. The relative rates at which they threw were systematically varied. On trials where the rates were not equal, the experimenter who threw at the higher rate was chosen randomly and could not be predicted from trial to trial. From the outset of the experimental trials, the ducks very rapidly distributed themselves in front of the two experimenters in proportion to the relative rates of throwing. A distribution proportionate to the rates of throwing was achieved in just a little over 1 minute, during which time only 12 to 18 pieces of bread were thrown by the two experimenters combined. As with the fish, the apportionment of the ducks was achieved before most ducks had obtained a single morsel and before any duck had obtained morsels from both patches.

The sophistication of the computations that animals make in the process of determining their relative tendency to switch from one patch to another is shown by the final experiment in the Harper (1982) series. In some trials of this final experiment, the food was thrown at the same frequency into both patches, but the morsels being thrown by one experimenter were twice as big. On these trials, the ducks initially distributed themselves in accord with the relative rates at which morsels were being thrown (that is, fifty-fifty), but discovered within the first 5 or 6 minutes that the morsels were larger in the one patch and adjusted their individual choice likelihoods accordingly. The distribution after 5 minutes accurately reflected the ratio of the net rates of provisioning, that is, the ratio between the products of morsel magnitude and morsel rate. This result suggests that birds accurately represent rates, that they accurately represent morsel magnitudes, and that they can multiply the representation of morsels per unit time by the representation of morsel

magnitude to compute the internal variables that determine the relative likelihood of their choosing one foraging patch over the other.

Attempts to model the rate matching behavior associatively have not been successful (Lea & Dow, 1984). Gallistel (1989; Gallistel, 1990, chap. 11) has argued that the ability to match the allocation of foraging time to the relative abundances of locations depends on a representation of the rate of food occurrence derived from two more primitive representations, a representation of the temporal interval over which a location has been sampled and a representation of the total number of occurrences during that interval. He reviews the extensive literature showing that the common laboratory animals do represent numerosity and temporal intervals and that they can perform the common arithmetic operations on their representatives of these quantities. He has argued that these abilities depend in substantial measure on innately specified computational machinery specifically dedicated to particular representational tasks—in other words, on what Marler has called “instincts to learn.”

Bird Song

Of the 8,600 known species of birds extant today, less than half are songbirds (Burton, 1985). These include the sparrows, wrens, finches, canaries, cardinals, mockingbirds, nightingales, thrashers, warblers, and many others. The mechanisms that ensure successful learning of a bird's conspecific song differ from species to species, in ways that can be understood in terms of differences in the nature and function of song. The evolutionary history of song-learning mechanisms cannot be characterized in terms of a general association-plus-constraint model. Rather, songbird learning mechanisms are specific adaptations, designed to operate in environmentally specific contexts to ensure gaining of adaptive information. Innately determined representations guide selection of what is to be learned, how that which is attended to is used in constructing a song, and how learning to interpret informative features of a conspecific song proceeds. Textbooks in associative learning acknowledge this nonassociative characterization of bird-song learning and treat it as a special case or exception to the view that learning can be described with the general laws of association. We do not see the learning of bird song as an exception to an account of learning; rather, it stands as another example of the more general truth that learning is domain-specific.

Within many species of songbirds, spectrographic recordings reveal systematic differences among the songs produced in different geographical regions. The dialects revealed by spectrographic recording are behaviorally relevant. For example, male sparrows establish and defend territories. If one maps a male's territory and places a speaker well within it, one can play field-

recorded conspecific song, synthetic song, and other species' song over the speaker. Males will approach and threaten the speaker when conspecific song is played. The dialects of chaff-chaffs can differ one from another so much that one from Germany, for example, does not recognize the song of a conspecific from Spain or Portugal (Burton, 1985). This fact alone establishes that songs must be learned—birds of the same species end up singing different songs, namely, those characteristic of the dialect they are exposed to. But there are also many types of direct evidence for the learning of song.

Marler (this volume) reviews his extensive experiments on the learning of song in white-crowned sparrows and other songbirds, emphasizing the contribution of innate learning mechanisms (instincts to learn). Here, we only emphasize the salient lessons to be drawn from this literature:

1. The mechanisms by which different species learn their song differ from species to species, even for closely related species.
2. The learning of song is usually the elaboration through experience of an innately given but incomplete representation of what is to be learned.

Within-Species Differences. There are several dimensions on which song-learning mechanisms differ, including whether there is a critical period and/or a process of crystallization, the method by which models are identified, and the need for models, and the extent to which the singer imitates or improvises. Many songbirds are like white-crowned sparrows (e.g., song sparrows, swamp sparrows, zebra finches), having sensitive periods in the first year of their life, a gap between the end of the sensitive period and the beginning of subsong, and crystallization at the end of the first year, after which no further learning occurs. At the other extreme are birds with larger song repertoires, who continue learning throughout their lives (e.g., canaries and mockingbirds). In the case of canaries, not only does crystallization fail to occur; but deafening at any time disrupts singing of the known repertoire, as well as the learning of new song.

