

The Vienna Series in Theoretical Biology

Cognitive Evolution: A Psychological Perspective  
M.E. Bitterman

---

# The Evolution of Cognition

---

edited by  
Cecilia Heyes and  
Ludwig Huber

The MIT Press, Cambridge, Massachusetts, 2000

## 4 Cognitive Evolution: A Psychological Perspective

M. E. Bitterman

In this initial staking out of positions with respect to the evolution of cognition (which I interpret as "knowing" in the classical sense of the term, encompassing perception, learning, and understanding), my task is to represent the psychological tradition rooted in the work of Thorndike (1911) and Pavlov (1927)—the Thorndikian tradition. The views of Thorndike and Pavlov differed considerably, of course, and so also did the views of their various influential successors, such as Watson, Lashley, Tolman, Guthrie, Skinner, Hull, Spence, and Mowrer (Bitterman, 1967). Skinner's well-popularized views were especially deviant, although outsiders often assumed them to be typical. In fact, it would be difficult to find sharper criticisms of Skinner than those made by insiders. I remember, for example, H. L. Teuber's description of the Skinner Box as a bloodless technique of decortication, which affects both the experimenter and the animal, and is irreversible for the experimenter. Among the contemporary descendants of Thorndike and Pavlov, there is no less diversity of opinion, and yet there are some clearly discernable common assumptions. For all the publicized disagreement between psychologists and ethologists, the same assumptions are to be found in Lorenz's *Behind the Mirror* (1977).

There is general agreement that information about the world comes from sensory systems whose outputs are filtered and organized in critical ways by genetically structured perceptual mechanisms; that the mechanisms of learning, which permit adaptation to a much wider range of environments than can possibly be provided for in the genome, are themselves products of evolution; that much of learning is associative in character; that the modification of behavior by reward and punishment is of special—Lorenz (p. 84) says "epoch-making"—importance; and that understanding must depend on information supplied by learning.

The central concern of psychologists working in the Thorndikian tradition has been with learning and memory. Their earliest interest was in whether something like human understanding could be found in animals, but the results of early experiments were largely negative. Only highly experienced subjects sometimes seemed to solve problems insightfully, which suggested that, if there was something like understanding in animals, it was grounded in learning, and that was where the inquiry should begin. Questions about learning soon gave rise to questions about perception (leading to a great deal of interesting work on generalization, discrimination, and attention), as well as to questions about motivation and about the interplay of learned and unlearned behavior; for a proper appreciation of the scope of that work, see the textbook by Mackintosh (1974), a landmark in its field. Interest in the discovery of conceptual abilities did not, however, entirely disappear and in recent years has

revived considerably, although still without clear outcome; see, for example, the critical analysis by Heyes (1998) of evidence for "theory of mind" in nonhuman primates.

An old criticism of Thorndikian research is that it is done in unnatural situations, although laboratory procedures for the study of learning in animals were designed from the very beginning with the behavior of the subjects in more worldly settings in mind—Thorndike's puzzleboxes for cats, Small's maze for rats, and even Skinner's key-pecking apparatus for pigeons (now commonly encountered in ecological laboratories). In *Behind the Mirror*, Lorenz does not hesitate to rely on results of maze experiments with rats and mice, and (in a discussion of Pavlov's experiments) recognizes the value of isolating specific responses "artificially" (p. 86) for purposes of quantitative analysis. In trying to understand an animal, we want to know about its behavior in as wide a range of situations as possible, and settings far removed from those in which the animal normally is found may be especially instructive. H. F. Harlow once remarked that field observations of rhesus monkeys gave little hint of the intellectual capabilities displayed in the Wisconsin General Test Apparatus.

Another criticism of Thorndikian research is that it has been concentrated on a very small number of species, and the wrong ones at that. Particularly disturbing for a time was the amount of effort devoted to rats. The answer to the objection is that, with limited resources, it is more instructive to study a small number of species intensively than a large number of species superficially; the laws of learning in any species are not given immediately in its behavior, but must be extracted painstakingly from the data of a long series of analytical experiments. In choosing a species for intensive study, we have to consider such practical questions as whether it is readily available; whether it lives well in the laboratory; and whether its sensory, motor, and motivational properties are suitable for the work. Having decided some 40 years ago that it was important to have a body of detailed information about learning in a vertebrate very different from the rat in its evolutionary history, I was led by just such practical considerations to choose the African mouthbreeding fish, *Tilapia macrocephala*, which L. R. Aronson bred in great quantity at the nearby American Museum of Natural History in New York, and which had the special advantage of a large appetite for dry food (Bitterman et al., 1958). With the development of automatic devices for feeding liquid food and small worms, the goldfish (abundant almost everywhere) proved to be even more practical. Later on, when I decided that it was important also to have a body of detailed information about learning in an invertebrate, I was led again by practical considerations to the honeybee.

And what of the early focus on learning in rats? Using data from Simpson (1945) and Walker (1964), R. B. Masterton once suggested to me that if we were starting

over again and had to select a single mammalian species for intensive study, rats would be prime candidates on demographic grounds. Of the living genera of mammals, more than a third are rodents—three times the number in either of the next two largest orders. Of the rodent genera, almost two-thirds are in one or the other of two main families generally referred to as “rats”—the old-world and new-world rats and mice. *Rattus*, one of the old-world genera, has many more named forms than any other mammalian genus, and even if only 50 percent of them were true species, the number of *Rattus* species would be larger than the number in any other genus. It follows that a random sample from *Mammalia* would most probably yield a rodent, and a sample of *Rodentia* would most probably yield a rat—which, having been selected for consideration, would pass the practical tests. If we were looking for any vertebrate, the probability is somewhat greater that we would hit on a bony fish.

