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The Comparative Analysis of Learning

Are the laws of learning the same in all animals?

M. E. Bitterman

A surprisingly influential recent paper raises the question of "why there is no theory in comparative psychology" and answers that it is because of the inability of animal psychologists to deal with the "intricacies" of evolutionary history (*1*). The question is the wrong one, at least as it relates to learning, long the principal concern of animal psychologists (*2*). A better question is why there has been so little comparative research, and the answer is that work on learning has been dominated almost from the outset by a powerful theory which denies that learning has undergone any fundamental evolutionary change.

The comparative analysis of learning was begun by Edward L. Thorndike, the 100th anniversary of whose birth was celebrated last year. Darwin and his followers could only speculate about intellectual evolution on the basis of the rather questionable anecdotal materials available to them (*3*), but Thorndike brought the problem into the laboratory, systematically comparing the performance of fishes, chickens, cats, dogs, and monkeys in a series of analogous tasks (*4*). His results are, or should be, well known. While substantial quantitative differences were to be found in the performance of his various animals (monkeys, for example, seemed able to learn more than cats, and more quickly), the qualitative features of their performance were very much the same, and Thorndike suggested that the underlying processes also might be the same—not only in his own animals, but in all animals, including man (*5, 6*). The same opinion was arrived at independently by Pavlov, that other great innovator in research on animal intelligence, who confidently asserted the generality of the principles discovered in his experiments with dogs (*7, 8*). After a relatively brief period of dissent, during which many different animals were studied, Thorndike's view gained wide acceptance among psychologists. In consequence of that acceptance, there was a rapid decline in the scope of comparative

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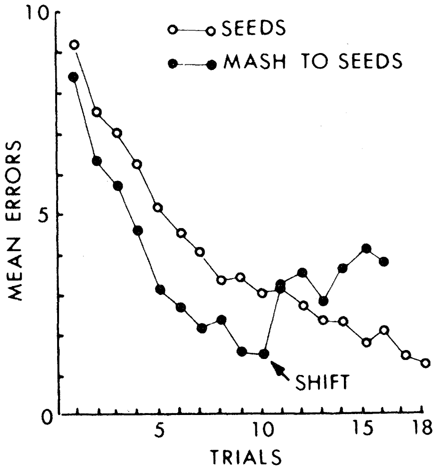


Fig. 1. Maze performance of two groups of rats, one rewarded throughout with sunflower seeds, the other shifted to sunflower seeds after nine trials with bran mash (*15*).

work as students of animal learning set about to elucidate in a few favored species, selected for reasons of custom or convenience, the laws of learning assumed to be common to all (*9*).

Only in recent years has this old assumption been called once more into question. Two alternative views may be distinguished, one deriving from the Thorndikian tradition and one, quite antithetical, which is rooted in ethology. The derivative view is that there certainly may be some common processes of learning but that the assumption of complete communality deserves more detailed scrutiny than it yet has received, and that further comparisons of diverse animals in contemporary experiments do indeed point to the possibility of rather fundamental evolutionary change (*10*). The ethological view, based on the fact already evident to Thorndike that a given animal may be better equipped to learn certain things than to learn others (*11*), is that learning processes cannot be considered apart from their organismic constraints (*12, 13*). In its most extreme statement, it carries the implication that each instance of learning must be treated as a specialized capability shaped by selective pressures and understandable only by reference to the ecology of the animal or of its ancestors—that there are no general laws of learning at all. My main purpose here is to examine the first view, with which I have been associated closely, but I shall take occasion also to comment briefly on the second.

Some Qualitative Differences in Performance

That there are many qualitative similarities in the performance of taxonomically disparate animals trained under analogous conditions cannot, of course, be doubted (*14*). It was the early discovery of such similarities which suggested the theory that the laws of learning are the same in all animals. Nevertheless, the suspicion has lingered that there are qualitative differences as well, and the work of recent years has in fact begun to show such differences—"qualitative" in the sense that phenomena of learning characteristic of some animals fail entirely to occur in others. To establish the existence of such differences is more difficult, however, than it may appear. Let us look at some evidence, first from experiments on the role of reward and then from experiments on discriminative learning.

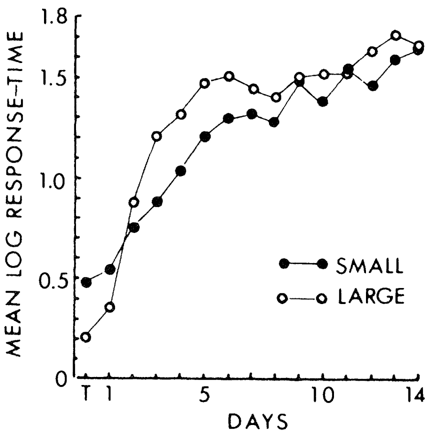


Fig. 3. Runway performance of two groups of rats on the last day of training (*T*) with small or large reward and in subsequent trials without reward (*25*).