Between the extremes of the sparrows and the canaries lie many other ways in which the temporal restrictions on learning may vary. To give one further example, in some cases in which crystallization occurs, improvisation plays a major role in determining song, resulting in highly distinctive songs from individual to individual. In some such cases, the sensitive period overlaps with the beginning of subsong. This allows the animal's own vocalizations to affect the template, yielding a progressively more complex product that goes beyond the model. Cardinals fit this pattern. Because cardinals recognize individuals by their song, a learning mechanism that ensures distinctive song is adaptive. In the cardinal's case, this is achieved

through overlapping temporal stages of song development often kept separate in other species of songbirds.

There are two broad classes of mechanisms for the selection of songs to learn: those that make use of acoustic properties of the songs the bird is exposed to and those that make use of information about who is doing the singing. Many birds, like the white-crowned sparrow, select song purely on the basis of acoustic parameters. Social factors seem to play no role whatsoever, as demonstrated by the finding that social isolates tutored with tapes learn entirely normal song. Other birds, to varying degrees, select song on the basis of social factors. For nightingales, imitation depends upon visual contact with the tutor, and the filial bond, specifically, is important to several finches. Male zebra finches, when raised in nests of bengalese finches, learn the bengalese finch song, even when male zebra finch song is within earshot. In many cases, selection mechanisms that incorporate both acoustic and social factors are in place. For example, whereas the socially reared zebra finch will learn the song of his bengalese foster father, if he is raised in isolation and tutored with tapes of zebra and bengalese finches, he learns zebra finch song. The bullfinch also selects song partly on the basis of social cues. Female, as well as male, bullfinches sing, but young males learn only the song of the male who raises them. Under laboratory conditions, bullfinches can be induced to sing an enormous variety of natural and synthetic songs, even nonsongbird sounds (Thorpe, 1963).

Songbirds differ with respect to the necessity of a model for the development of normal song and also with respect to the use to which models are put. Very rarely, normal song is developed in complete absence of a model. Black birds recombine elements to form new song patterns even if raised in social and acoustical isolation—indeed, even if deafened. Cardinals acquire some normal syllables and some properties of normal song when raised in isolation, but they require models to develop song fully. At the other extreme are some sparrows, who need models to acquire even minimally normal song.

In some cases, models are faithfully imitated, whereas at the other extreme, models provide only the most generalized stimulus necessary for improvisation. White-crowned sparrows fall in the former category; juncos in the latter. For juncos, even the immature songs of other juncos sustain normal learning. Improvisation takes several forms. In some cases, syllables are faithfully copied and then recombined into novel song. In other cases, syllables themselves are gradually modified as the song is elaborated. The notorious mimic, the mockingbird, combines both processes. Syllables are copied from songs of other species, sometimes modified and sometimes not, and then incorporated into a specific temporal pattern.

In short, there is no single process sustaining the learning of bird song in different species; rather, just as the song of each songbird is unique, the

process that supports its development is also unique. The differences are not merely minor variations on a common theme. Rather, the differences are profound and can be understood in terms of the different requirements for flexibility of various types placed on the song of different species by the song's role in mate selection, territory defense, and so forth. Cataloging the differences among song learning mechanisms is crucial for understanding the evolution and function of bird song. Further, understanding the unique properties of each learning process is necessary for progress in explaining learning.

The Complex Roles of Innate Representations. Our explanation of learning proceeds at two levels: representational and neurological. A full representational characterization of mechanism details the representations that guide selection of models, characterizes what is represented from the original model, characterizes the representations that guide improvisation and phrase construction, and characterizes the bird's final representation of conspecific song that supports song recognition as well as song production. A full neurological characterization of mechanism provides the neural substrate for all of this. Bottjer and Arnold (1986) provided an excellent review of recent progress in the discovery of the neural substrate of song production and song learning. Particularly interesting is evidence for a neural center in the zebra finch that is crucially involved only during learning. Lesions in this area during subsong or plastic song disrupt song crystallization, but lesions after crystallization do not affect normal singing.

When infant songbirds select conspecific models from acoustical properties, they must do so on the basis of an innately specified representation of conspecific song. That representation must be incomplete, for if they had a complete representation of conspecific song, they would hardly need a model, and dialect acquisition would be impossible. Also, in the course of learning, their representation of song must be enriched, for we know that a song that would support learning (e.g., any dialect of conspecific song) will not necessarily be recognized as conspecific after the bird has learned a particular dialect. This much follows logically from the characterization of song learning mechanisms already presented. Marler and Peters' (1977, 1981) work on the representations guiding learning of swamp sparrow and white crowned sparrow song fills in the details in these two cases and adds one additional generalization: Some aspects of song that are innately specified are not used in the initial selection of song, but come into play later as the bird puts together what he has represented from the models into his own crystallized song.