### General-Process Theory

Of course, there has also been considerable work on learning in mammals other than rats, in vertebrates other than mammals, and in invertebrates, and nothing has so earned the skepticism of outsiders as the hypothesis, conceived early in the course of the work, that there are some quite general laws of learning. The first formulation of the so-called *general-process* view we owe to Thorndike (1911), who studied cats, dogs, chickens, monkeys, and even a species of fish (*Fundulus*), and who found only quantitative differences in their learning. The various animals learned different things, and some seemed to learn more quickly than others, but all could be understood as systems of connections governed by the Laws of Exercise and Effect. Thorndike's distinction between the content and rate of learning on the one hand, and the laws of learning on the other, is an important one. Hull (1945) puts the question about the generality of the laws of learning in a very clear way. He asks whether the equations that describe learning in various species (when we have them) will be of the same form, differing only in the values of their constants (as, in his example, the gravitational constant at Hammerfest and Madras), or whether the equations themselves will be different.

Consider the S-S contiguity principle, according to which the pairing of two stimuli—such as the pairing of a tone (the conditioned stimulus, or CS) and a bit of food (the unconditioned stimulus, or US) in Pavlovian conditioning—results in the formation of an association between them. Bush and Mosteller (1951) suggest that the growth of associative strength in the course of training can be described by a simple linear equation currently more familiar in the notation of Rescorla and Wagner (1972):

$$\Delta V = \alpha \cdot U\beta(\lambda - V) \quad [1]$$

with  $V$  representing the strength of association at the beginning of each trial;  $\Delta V$ , the change in  $V$  produced by the pairing of the CS and the US on that trial;  $\alpha$ , the salience of the CS;  $U\beta$ , the learning rate; and  $\lambda$ , the maximal strength of association that can be achieved with a given US—the asymptote of the growth function. On nonreinforced trials (that is, on trials with the CS alone),  $\lambda = 0$ ,  $\Delta V$  is negative, and  $V$  declines at a rate ( $D\beta$ ) that may be different from  $U\beta$ . The constants  $\alpha$ ,  $U\beta$ ,  $D\beta$ , and  $\lambda$ , may vary widely in value from situation to situation and from species to species, as may the conditioned response (CR) itself, and so also the relation between  $V$  and the measure of response (specified in a supplementary performance equation); but the learning equation (and the conditioning process it describes) may be the same. There is a good deal of contemporary interest in the development of quantitative theories of learning that will permit exact rather than merely ordinal predictions of experimental outcomes. Equation [1] has proved useful in deriving the results of experiments on such diverse phenomena as transitive inference in pigeons (Couvillon and Bitterman, 1992), avoidance conditioning in goldfish (Zhuikov et al., 1994), and (by Martin Shapiro in doctoral research at the University of Hawaii) risk-sensitive foraging in honeybees.

Although what many have come to think of as the ethological view is that there are no general laws of learning, we find general-process thinking by Lorenz himself in *Behind the Mirror*. There he considers at length some phenomena of learning in animals as diverse as cuttlefish, flatworms, human infants, wasps, dogs, and birds of various species. Two of the phenomena—*facilitation by practice* and *sensitization*—are interpreted as frequency or practice effects and attributed to a process like that of “‘running in’ an automobile” (p. 69). Thorndike’s Law of Exercise comes to mind here. Four other phenomena—*habituation*, *habit*, *traumatic avoidance*, and *imprinting*—are explained in terms of association, which is defined as “the forming of a linkage between two nervous processes hitherto not causally connected” (p. 81). A seventh phenomenon is *conditioning by reinforcement* or “learning through success and failure,” which Lorenz thinks of as “true conditioning” rather than “mere association.” It is based, he assumes, on a feedback process found in all animals except “unicellular and lower multicellular creatures which have no centralized nervous systems” (pp. 84–87). Here, of course, Thorndike’s Law of Effect comes to mind. In sum, three general processes are postulated—a frequency process and a contiguity process that are perfectly general, and a reinforcement process that operates in all but the simplest animals. Psychologists working in the Thorndikian tradition would quarrel with the substance of the theory, which is summarized in table 4.1, but would not find its form or intent at all foreign.

Table 4.1  
General-process theory in *Behind the Mirror* (Lorenz, 1977)

Process	Locus of operation	Representative phenomena
Frequency	All animals	Facilitation by practice Sensitization
Association	All animals	Habituation Habit Traumatic avoidance Imprinting
Reinforcement	All animals with "centralized nervous systems"	Learning by trial and success ("true conditioning")

General-process theory is often thought to be contradicted by *adaptive specialization*—the alleged evolutionary tailoring of learning processes to the needs of particular species in particular situations—although the assumption of tailoring implies the existence of general processes to be tailored, as when Lorenz proposes that the associations involved in imprinting and traumatic avoidance may be especially persistent. One line of evidence for adaptive specialization comes from experiments in which the performance of the same species in different situations is compared. Why, asks Huber (this volume), should it be easier to train rats to avoid shock by running away from the danger signal than by making copulatory responses? The Thorndikian answer is that a response must occur before it can be rewarded, and the signal, which is paired with shock whenever the animal fails to avoid, is more likely in consequence of the pairing to elicit running than copulation. The once popular conviction that food-aversion experiments point to the operation of specialized learning processes is now widely understood to be groundless (Klosterhalfen and Klosterhalfen, 1985). The primordial finding—that rats poisoned after eating a novel food may develop an aversion to the taste of the food but not to its appearance—follows directly from the contiguity principle, given that the traces of visual stimuli fade rapidly in the relatively long interval between poisoning and illness while food remains in the gut (Bitterman, 1975). Without controls for the effects of the many variables other than learning that influence performance in such experiments, conclusions about learning are unwarranted.