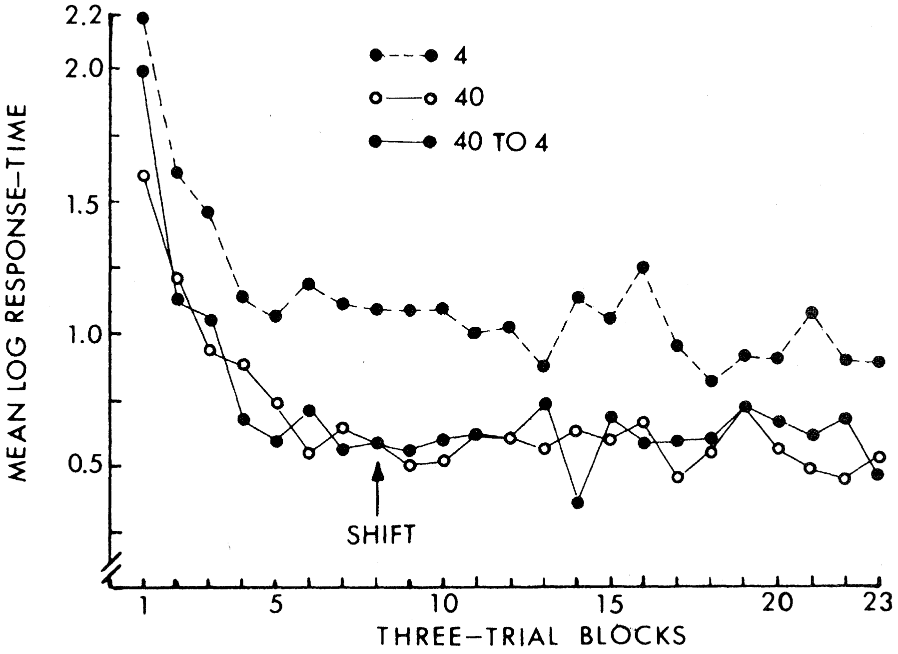


Fig. 2. Target-striking performance of three groups of goldfish, one rewarded throughout with four worms, one rewarded throughout with 40 worms, and one shifted from 40 to four worms (*19*).

After training with a preferred reward laboratory rats work less well for a less-favored reward than do control animals trained from the outset with the less-favored reward. This so-called depression effect was demonstrated first in an experiment whose results are plotted in Fig. 1 (*15*). Two groups of rats were trained in spaced trials to run a maze of 14 choice-points, and the incorrect choices made on each trial were counted. Performance was better for bran mash than for sunflower seeds, but the animals would work reasonably well for the sunflower seeds unless they had previously experienced the bran mash. Subsequent experiments with rats have shown the depression effect also in simple instrumental conditioning situations and with differences in quantity rather than in kind of reward (*16*).

These results bear directly, of course, on the role of reward in learning. According to the S-R (stimulus-response) reinforcement principle, which first was formulated by Thorndike as the law of effect and which dominated the thinking of American learning theorists for half a century, the role of reward is simply to connect responses to stimuli; large rewards produce stronger connections than small rewards, and strong connections produce better performance than weak connections (*6, 17*). An alternative assumption, often characterized as "cognitive," is that reward does not affect learning but is itself "learned about" and therefore comes to be "anticipated," as food which follows the sounding of a metronome may be said to be anticipated by a Pavlovian dog; large rewards produce not better learning but different learning, with level of performance determined by the hedonic value of the anticipated consequences (*18*). The depression effect certainly suggests learning about reward in that shifted animals seem to be affected by the discrepancy between previously encountered and presently encountered rewards. Perhaps more than any other finding, the depression effect was responsible for loss of interest in the S-R reinforcement principle, according to which it is difficult to understand why the shifted animals should show any decrement in performance at all.

From an anthropomorphic standpoint the depression effect seems perfectly reasonable, and one may wonder after the fact why the possibility of any other outcome should ever be considered. Yet analogous experiments with goldfish do, in fact, have quite another outcome. Consider, for example, the results shown in Fig. 2. Goldfish were trained in spaced trials to strike at a target for *Tubifex* worms as reward, and the time between the introduction of the target and the occurrence of the response was measured on each trial (*19*). The curves picture the performance of three groups of animals, one rewarded throughout with four worms for each response, one rewarded throughout with 40 worms, and one shifted to four worms after a period of training with 40 worms. Although the smaller reward produced poorer performance (longer response-time) than the larger reward in the two unshifted groups, the shifted group was entirely unaffected by the change from 40 to four worms, continuing to respond as it had for 40 worms. These results suggest that goldfish do have some respect for the S-R reinforcement principle. It should be noted that the depression effect has failed also to appear in runway (swimway) experiments with goldfish (*20, 21*) and in a runway experiment with painted turtles (*22*).