The case of bird-song learning is complex. It highlights the role of representations in selective attention and learning. It also serves as a challenge to a general process learning theory. Different species rely on

different mechanisms of learning. Indeed, species that are very similar genetically may learn in different ways. A consideration of the problems that different birds have to solve helps explain why one learning path is chosen over another.

It is not that there is nothing in common about the way birds learn their songs: The vast majority are born with some attentional predispositions that focus learning on songs and not other materials. The work of Marler and his colleagues serves as a model for a research program that would allow us to characterize the nature of the representations that would determine attention to start as well as the nature these templates come to have as a consequence of learning opportunities. Marler and his colleagues have also begun to apply the same program of research to another case where initial representations guide learning—the case of how vervet monkeys recognize predators.

Predator Recognition in Vervet Monkeys

Vervet monkeys give different alarm calls to three different kinds of predators: pythons, martial eagles, and leopards (Seyfarth, Cheney, & Marler, 1980; Struhsaker, 1967). Each call evokes a different behavior pattern. Snake calls lead the monkeys to look down at the ground; leopard calls lead them to run up into trees if on the ground or stay in the trees if already there; and eagle calls cause them to run into the bushes and/or look up. These reactions are evoked whether the calls are produced by a vervet or by playback of recorded calls through a hidden speaker (Seyfarth et al., 1980). The ability to respond selectively to these calls reflects learning guided by an innate tendency to represent some but not all of the characteristics of the class of stimuli involved, a conclusion arrived at by considering how infant vervet monkeys react to the stimuli that elicit these calls.

Although the infants give the respective calls to broader classes of objects than do adults, they do not respond randomly. Leopard calls are given to terrestrial animals and not to snakes or birds; eagle calls are given to birds and not to snakes or land animals; and snake calls are given to snakes or long thin things. With development, the monkeys learn to restrict their calls to just those subclasses of these broader class of stimuli that their parents respond to. Seyfarth et al. (1980) suggested that the infants' response to "bird" is to things that move overhead in the sky; their response to "animals," things that walk; and their response to "snakes," things that are thin and move along the ground. Such general characteristics guarantee that the infants will attend to and respond correctly to each set of stimuli that have these properties. The task of learning is to shape them to respond to only those which are relevant in their environment. Presumably, more detailed representations of the relevant objects are developed to capture critical features of local predators.

Evidence regarding the exact nature of the representations is not available yet, but it would be surprising if the pattern of movement and shape were not crucial features captured in the initial representation. Indeed, it is hard to account for the results if this is not the case.

The Representations of Spatial Position

One of the most basic things to be learned by a mobile organism is where it is and which way it is headed, so that it may orient toward and return to the special places in its environment, such as food sources and its nest or resting place. A number of special learning mechanisms have evolved under the selection pressure exerted by this fundamental requirement for positional and directional knowledge.

Dead Reckoning. One such mechanism is that by which the animal keeps track of its position as it moves. The foraging ant follows a tortuous course as it ranges farther and farther from the nest entrance in search of food to bring back, but when it finds something, it turns to orient to within a degree or two of its nest entrance and runs in a fairly straight line back toward the entrance (Harkness & Maroudas, 1985), stopping to search for the entrance when it has gone approximately the right distance (Wehner & Srinivasan, 1981). Thus, the foraging ant knows the approximate direction and distance of the nest entrance at every moment. Its homeward run is governed by this acquired knowledge, not by any odor trail it has laid down on the way out, nor by the sight, sound, or smell of the nest entrance. This can be shown by picking up a large fast-moving desert ant, *Cataglyphis bicolor*, as it starts its homeward run and displacing it into unfamiliar territory (Wehner & Srinivasan, 1981). The ant runs across the flat featureless desert floor in the direction in which the nest would have been had the ant not been displaced and breaks off its run to search for the nest when it is within a meter or two of where the nest should be.

The search pattern is even more tortuous than the pattern pursued during foraging, involving innumerable ever widening loops, but it has the property that the ant returns again and again to the place where it initially estimated the nest to be, much as we do when searching for our misplaced eyeglasses, for example. Thus, the ant keeps track of where it is relative to the start of its search. It does so entirely by dead reckoning, as may be shown by displacing it in mid search. Displacing the ant in midsearch displaces the center of its search pattern, that is, the point to which it loops back time and again.