Another line of evidence for adaptive specialization comes from experiments in which the performance of different species is compared in what is purported to be the same situation, and here similar difficulties are encountered. Better performance of food-storing birds as compared with nonstorerers in spatial learning tasks might well be due, as Shettleworth (1993) admits, to evolutionary tailoring of their sensory or motivational properties rather than of their learning; spatial cues, she suggests, may be more salient for the black-capped chickadee than for the dark-eyed junco. Even if

a difference in what she refers to as the capacity and persistence of spatial memory could somehow be demonstrated, of course, the finding would not go to the generality of whatever learning process is involved—not to the form of the learning equation, as Hull put it, but only to the values of the constants. It is often implied that certain seemingly specialized instances of learning, such as the much-advertised song learning of birds, involve processes that are entirely unique—that the tailoring is qualitative rather than merely quantitative—but little interest has been evidenced in what the unique processes might be, or how they might differ from those delineated by conventional laboratory experiments. The accommodating modular view expounded here by Shettleworth may be attractive because it suggests that we need not worry very much about such matters. The Law of Least Effort holds for mind as well as for muscle.

Scattered allegations of adaptive specialization should not be permitted to obscure the fact that there are a great many phenomena of learning that transcend particular sensory, motor, and motivational contexts, which are found in many different species, and which point to the operation of common processes—although we are still not clear as to the nature of some of those processes. The strategy of psychologists working in the Thorndikian tradition is to continue in given species to try to discover what the processes are, and in comparative experiments to examine their generality over a range of widely divergent species chosen to provide clues to their evolutionary history. Because a variety of general learning processes seem to be at work in the species that we have been studying intensively, and because it is unlikely that the whole set of them appeared together, or are inextricably linked, we should not be surprised to find animals in which certain of them are absent, or are present in a different form. It is possible, however, as Macphail (1982) suggests, that there may be no differences among existing vertebrates because the critical developments occurred at an early stage of evolution in animals now extinct.

#### **Learning in Vertebrates and Honeybees**

That there are many phenomena of learning common to our favorite vertebrate subjects, as diverse as they are, is perhaps not difficult to understand on the assumption of common processes evolved in common ancestors. That many of what appear to be the same phenomena are found also in honeybees is perhaps more difficult to understand in view of the greater remoteness of the evolutionary relationship and the presumed simplicity of even the most advanced common ancestors. Because, as Simpson (1964) notes, convergence to the point of identity or even of seriously confusing similarity is unlikely in what he refers to as elaborately polygenic behavioral

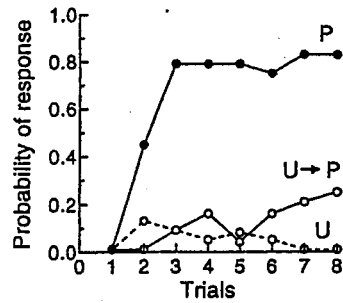


Figure 4.1  
Classical conditioning in honeybees (P, paired; U, unpaired; U → P, unpaired to paired).

systems, it might be expected that resemblances in the learning of honeybees and vertebrates would be no more than superficial, but an examination of a small sample of them will show that they are quite detailed.

Consider, for example, the performance of a group of honeybee foragers (Group P) harnessed in small tubes and subjected to a series of conditioning trials with odor as the CS and a small drop of sucrose solution, applied to antennae and proboscis, as the US. As figure 4.1 shows, the odor soon comes to elicit extension of the proboscis (the CR), which at the outset is elicited only by the sucrose (Bitterman et al., 1983). The results look very much like salivary conditioning in a Pavlovian dog standing on laboratory table in Petrograd. The stimuli and responses are different, and so also is the rate of change in performance over trials (which is actually much greater in the honeybees), but the learning process may be the same—the process described by equation [1].

The possibility that the change in responding to the odor is due to experience with the stimuli apart from their pairing—say, to sensitization of the response by the experience with sucrose—is evaluated with a control procedure common in work with vertebrates. Another group of honeybees (Group U) is given the same experience with the odor and sucrose, except that the two stimuli are presented separately in random sequence (*explicitly unpaired training*). As figure 4.1 shows, these animals respond very little to the odor, which suggests that the pairing of the stimuli really is a critical factor in the performance of Group P. In vertebrates, the explicitly unpaired procedure is found not to be associatively neutral, as evidenced by the fact that a stimulus explicitly unpaired with a US is slow to condition when subsequently paired with it. Figure 4.1 shows that the same is true for honeybees; as compared with the rate of conditioning in Group P, the rate of conditioning in Group U—shown

in the curve labeled U→P—is indeed slow. As to why explicitly unpaired training should retard subsequent conditioning, there is some disagreement in the vertebrate literature.