Another phenomenon with implications for the validity of the S-R reinforcement principle is the inverse relation shown by rats between resistance to extinction of a learned response (that is, persistence of the previously rewarded response after it has ceased to be rewarded) and amount of reward encountered in training (*23, 24*). The relation should be direct rather than inverse if larger rewards produce stronger connections and they in turn produce greater resistance to extinction. As may be seen in Fig. 3, in two groups of rats trained in spaced trials with different amounts of dry food as reward the larger reward produced better performance (quicker response) in training but less resistance to extinction (*25*). Goldfish studied in analogous experiments show more respect for the S-R reinforcement principle (*26, 27*). For example (Fig. 4), in three groups of goldfish rewarded in training with one, four, or 40 worms larger reward produced better performance both in training and in extinction trials (*21*). In painted turtles (Fig. 5) trained with either a small or a large piece of fish as reward the relation between amount of reward and resistance to extinction of the response is direct (*22*). In pigeons rewarded with food for pecking at a transilluminated plastic disk the relationship appears to be inverse (*28*).

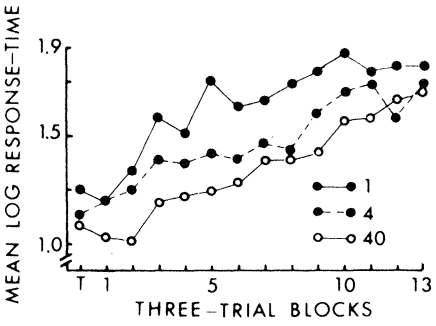


Fig. 4 (left). Runway performance of three groups of goldfish in the last block of training trials (*T*) with one, four, or 40 worms as reward and in subsequent trials without reward (*21*).

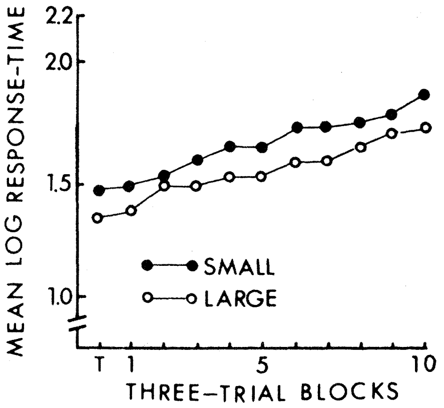


Fig. 5 (right). Runway performance of two groups of painted turtles in the last block of training trials (*T*) with small or large reward and in subsequent trials without reward (*22*).

Experiments on discriminative learning also reveal qualitative differences in the performance of vertebrates of different classes. Consider first the phenomenon of random probability matching. Suppose a goldfish or an African mouthbreeder is trained to discriminate between two stimuli, say, red and green, with the choice of red being rewarded on a random 70 percent of trials and choice of green on the remaining 30 percent. The animal is permitted to correct itself whenever an error is made, so that each trial ends with reward and the red-green reward ratio is in fact 70 : 30. Under these circumstances, typically, the animal's choice ratio comes to equal (that is, to "match") the reward ratio—the animal chooses red on a random 70 percent of trials and green on the remaining 30 percent (*29, 30*). Some representative data for three individual goldfish are plotted in Fig. 6; as the reward-ratio shifted from 70 : 30 to 50 : 50, the choice ratio of each animal did the same (*31*). Comparable results have been obtained in experiments with painted turtles and with pigeons (*32*). An essential feature of the asymptotic behavior at any reward ratio is that it gives no evidence of sequential dependency, hence the term "random."

Occasionally in such experiments nonrandom matching is found—that is, a correspondence of choice ratio to reward ratio which stems from some strategic behavior on the part of the animal. For example, the animal may choose on each trial the rewarded alternative of the immediately preceding trial ("reward following") or it may systematically avoid the rewarded alternative of the immediately preceding trial ("negative recency"). Shown in Fig. 7 is the performance of two rhesus monkeys trained in a red-green discrimination at ratios of 70 : 30, 50 : 50, and 30 : 70. In the 70 : 30 and 30 : 70 problems the animals tended to "maximize," which is to say that they tended consistently to choose the

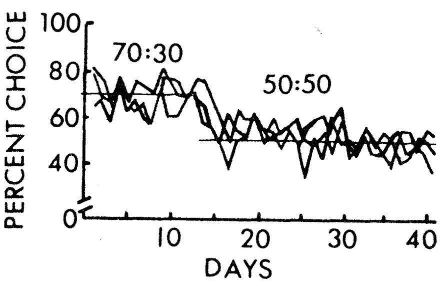


Fig. 6 (left). Percentage of choice of the original 70 percent color by three goldfish trained with a 70 : 30 reward ratio and shifted to 50 : 50 (*31*).