Dead reckoning is a nautical corruption of the "deduced reckoning" of the ship's position that the navigator makes at regular intervals by decomposing the ship's movement into its north-south (latitudinal) and east-west (longitu-

dinal) components to get its velocity vector, then multiplying its north-south speed and its east-west speed by the amount of time it has been holding that course and speed. The result is the ship's change in latitude and longitude. By plotting this change from the ship's position at the last reckoning, the navigator gets the dead reckoning estimate of its current position. When this computation of the ship's new position is made at shorter and shorter intervals, it approaches in the limit the operation of integrating the ship's velocity with respect to time. In fact, on large modern ships, there is a small computer that does this integration, taking the speed from the rate at which the ship's screw is turning and the requisite directional information from the ship's compass, and plotting the ship's position continuously on a nautical chart. A similar dead reckoning mechanism operates in the systems just now becoming commercially available that show the moment-to-moment position and heading of one's car on a road map scrolling across a video monitor.

Here we have a spectacular example of a dedicated specialized learning mechanism that makes possible the moment-to-moment acquisition of positional information. People's reaction to the claim that this is a learning mechanism is also revelatory of the (we believe erroneous) conceptual framework within which most of us think about learning. Students readily agree that learning is the acquisition of knowledge. When confronted with the experimental evidence, they agree that the foraging ant knows where it is at every moment. From the experimental evidence, they also agree that the ant acquires this knowledge of its position by integrating its velocity over time, but when one then draws the conclusion to the syllogism, namely, that in this case the learning mechanism is the mechanism that integrates velocity with respect to time, they balk. Somehow, this "just isn't learning." In that case, they confront the paradox of an instance of knowledge acquisition that does not involve learning. We believe the way out of this paradox is to recognize that learning is, generally speaking, the acquisition of particular kinds of knowledge through the operation of specialized computational mechanisms dedicated to the acquisition of particular kinds of representations—in this case, a representation of the animal's momentary spatial position.

Learning the Ephemeris. The ephemeris is the position of an astronomical body as a function of the date and time. Knowledge of the azimuthal component of the sun's ephemeris (the point on the horizon directly under the sun) is crucial to any animal that orients by reference to it, as do many (perhaps all?) birds, insects, mammals, and so on. Animals must acquire their knowledge of the sun's ephemeris, because it changes from season to season, and place to place. For a honey bee north of the tropics, the sun moves clockwise along the horizon; for a honey bee south of the tropics, it moves

counterclockwise along the horizon, and for a honey bee in the tropics, it moves clockwise part of the year and counterclockwise the other part. The sun's azimuth changes more rapidly at midday than in the morning or evening, but how much more rapidly varies markedly depending on the season and one's latitude. In short, an animal cannot be born with a knowledge of the sun's azimuthal ephemeris; it must acquire this knowledge.

There is another reason why the knowledge of the sun's ephemeris must be acquired: The ephemeris function is a specification of the sun's azimuthal position with respect to the time of day and the azimuthal position is itself defined with respect to the local terrain, which provides the landmarks that make it possible to track the changing position of the sun. On cloudy days, when the sun is hidden from view, foraging bees orient with respect to these landmarks, but when they dance to indicate the direction of a food source to fellow foragers back in the hive, they orient their dance with respect to the invisible sun, estimating its position relative to the terrain around the hive from the time on their internal clock and their knowledge of the sun's ephemeris (Dyer & Gould, 1983). Thus, their cognitive map of the terrain over which they forage, which must, of course, be acquired, makes it possible to define the position of the sun. Thus, the specification of the sun's ephemeris depends on a map of the terrain around the hive, which must itself be acquired.

There is every reason to think that the learning of the sun's azimuthal ephemeris is based on a special-purpose learning mechanism, without which animals would be incapable of sun-compass navigation (see Gould, 1984, for an experimental study of this learning mechanism in the honey bee).

The Cognitive Map. A map is a representation of the relative positions of points, lines, and surfaces. It makes it possible to direct one's movements toward a point one cannot or does not currently perceive by reference to points one does perceive. Gallistel (1990) has reviewed a large body of experimental and observational literature demonstrating the ubiquitous tendency of animals of all kinds to orient toward goals by reference not to the goals themselves but rather to the global configuration of the terrain—that is, the macroscopic shape of their environment. One recent demonstration of this in the rat comes from experiments with a water maze (Morris, 1981). The rats were dropped into a pool of opaque water and had to find a barely submerged brick on which they could perch. Once they had found it, they could make directly for it from any point in the pool, whether its location was marked by a local cue (a flag on the brick) or not. In other words, they could readily find the brick by reference to the framework established by the experimental room. This ubiquitous tendency to find a goal by reference to the surrounding environment implies an equally ubiquitous use of cognitive

maps, because this kind of orientation is only possible when the animal has a map that gives the position of its goal within the framework established by the macroscopic shape of its environment.