Now there is another question worth asking, which has been asked also about appetitive conditioning in vertebrates. Is the change in response to the CS a product of CS-US contiguity per se, or of the CR-US contiguity (the contiguity of response and sucrose) that the pairing of the two stimuli occasions? Although the sucrose is presented whether or not the CR occurs, the CR is always closely followed by the sucrose when it does occur, which gives us reason to suspect that what we may really have here is instrumental learning in disguise (Lorenz's "true conditioning" rather than "mere association"). We answer the question by training a new group of honeybees with two different odors. On some trials, one of the odors (S+) is paired with sucrose, but only when the CR fails to occur (*omission training*). On the remaining trials, the other odor (S-) is presented alone, serving to control for the possibility that any responding to S+ is due simply to sensitization. The results are like those for vertebrates. There is little response to S-, but a good deal of response to S+, which (because there is no CR-US contiguity) must be attributed to the contiguity of CS and US on the few trials on which the CR does not occur. It is interesting to note that Pavlov found good salivary conditioning in dogs even when the CS was paired with the US on only a small percentage of trials.

As Pavlov also found, a CS can itself act as a US in the conditioning of a novel stimulus (*second-order conditioning*), and the same is true of honeybees. After one odor has been paired with sucrose in a series of trials, a second odor that is paired with the first odor soon comes to elicit the CR. That does not happen if the two odors are explicitly unpaired in the second stage of the experiment. It does not happen either if the first odor has been explicitly unpaired with sucrose in the first stage of the experiment—the paired odors may be associated in the second stage, but the second odor will not evoke the response if the first odor does not. The vertebrate literature shows that contiguous neutral stimuli are, in fact, associated (that classical conditioning does not require a motivationally significant US), and that the same is true of honeybees has been shown by experiments on what in the vertebrate literature is called *within-compound association* (Couvillon and Bitterman, 1982).

The work on within-compound association in honeybees was done with free-flying subjects that were pretrained individually to forage for sucrose solution at a laboratory window—feeding to repletion on each visit, leaving for the hive to deposit the sucrose, and returning of their own accord a few minutes later to collect more. (The window used in such experiments is so situated as to minimize following by nest-mates, a technique that Professor B. Hassenstein taught me in his laboratory at

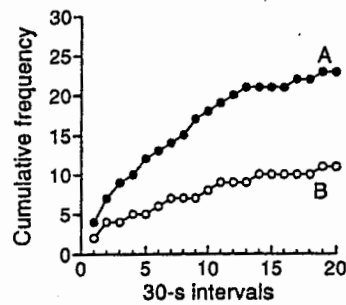


Figure 4.2

Within-compound association in honeybees. Responses in a choice test with A and B after experience with AX and BY followed by training with X+ and Y-.

Freiburg, where I first learned to work with honeybees.) In the first stage of training, the subjects were exposed on a series of visits to two gray targets, one (AX) labeled with a color (A) and an odor (X), and another (BY) labeled with a different color (B) and a different odor (Y). In the second stage of the experiment, the subjects were trained to discriminate between two gray targets labeled with the odors, only one of which (X) contained sucrose solution. When, in the third stage of the experiment, the subjects were tested with two gray targets labeled only with the colors, neither containing sucrose solution, they showed a strong preference for A (the color paired in the first stage with the odor reinforced in the second stage). In figure 4.2, some sample results are plotted in terms of the mean cumulative frequency of responding to each of the targets in a 10-min choice test. It seems reasonable to conclude that color-odor associations are formed in the first stage, although not then evident in behavior—an instance of what is called *latent learning* in the vertebrate literature.

Experiments with compound stimuli show a variety of other phenomena first discovered in vertebrates. One of them is *blocking*, which has been found both in proboscis-extension conditioning (Smith and Cobey, 1994) and in the performance of free-flying foragers (Couvillon et al., 1997). After reinforced training with a compound of two odors or two colors (AB), there is less response to B alone if A has previously been paired with the same reinforcer; that is, the conditioning of B is impaired (blocked) by the presence of the previously conditioned A. Blocking in vertebrates is commonly explained on the assumption that the components of a reinforced compound compete with each other for associative strength or for attention, and the same explanation may well hold for honeybees. In any case, it is clear from the data both for vertebrates and for honeybees that CS-US contiguity, although necessary, is not sufficient for conditioning.

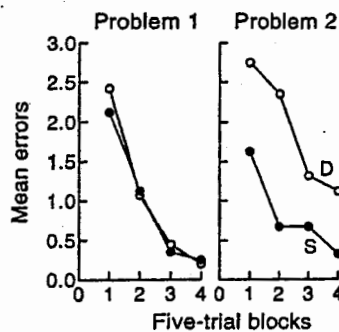


Figure 4.3

Performance of honeybees in two color-position discrimination problems with the relevant dimension the same (S) or different (D) in the two problems.

Competition for attention has been demonstrated in honeybees, again in an experiment patterned after work with vertebrates (Klosterhalfen et al., 1978). Free-flying foragers were trained with targets of two different colors in two different positions, some rewarded for choosing one of the colors independently of position (color-relevant training), and others for choosing one of the positions independently of color (position-relevant training). In a second problem, with targets of two new colors in two new positions, learning was more rapid when the relevant dimension was the same as in the first problem than when it was different. In figure 4.3, the results are plotted in terms of the mean number of errors made in each of the two problems. The results suggest that the animals learn first of all in such problems to single out the relevant stimulus dimension (see also Shapiro and Bitterman, 1998); and that dimensional selection is influenced by prior training. It is interesting to note that the results of like experiments on discriminative learning in octopuses have been interpreted in the same way (Sutherland and Mackintosh, 1971).

Another interesting phenomenon of compound conditioning found in honeybees as well as in vertebrates is *conditional discrimination* (Couvillon and Bitterman, 1988). Honeybees can learn to choose, say, a green rather than a blue target when both are scented with geraniol, but a blue rather than a green target when both are scented with peppermint. Because each of the components is equally often reinforced and nonreinforced, differential responding to the compounds cannot be understood in terms of the summed associative strengths of the components. *Spontaneous* discrimination of compounds *qua* compounds also has been demonstrated in honeybees (Couvillon and Bitterman, 1982). Subjects that have found sucrose solution on each of two targets labeled with different color-odor compounds (AX and BY) clearly

prefer them to two targets labeled with the same colors and odors paired differently (AY and BX) in a subsequent choice test. The simplest interpretation in the vertebrate literature is that we are dealing in such experiments with perceptual rather than conceptual effects—that the animals learn about configural properties in the same way they learn about component properties (which also may sometimes be quite subtle)—although there is some disagreement as to how the perceptual effects are best conceived.

These detailed similarities in the results for honeybees and vertebrates represent only a very small proportion of those that have been found in a wide range of experiments (Bitterman, 1988, 1996). Differences also have turned up occasionally. The results of initial blocking experiments (Funayama et al., 1995) were negative, for example, although for reasons that now seem to be purely perceptual (Couvillon et al., 1997). A long series of recent experiments designed to look for evidence of inhibitory conditioning produced only negative results (Couvillon et al., 1999), but their meaning is uncertain because the evidence of inhibitory conditioning in vertebrates (commonly taken for granted since the time of Pavlov) is unimpressive (Papini and Bitterman, 1993). Noteworthy, too, is our failure in other recent experiments to find evidence that the control of performance by short-term memory can be modified by learning (Couvillon et al., 1998). On the whole, however, the differences are far outweighed by the similarities.

Why should it be so difficult to discover differences in the learning of animals whose most recent common ancestor lived half a billion years ago and had hardly any brain at all? At least part of the answer may be that honeybees can be studied properly only in relatively massed trials and for relatively brief periods, which rules out a search for many interesting and seemingly more complex phenomena of vertebrate learning. On these grounds alone, although for other obvious reasons as well, it seems necessary to extend the work to other invertebrates, and the trick, of course, is to find a suitable one. With a huge research budget (because to do the work well would be enormously expensive), I might be tempted to turn again to octopuses (Walker et al., 1970).

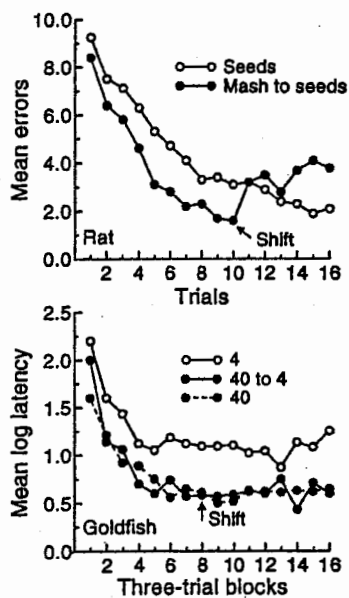
#### **Divergence in Vertebrate Learning**

When we ask whether there are differences in the learning of honeybees and vertebrates, we are referring to what we conceive to be general phenomena of vertebrate learning—phenomena that have been found, or that we assume can be found, in vertebrates of all classes. The question does not imply that there has been no diver-

gence in vertebrate learning, although evidence of divergence is scarce indeed, and the scarcity is not due simply to the fact that psychologists have not bothered to look for it. Macphail (1982) has reviewed in considerable detail the results of a large number of comparative experiments with fishes, reptiles, birds, and mammals, including primates, which in his opinion provide no compelling evidence of qualitative differences in learning. I agree with many of his evaluations; the difficulty in establishing such differences, of course, is that performance in learning situations is influenced by variables other than learning. There are, however, several series of experiments that I think deserve further consideration, among them experiments on the so-called *paradoxical reward effects* discovered in work with rats.

One of the effects is *negative incentive contrast*, found first in a famous experiment by Elliott (1928). Two groups of rats were trained in a maze, one with bran mash as reward, and the second with (less acceptable) sunflower seeds. (Except where otherwise noted, the intertrial interval in all of the instrumental learning experiments considered here was 24 hours—a procedure that has the important advantage, among others, that the sensory antecedents of response on one trial are not contaminated by the sensory consequences of response on preceding trials.) The performance of the bran mash animals was much better than that of the sunflower seed animals until the bran mash animals were shifted to sunflower seeds. Finding sunflower seeds for the first time, they showed a good deal of disturbance, and their performance on subsequent days fell precipitously below that of the animals rewarded with sunflower seeds from the outset. In the upper portion of figure 4.4, the performance of the two groups is plotted in terms of mean errors per trial. These results, and those of like experiments with differences only in quantity of reward, suggest that instrumental behavior in rats is modulated by anticipation of its remembered consequences—energized by remembered reward and impaired by remembered frustration (Amsel, 1958)—all of which may seem perfectly commonplace until it is appreciated that quite different results are obtained in analogous experiments with other animals.