Gallistel (1990) has given a computational model of the process by which an animal builds its cognitive map. It uses a variety of sophisticated sensory-perceptual processes to determine the direction and distance of points, lines, and surfaces from its current vantage point, thereby building up an egocentric spatial representation of the terrain surrounding a vantage point. It integrates this vantage-point-specific egocentric representation with the geocentric representation of its current position and heading supplied by the dead reckoning mechanism to generate a geocentric representation of the relative positions of environmental features that have been perceived at different times and from different vantage points. Again, we see that a special-purpose computational mechanism makes possible the learning of a particular kind of representation—in this case, a representation of the macroscopic shape of the environment.

Cheng (1986) and Margules and Gallistel (1988) have shown that, in the rat at least, the process of getting oriented within the environment relies almost exclusively on this representation of its macroscopic shape, ignoring to an astonishing degree other relevant positional information, such as the position of distinctively painted walls or the position of the sources of distinctive odors. When the rat has to find buried food in a rectangular environment, it gets misoriented by 180° on half the trials, just as one often gets misoriented with respect to the street plan of grid cities when emerging from a subway stop or a movie theater. The rat digs at the rotational equivalent of the correct location, the place where the food would be if the floor of the rectangle were rotated 180° with respect to the walls. The surprising finding is that polarizing the rectangular environment with various highly salient stimuli—one white wall in an otherwise black enclosure or distinctively patterned and distinctly smelling panels in the corners—does not improve the rat's performance. In getting oriented within the environment, the rat ignores these stimuli, which do not contribute to the definition of the shape of the environment, even though it uses these distinctive stimulus contrasts under other conditions.

For the rat, and perhaps for most other animals as well, place as well as direction is defined by reference to the macroscopic shape of the environment rather than by reference to other localized distinctive attributes. Cheng (1986) contrasted the performance of rats required to dig for food located at any one of 80 positions within a rectangular enclosure with the performance of rats required to dig for food located in front of a corner panel of distinctive appearance and odor, which changed its position in the enclosure between the time when the rat was shown the location of the food and the time when the rat had to dig for it. In the first group, the rats were shown the location

of the food at the beginning of a trial, removed from the environment for a little more than a minute and then required to locate and dig out the food they had been shown. In the second group, the rats were shown the food buried in front of one of the four distinctive panels in the four corners of the enclosure, removed for a little more than a minute while the panels and the buried bait were shifted around one corner, and then returned to the enclosure to dig for the food, which they could get by digging in front of the correct panel, now located in a new position in the rectangular enclosure. The rats in the first group, which could rely on the location of the food relative to the rectangular shape of the enclosure, dug at the correct location and its rotational equivalent on substantially more than 50% of the trials, even though the location of the food varied from trial to trial among 80 different locations. By contrast, the rats in the second group, which had to locate the food by reference to the panel in front of which it was buried, rather than by reference to the food's position in the enclosure, never dug in front of the correct panel at greater than the chance level. The chance level was 25%, because the food was always in a corner, and the rats rapidly learned to dig for it only in the corners—that is, they rapidly learned the location of the possible burial sites relative to the shape of the enclosure, but they never learned to locate the food relative to the distinctive features of the panel in front of which it was buried.

Here, as in the other examples we have surveyed, we see the animal relying on a particular kind of representation extracted from its experience through the operation of problem-specific computational mechanisms that make a particular form of learning possible while at the same time constraining what is learned and what can be done with it.

SUMMARY AND CONCLUSIONS

Within each functionally defined domain of animal endeavor, there can be dramatic differences in the need for flexibility and, thus, in the need for learning. There must always be a strong learning component in any mobile organism's ability to develop a representation of the spatial location of objects in the world, insofar as it is extremely implausible that that information is prewired. In other domains, however, such as the identification of food or the recognition of conspecifics, species differ as to how much demand on learning their solution to the problem requires. These differences are reflected in the existence and the complexity of specific learning mechanisms.

The major source of evidence for domain specific learning mechanisms is selectivity, or what we have called in this chapter "privilege." We have repeatedly seen examples of privileged learning—as in Garcia's demonstrations of privileged pairing of noise and shock, on the one hand, and taste

and nausea, on the other; in Marler's and his colleagues' demonstrations of the basis of song selection; and in Cheng's and Margules' and Gallistel's demonstrations of the rat's nearly exclusive reliance on geometric information to specify orientation and spatial position.

Besides providing evidence for domain-specific learning devices, selectivity in learning provides the beginning point for characterizing those mechanisms. Sometimes, different cases of learning within an animal, or different cases of learning across different species of animals, can be abstractly characterized in terms of a common model, the differences captured in terms of different parameter settings. Examples in this chapter are the diverse applications of the Rescorla-Wagner learning model and, to some extent, the differences in bird-song learning mechanisms. Parameter setting may vary across species (as in bird song) or across domains within species (as in the different applications of the Rescorla-Wagner law).