Lowes and Bitterman (1967) trained goldfish to strike a target lowered into the water at the start of each trial. The reward was a cluster of 40 (*Tubifex*) worms for one group, which then was shifted to four worms; a second group was rewarded throughout with four worms. In the lower portion of figure 4.4, the results are plotted in terms of the mean log latency of response (in seconds). Performance was better for the larger reward in the first stage, but the group shifted from the larger to the smaller reward showed no disturbance whatsoever, continuing to respond as rapidly as before the shift, and just as rapidly as a third group that continued to find the larger reward. The results suggest that instrumental learning in goldfish is different in some important way from instrumental learning in rats.



**Figure 4.4**  
Performance of rats and goldfish shifted from preferred to less-preferred rewards compared with the performance of unshifted control groups.

It is possible, of course, that the explanation lies elsewhere. The training situations are different, the response measures are different, the rewards are different, and so also may be the differential attractiveness of the rewards. The only way to deal with such possibilities seems to be to do the same kind of experiment under systematically varied training conditions (Bitterman, 1975). It may never be possible to find conditions of whose functional equivalence for the two species we can be confident; but to the extent that the qualitative difference in their performance remains the same with variation in the training conditions, we can give less weight to the interpretation in terms of contextual variables alone. Consider an experiment in which goldfish were trained to swim in a runway rather than to strike a target, with either 40 worms or only a single worm as reward (Gonzalez et al., 1972). The 40-worm group swam more rapidly than the one-worm group, and when shifted to the smaller reward continued to swim as rapidly as before, although a group shifted from 40 worms to none soon stopped responding. With a new instrumental response and a greater discrepancy between the two reward magnitudes, the contrast effect failed again to appear.

Parallel results for the two species are obtained in experiments in which consummatory rather than instrumental responding is measured—rats licking a drinking tube, and goldfish sucking liquid food from a nipple. In each experiment, there are two groups of subjects, one fed for a brief period each day with a preferred food, and the second with a less preferred food. Both the rats and the goldfish take much more of the preferred food. Then comes a day when the animals that have been given the preferred food find the less preferred food instead. The feeding behavior of the rats is disrupted; they take much less of the less preferred food than do the rats that have known only that food (e.g., Flaherty et al., 1983)—that is, they show negative contrast. The performance of the shifted goldfish is entirely unaffected; they continue to take as much of the less preferred food as they have been taking of the preferred food (Couvillon and Bitterman, 1985).

A variation of Elliott's paradigm produces another paradoxical effect in rats—an *inverse relation* between amount of reward and resistance to extinction. One group is trained with large reward, a second with small reward, and then both groups are extinguished, which is to say that they are no longer rewarded at all. The outcome of a considerable number of such experiments with rats (e.g., Gonzalez and Bitterman, 1969) is that the large reward group performs better in training, but extinguishes more rapidly; nonreward seems to be more frustrating for rats that anticipate a large reward than for rats that anticipate only a small reward. In a runway experiment with three groups of goldfish, one trained with 40 worms, a second with four worms, and a third with a single worm, performance both in training and in extinction was directly related to amount of reward—the larger the reward, the more vigorous the performance in extinction as well as in training (Gonzalez et al., 1972).

A third paradoxical effect found repeatedly in rats is the *partial reinforcement effect* or PRE (e.g., Gonzalez and Bitterman, 1969). The procedure is to train two groups with large rewards (the effect does not occur in widely spaced trials when the reward is small)—a Consistent group rewarded on every trial, and a Partial group only on half the trials (the remaining trials unrewarded). When the reward for both groups is then discontinued, the Partial group extinguishes less rapidly than the Consistent group; that is, nonreward in extinction is less frustrating for the Partial animals, perhaps because they have already encountered it in training, where it has been followed eventually by large reward. In analogous experiments, African mouthbreeders rewarded with food pellets for striking a target (Longo and Bitterman, 1960) and goldfish rewarded with worms in a runway (Schutz and Bitterman, 1969) have failed to show the PRE.

That we are not dealing here merely with idiosyncratic properties of the species being compared is suggested by the results of analogous experiments with a variety of

other animals. Negative incentive contrast has been found in consummatory experiments with opossums of two species (Papini et al., 1988), and unmistakable evidence of disturbance produced by unrealized anticipation of a preferred reward has appeared also in delayed response experiments with rhesus monkeys (Tinklepaugh, 1928) and chimpanzees (Cowles and Nissen, 1937). The PRE has been found in pigeons (Roberts et al., 1963), but neither negative contrast nor the inverse relation (Papini, 1997). The PRE also has been found in pigeons, although not in goldfish, under conditions in which the intertrial intervals were relatively short but trials with other stimuli were interpolated to control for sensory carryover (Bitterman, 1994). All three paradoxical effects have failed to appear in experiments with animals of two older vertebrate lines—turtles of two species (Papini and Ishida, 1994; Pert and Bitterman, 1970) and toads (Schmajuk et al., 1981; Muzio et al., 1992). The paradoxical effects fail also to appear in very young rats trained (necessarily) with relatively short intertrial intervals, and it is interesting in view of the dissociation evident in the pigeon data that the PRE is the earliest of the three effects to appear as the rats develop (Amsel, 1992).

This striking pattern of results, which is obscured in Macphail's (1982) treatment, suggests that instrumental learning may have undergone some important changes in common reptilian ancestors of birds and mammals, and it is regrettable that there is still so little evidence as to the nature of those changes. Funding for my own work on the problem ended rather abruptly several decades ago when peer reviewers of a new breed maligned it as a primitive Aristotelian enterprise; comparisons of rats and goldfish could not be expected to tell us anything about evolution, they advised, because rats are not descended from goldfish. In recent years, the intellectual climate has improved somewhat—nobody at least has yet felt compelled to warn the agency supporting my current work that vertebrates are not descended from honeybees—and it may be that a proposal for continuation of the vertebrate experiments would now be more favorably received, although misunderstanding lingers.

I am baffled by Shettleworth's insistence that traditional comparative psychologists, despite their "claim" to be interested in the "commonality of cognitive processes," really think of evolution as a "ladder of improvement" (1993, p. 179) and "expect that a single hierarchical ordering of mechanisms will be found with capacities possessed only by humans at the 'most complex' or 'most advanced' end" (this volume, p. 57). Whether we are judged to be disingenuous or merely confused, the implication is incorrect that the recognition both of commonality and divergence is inherently contradictory. As to improvement, it would be absurd to deny historic advance in the ability of animals to know the world, or to question the cognitive preeminence of humans. One has but to compare (at one extreme) the animals of the oldest lines that

have been found in our experiments to be incapable even of simple associative learning, and (at the other) our nearest primate relatives, however impressive their perceptual and mnemonic competence, that would be hard put to design such experiments, or to evaluate the results—which is not, of course, to say that the molecular geometry of evolution is linear. Rats, as we now know, are certainly not descended from goldfish, and early Japanese horror films have prepared us well enough for the possibility that before the sun fades or the earth is destroyed by an errant comet some superordinate intelligence will appear in a crustacean. I suspect, in any case, that for the prosaic present, their confidence undiminished by an airy sermon on modularity, traditional comparative psychologists will continue to work in much the same way as before.

### Summary

Comparative psychologists have been interested in perception and in the precursors of human understanding, but the main focus thus far of their work on the evolution of cognition has been on learning and memory. Conditioning experiments with a small number of widely divergent vertebrate species have yielded a lengthy list of phenomena that may reasonably be assumed on the basis of the taxonomic diversity of the subjects to be general phenomena of vertebrate learning; the results vary quantitatively with species and with training techniques, but there are common qualitative patterns that are understandable in terms of common functional principles and may well reflect the operation of homologous mechanisms of information storage and retrieval. Despite the remoteness of the evolutionary relationship, many of the vertebrate principles seem to hold also for honeybees, whose performance in conditioning experiments shows detailed similarities to that of vertebrates, although here we may suspect that the similarities are, at least in large measure, convergent. In the learning of vertebrates, there is not only extensive commonality, but evidence of broad evolutionary divergence as well; some of that evidence is provided by a set of experiments on the control of instrumental behavior by its remembered and anticipated consequences, whose results for birds and mammals are qualitatively different from those for animals of older vertebrate lines. Familiar objections to the way in which comparative psychologists have approached the problem of cognitive evolution and the conclusions to which they have been led are reviewed and evaluated.

### References

- Amsel A. (1958) The role of frustrative nonreward in noncontinuous reward situations. *Psychological Bulletin*, 55: 102–119.

- Amsel A (1992) Frustration theory. Cambridge: Cambridge University Press.
- Bitterman ME (1967) Learning in animals. In: Contemporary approaches to psychology (Helson H, Bevan W, ed), pp 140-179. New York: D. Van Nostrand.
- Bitterman ME (1975) The comparative analysis of learning. Are the laws of learning the same in all animals? *Science*, 188: 699-709.
- Bitterman ME (1988) Vertebrate-invertebrate comparisons. In: Intelligence and evolutionary biology (Jerison HJ, Jerison IL, ed), pp 251-276. Berlin: Springer Verlag.
- Bitterman ME (1994) Amsel's analysis of reward-schedule effects. *Psychonomic Bulletin and Review*, 1: 297-302.
- Bitterman ME (1996) Comparative analysis of learning in honeybees. *Animal Learning and Behavior*, 24: 123-141.
- Bitterman ME, Menzel R, Fietz A, Schäfer S (1983) Classical conditioning of proboscis-extension in honeybees (*Apis mellifera*). *Journal of Comparative Psychology*, 97: 107-119.
- Bitterman ME, Wodinsky J, Candland DK (1958) Some comparative psychology. *American Journal of Psychology*, 71: 94-110.
- Bush RR, Mosteller F (1951) A mathematical model for simple learning. *Psychological Review*, 58: 313-323.
- Couvillon PA, Ablan CD, Bitterman ME (1999) Exploratory studies of inhibitory conditioning in honeybees. *Journal of Experimental Psychology: Animal Behavior Processes*, 25: 103-112.
- Couvillon PA, Arakaki L, Bitterman ME (1997) Intramodal blocking in honeybees. *Animal Learning and Behavior*, 25: 277-282.
- Couvillon PA, Arincorayan NM, Bitterman ME (1998) Control of performance by short-term memory in honeybees. *Animal Learning and Behavior*, 26: 469-474.
- Couvillon PA, Bitterman ME (1982) Compound conditioning in honeybees. *Journal of Comparative and Physiological Psychology*, 96: 192-199.
- Couvillon PA, Bitterman ME (1985) Effect of experience with a preferred food on consummatory responding for a less preferred food in goldfish. *Animal Learning and Behavior*, 13: 433-438.
- Couvillon PA, Bitterman ME (1988) Compound-component and conditional discrimination of colors and odors by honeybees: Further tests of a continuity model. *Animal Learning and Behavior*, 16: 67-74.
- Couvillon PA, Bitterman ME (1992) A conventional conditioning analysis of "transitive inference" in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 18: 308-310.
- Cowles JT, Nissen HW (1937) Reward-expectancies in delayed-responses of chimpanzees. *Journal of Comparative Psychology*, 24: 345-358.
- Elliott MH (1928) The effect of change of reward on the maze performance of rats. *University of California Publications in Psychology*, 4: 19-30.
- Flaherty CF, Becker HC, Checke S (1983) Repeated successive contrast in consummatory behavior with repeated shifts in sucrose concentration. *Animal Learning and Behavior*, 11: 407-414.
- Funayama ES, Couvillon PA, Bitterman ME (1995) Compound conditioning in honeybees: Blocking tests of the independence assumption. *Animal Learning and Behavior*, 23: 429-437.
- Gonzalez RC, Bitterman ME (1969) Spaced-trials partial reinforcement effect as a function of contrast. *Journal of Comparative and Physiological Psychology*, 67: 94-103.
- Gonzalez RC, Potts AK, Pitkoff K, Bitterman ME (1972) Runway performance of goldfish as a function of complete and incomplete reduction in amount of reward. *Psychonomic Science*, 27: 305-307.
- Heyes CM (1998) Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, 21: 101-134.
- Hull CL (1945) The place of innate individual and species differences in a natural-science theory of behavior. *Psychological Review*, 52: 55-60.