In this chapter we have concentrated on learning mechanisms with a clear representational component. This is because of the problems that we chose to analyze—the recognition of danger in vervet monkeys, the recognition of conspecifics in birds, the recognition of food (and nonfood), the representation of space, and so on. These choices were hardly arbitrary, for they seem to be among the best animal cases to analyze with the analogy to human cognition in mind. We concluded that within the same domain (e.g., recognition of conspecifics by songbirds) different species may have different learning mechanisms. In such cases, the learning mechanisms may be part of a family that shares an abstractly characterizable structure. Within that structure, though, each species differs in terms of the specific representations that are built, in the limits on the elaboration of those representations, the nature and time course of the elaboration process, and so on.

We may abstract a research strategy from the work we have sketched in this chapter. The search for domain-specific learning mechanisms proceeds in three steps. First, a candidate domain must be identified. In all of the cases we have described here, the candidate domains are defined functionally. A problem that a given animal (or all animals) must solve in order to survive is identified—the animal must be able to recognize danger, recognize food, choose where and when to forage, recognize conspecifics in order to mate and defend territory, represent the location of itself and other objects in a spatial framework, and so on. Any such candidate domain must then be analyzed: Is there a computational account of the optimal solution to that problem, can one characterize the representations uniquely relevant to that problem, and so on? Finally, can one find evidence that animals have evolved learning devices that accomplish the optimal strategies, or exploit the relevant representations? This evidence will be of several sorts—such as successful explanation of particular parameters of general laws, the violation of general laws of learning altogether, the evidence that different animals solve the same

problem differently, privileged pairings of stimuli or of stimuli and responses, domain-specific critical periods, and physiological or anatomical evidence of specialized neural support for learning in the relevant domain.

Domain General Learning Devices

Although we have concentrated on domain-specific constraints, we do not want to seem to be denying the existence of nor the importance of domain-general constraints on learning. Some general properties of learning cut across learning within specific functional domains in two different ways. First, there may well be some general laws of learning, such as the Rescorla-Wagner law describing the increment in associative strength as a function of repeated trials of classical conditioning, that apply across a wide variety of functionally defined domains and across a wide variety of animal species. Such laws may be analogous to the psychophysical laws (Weber's, Fechner's, and Tversky's). Second, some functionally defined specific domains are used in other such domains. Thus, the food foraging models and ephemeris learning models and many, many other models require spatial representations. Keeping a constantly updated representation of where one is is crucial for success at many life maintaining tasks. The device that represents space, and that learns where things are, is thus more generally applied than the device that sets foraging policy. This latter sense of generality poses no unique problems of analysis—while the learning and utilization of spatial relations may play a role in many different kinds of learning, the learning of spatial layouts and the locations of particular objects within them remains a paradigmatic example of domain-specific learning.

It is the first kind of domain-general laws or principles that require further comment. In each case of a domain-general principle, we would want to know the answer to two questions. First, is there a separate learning device whose domain is learning of that sort—in the case of the Rescorla-Wagner law, is there a classical conditioning organ? Alternatively, the general law may reflect some property that is common to many domain-specific learning devices. Second, we would want to know the source of the domain general principle or law. Does it reflect some computational or representational property of successful learning that has been repeatedly and independently selected for? Alternatively, is it a by-product (even an accidental by-product) of the nature of the nervous system? Common laws of learning may bespeak evolutionary continuity in properties of the nervous system, just as common properties of animal cells reflect evolutionary continuity in the animal kingdom.

The distinction between domain-specific and domain-general learning devices is one of degree and, to some extent, one of emphasis. When

discussing bird-song learning, for example, we alternately stressed the uniqueness of each bird-song learning device and the communalities among song-learning mechanisms that allow us to see each unique song-learning device as defined by parameter values on the several dimensions that differentiate one learning strategy from another. Thus, the same two questions arise in the case of domain-specific learning devices. In most cases of domain-specific principles of learning, we would expect these principles to reflect the properties of specialized devices evolved to carry out the computations in the relevant domain. Sometimes, as in the case of song learning, there may even be neural specialization for a learning device itself (Bottjer & Arnold, 1986). The explanation for the commonality among bird-song learning devices is very likely common evolutionary origin—presumably, all songbirds evolved from birds whose singing did not require learning, whose innate representation of song allowed both the recognition and production of species-specific song, and who began to sing at the end of the first year of their life. As we argued earlier, the explanation for commonality among food foraging strategies is likely to be entirely different. Selection pressure would be expected to make each species independently converge on optimized foraging patterns. Similarly, insofar as different animals have evolved common solutions to the problem of the representation of space, these common solutions most probably reflect the computational nature of the problem being solved.

In this chapter, we have not attempted to review all known domain-specific learning devices, nor have we attempted to begin to review all the candidates for domain-general learning principles. Rather, we have tried to show how the marriage between the ethological approach to learning and standard learning theory has led to a search for domain-specific principles of learning. All of this has implications for how we will approach issues in human cognitive development. We will attempt to carry out the research program outlined earlier—identify and analyze candidate functional domains and review the evidence for (and against) specialized learning mechanisms in these candidate domains: human language, intuitive physics, intuitive psychology, and number. We will consider the nature of domain-general learning devices in humans, and we will consider whether humans go beyond the initial principles that guide their learning in any given domain.

REFERENCES

- Atkinson, R. C., Bower, G. H., & Crothers, E. J. (1966). *An introduction to mathematical learning theory*. New York, NY: John Wiley and Sons.
- Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, 77, 32-48.

- Bottjer, S. W., & Arnold, A. P. (1986). The ontogeny of vocal learning in songbirds. *Developmental psychobiology and developmental neurobiology* (pp. 29-161). New York: Plenum Press.
- Burton, R. (1985). *Bird behavior*. New York: Alfred A. Knopf.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, 23, 149-178.
- Dyer, F. C., & Gould, J. L. (1983). Honey bee navigation. *American Scientist*, 71, 587-597.
- Elner, R. W., & Hughes, R. N. (1978). Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology*, 47, 103-116.
- Emlen, S. T. (1967). Migratory orientation in the indigo bunting, *Passerina cyanea*. Part I. Evidence for use of celestial cues. *Auk*, 84, 309-342.
- Emlen, S. T. (1969a). Bird migration: Influence of physiological state upon celestial orientation. *Science*, 165, 716-718.
- Emlen, S. T. (1969b). The development of migratory orientation in young indigo buntings. *Living Bird*, 8, 113-126.
- Emlen, S. T. (1972). The ontogenetic development of orientation capabilities. In *Symposium of animal orientation: NASA special publications SP-262* (pp. 191-210). Washington, DC: National Aeronautics and Space Administration.
- Fretwell, S. D. (1972). *Populations in seasonal environments*. Princeton, NJ: Princeton University Press.
- Fretwell, S. D., & Lucas, H. L. J. (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, 19, 16-36.
- Galef, B. G., McQuoid, L. M., & Whiskin, E. E. (1990). Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. *Animal Learning and Behavior*, 18(2), 199-205.
- Galef, B. G. J. (1987). Social influences on the identification of toxic foods by Norway rats. *Animal Learning and Behavior*, 15(3), 327-332.
- Gallistel, C. R. (1980). *The organization of action: A new synthesis*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Gallistel, C. R. (1989). Animal cognition: The representation of space, time and number. *Annual Review of Psychology*, 40, 155-189.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Garcia, J. (1981). The nature of learning explanations. *The Behavioral and Brain Sciences*, 4, 143-144.
- Garcia, J., & Koelling, R. A. (1966). The relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123-124.
- Godin, J.-G. J., & Keenleyside, M. H. A. (1984). Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): A test of the ideal free distribution theory. *Animal Behaviour*, 32, 120-131.
- Gould, J. L. (1984). Processing of sun-azimuth information by bees. *Animal Behaviour*, 32, 149-152.
- Graf, V., Bullock, D. H., & Bitterman, M. E. (1964). Further experiments on probability matching in the pigeon. *Journal of the Experimental Analysis of Behavior*, 7, 151-157.
- Harkness, R. D., & Maroudas, N. G. (1985). Central place foraging by an ant (*Cataglyphis bicolor* Fab.): A model of searching. *Animal Behaviour*, 33, 916-928.
- Harper, D. G. C. (1982). Competitive foraging in mallards: Ideal free ducks. *Animal Behaviour*, 30, 575-584.
- Heinrich, B. (1979). Majoring and minoring by foraging bumblebees. *Bombus vagans*: An experimental analysis. *Ecology*, 60, 245-255.
- Herrnstein, R. J. (1961). Relative and absolute strength of response as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behavior*, 4, 267-272.