- Klosterhalfen S, Fischer W, Bitterman ME (1978) Modification of attention in honeybees. *Science*, 201: 1241-1243.
- Klosterhalfen S, Klosterhalfen W (1985) Conditioned taste aversion and traditional learning. *Psychological Research*, 47: 71-94.
- Longo N, Bitterman ME (1960) The effect of partial reinforcement with spaced practice on resistance to extinction in the fish. *Journal of Comparative and Physiological Psychology*, 53: 169-172.
- Lorenz K (1977) *Behind the mirror*. New York: Harcourt Brace Jovanovich.
- Lowes G, Bitterman ME (1967) Reward and learning in the goldfish. *Science*, 157: 455-457.
- Mackintosh NJ (1974) *The psychology of animal learning*. London: Academic Press.
- Macphail EM (1982) *Brain and intelligence in vertebrates*. Oxford: Clarendon Press.
- Muzio RN, Segura ET, Papini MR (1992) Effect of schedule and magnitude of reinforcement on instrumental learning in the toad, *Bufo arenarum*. *Learning and Motivation*, 23: 406-429.
- Papini MR (1997) Role of reinforcement in spaced-trial operant learning in pigeons (*Columba livia*). *Journal of Comparative Psychology*, 111: 275-285.
- Papini MR, Bitterman ME (1993) The two-test strategy in the study of inhibitory conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, 97: 396-403.
- Papini MR, Ishida M (1994) Role of magnitude of reinforcement in spaced-trial instrumental learning in turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology*, 47B: 1-13.
- Papini MR, Mustaca AE, Bitterman ME (1988) Successive negative contrast in the consummatory responding of Didelphid marsupials. *Animal Learning and Behavior*, 16: 53-57.
- Pavlov IP (1927) *Conditioned reflexes*. Oxford: Oxford University Press.
- Pert A, Bitterman ME (1970) Reward and learning in the turtle. *Learning and Motivation*, 1: 121-128.
- Rescorla RA, Wagner AR (1972) A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In: *Classical conditioning II: Current research and theory* (Black AH, Prokasy WF, ed), pp 64-99. New York: Appleton-Century-Crofts.
- Roberts WA, Bullock DH, Bitterman ME (1963) Resistance to extinction in the pigeon after partially reinforced instrumental training under discrete-trials conditions. *American Journal of Psychology*, 76: 353-365.
- Schmajuk N, Segura E, Rudiaz A (1981) Reward downshift in the toad. *Behavioral and Neural Biology*, 28: 392-397.
- Schutz SL, Bitterman ME (1969) Spaced-trials partial reinforcement effect and resistance to extinction in the goldfish. *Journal of Comparative and Physiological Psychology*, 68: 126-128.
- Shapiro MS, Bitterman ME (1998) Intramodal competition for attention in honeybees. *Psychonomic Bulletin and Review*, 5: 334-338.
- Shettleworth SJ (1993) Where is the comparison in comparative cognition? *Alternative research programs. Psychological Science*, 4: 179-184.
- Simpson GG (1945) Principles of classification and a classification of mammals. *Bulletin of the Museum of Natural History*, 85: 1-350.
- Simpson GG (1964) Organisms and molecules in evolution. *Science*, 146: 1535-1538.
- Smith BH, Cobey S (1994) The olfactory memory of the honeybee *Apis mellifera*. *Journal of Experimental Biology*, 195: 91-108.
- Sutherland NS, Mackintosh NJ (1971) *Mechanisms of animal discrimination learning*. New York: Academic Press.
- Thorndike EL (1911) *Animal intelligence: Experimental studies*. New York: Macmillan.

- Tinklepaugh OL (1928) An experimental study of representative factors in monkeys. *Journal of Comparative Psychology*, 8: 197-236.
- Walker EP (1964) *Mammals of the world*. Baltimore, MD: Johns Hopkins University Press.
- Walker JJ, Longo N, Bitterman ME (1970) The octopus in the laboratory: Handling, maintenance, training. *Behavior Research Methods & Instruments*, 2: 15-18.
- Zhuikov AY, Couvillon PA, Bitterman ME (1994) A quantitative two-process analysis of avoidance conditioning in goldfish. *Journal of Experimental Psychology: Animal Behavior Processes*, 19: 342-352.