- Herrnstein, R. J., & Loveland, D. H. (1975). Maximizing and matching on concurrent ratio schedules. *Journal of the Experimental Analysis of Behavior*, 24, 107-116.
- Hinde, R. A., & Hinde, J. S. (1973). *Constraints on learning*. New York: Academic Press.
- Hineline, P. N., & Rachlin, H. (1969). Escape and avoidance of shock by pigeons pecking a key. *Journal of the Experimental Analysis of Behavior*, 12, 533-538.
- Kamin, L. J. (1969). Predictability, surprise, attention, and conditioning. In B. A. Campbell, & R. M. Church (Eds.), *Punishment and aversive behavior* (pp. 276-296). New York: Appleton-Century-Crofts.
- Knudsen, E. (1983). Early auditory experience aligns the auditory map of space in the optic tectum of the barn owl. *Science*, 222, 939-942.
- Knudsen, E. I., & Knudsen, P. F. (1990). Sensitive and critical periods for visual calibration of sound localization by barn owls. *Journal of Neuroscience*, 10(1), 222-232.
- Krebs, J. R., & Davis, N. B. (Eds.). (1984). *Behavioral ecology* (2nd ed.). Oxford, England: Blackwell Scientific Publications.
- Lea, S. E. G. (1981). Correlation and contiguity in foraging behavior. In P. Harzem & M. D. Zeiler (Eds.), *Advances in analysis of behavior: Vol. 2: Predictability, correlation, and contiguity* (pp. 344-406). New York: John Wiley.
- Lea, S. E. G., & Dow, S. M. (1984). The integration of reinforcements over time. In J. Gibbon & L. Allan (Eds.), *Timing and time perception* (pp. 269-277). New York: Annals of the New York Academy of Sciences.
- Lolordo, V. M., Jacobs, W. J., & Force, D. D. (1982). Failure to block control by a relevant stimulus. *Animal Learning and Behavior*, 10, 183-193.
- MacArthur, R. H., & Pianka, E. R. (1966). On the optimal use of a patchy environment. *American Naturalist*, 100, 603-609.
- Mackintosh, N. J. (1974). *The psychology of animal learning*. New York: Academic Press.
- Malone, J. C., Jr. (1981). A fourth approach to the study of learning: Are "processes" really necessary? *The Behavioral and Brain Sciences*, 4, 151-152.
- Margules, J., & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning and Behavior*, 16, 404-410.
- Marler, P., & Peters, S. (1977). Selective vocal learning in a sparrow. *Science*, 198, 519-521.
- Marler, P., & Peters, S. (1981). Sparrows learn adult song and more from memory. *Science*, 213, 780-782.
- Martin, D. D., & Meier, A. H. (1973). Temporal synergism of corticosterone and prolactin in regulating orientation in the migratory white-throated sparrow (*Zonotrichia albicollis*). *Condor*, 75, 369-374.
- Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation*, 12, 239-260.
- Petrinovich, L. (1981). A functional view of learning. *The Behavioral and Brain Sciences*, 4, 153-154.
- Pyke, G. H., Puliam, H. R., & Charnov, E. L. (1977). Optimal foraging: A selective review of theories and facts. *Quarterly Review of Biology*, 52, 137-154.
- Rescorla, R. A. (1968). Probability of shock in the presence and absence of CS in fear conditioning. *Journal of Comparative and Physiological Psychology*, 66(1), 1-5.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II* (pp. 64-99). New York: Appleton-Century-Crofts.
- Revusky, S., & Garcia, J. (1970). Learned associations over long delays. In G. H. Bower & J. T. Spence (Eds.), *The psychology of learning and motivation* (pp. 189). New York: Academic.
- Rozin, P., & Kalat, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Review*, 78, 459-486.

- Rozin, P., & Schull, J. (1988). The adaptive-evolutionary point of view in experimental psychology. In R. Atkinson, R. J. Herrnstein, G. Lindzey, R. D. Luce, & J. Wiley (Eds.), *Stevens' handbook of experimental psychology. Vol. 1: Perception and motivation* (pp. 503-546). New York: John Wiley & Sons.
- Schoener. (1971). Theory of feeding strategies. *Annual review of ecology and systematics*, 2, 369-404.
- Schwartz, B. (1981). The ecology of learning: The right answer to the wrong question. *The Behavioral and Brain Sciences*, 4, 159-160.
- Seligman, M. E. P., & Hager, J. L. (1972). *Biological boundaries of learning*. New York: Appleton-Century-Crofts.
- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, 210(14), 801-803.
- Shettleworth, S. J. (1975). Reinforcement and the organization of behavior in golden hamsters: Hunger, environment, and food reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, 1, 56-87.
- Shettleworth, S. J. (1981). An ecological theory of learning: Good goal, poor strategy. *The Behavioral and Brain Sciences*, 4, 159-160.
- Smith, J. N. M., & Dawkins, R. (1971). The hunting behavior of individual great tits in relation to spatial variations in their food density. *Animal Behavior*, 19, 695-706.
- Struhsaker, T. (1967). Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In S. Altmann (Ed.), *Social communication among primates*. Chicago: University of Chicago Press.
- Thorpe, W. H. (1963). *Learning and instinct in animals* (2nd ed.). London: Methuen.
- Tinbergen, N. (1951). *The study of instinct*. Oxford: Clarendon Press.
- Wagner, A. R., Logan, F. A., Haberlandt, K., & Price, T. (1968). Stimulus selection in animal discrimination learning. *Journal of Experimental Psychology*, 76(2), 171-180.
- Wehner, R., & Srinivasan, M. V. (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of Comparative Physiology*, 142, 315-338.