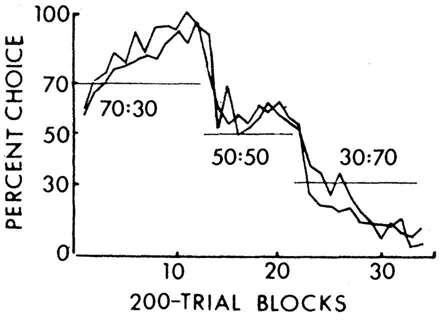


Fig. 7 (right). Percentage of choice of the original 70 percent color by two rhesus monkeys trained with 70 : 30, 50 : 50, and 30 : 70 reward ratios (*33*).

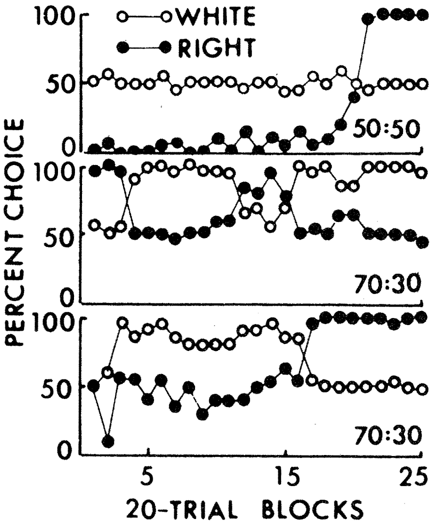


Fig. 8. Performance of three rats trained in 50 : 50 and 70 : 30 black-white problems (*34*).

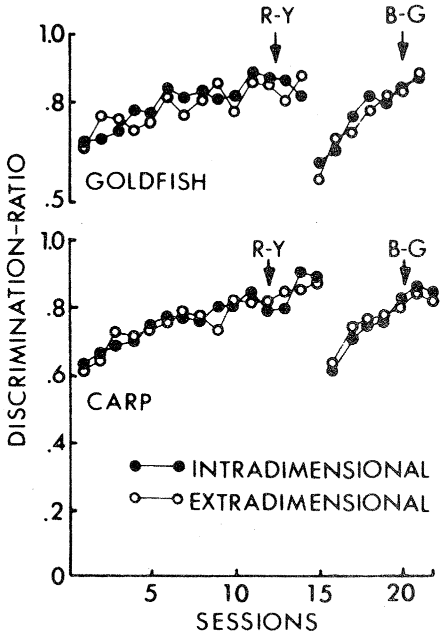


Fig. 9. Performance of groups of goldfish and carp matched for response in an initial discriminative problem with red and yellow horizontal lines (*R-Y*) and then tested in a second problem with blue and green diagonal lines (*B-G*). "Intradimensional" designates groups for which the relevant dimensions of the two problems were the same, "extradimensional" groups for which the relevant dimension of one problem was the irrelevant dimension of the other (*37*).

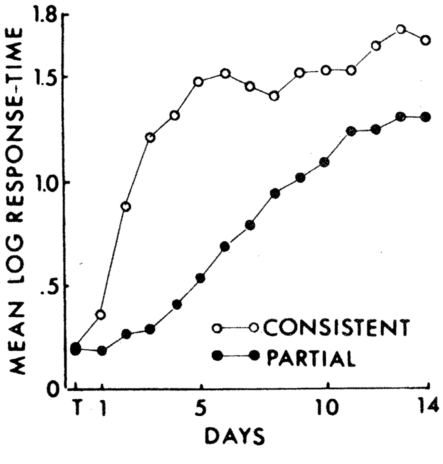
higher-probability alternative, but in the 50 : 50 training they showed negative recency, a strategy that rarely appears at other ratios, presumably because it is too costly (*33*). Rats tend in 50 : 50 problems to fall into rigid position habits and at discriminably different ratios tend to maximize, although often they reward-follow, and on occasion show precipitous shifts in the basis of choice. Some interesting examples are given in Fig. 8. One rat trained in a 50 : 50 white-black problem shows a strong left preference which gives way suddenly to a strong right preference; two other animals trained in a 70 : 30 white-black problem shift unpredictably from choice of white to choice of right (*34*). When the mammalian species studied in such experiments are not maximizing, they are displaying some sort of systematic behavior. Random matching is not always found in African mouthbreeders, goldfish, painted turtles, or pigeons—the conditions required to produce it have not yet been fully defined—but it never has been demonstrated in mammals (*35*).

Another phenomenon of discriminative learning whose generality may be questioned on the basis of recent experiments is the "dimensional transfer effect." Suppose that animals are trained with a set of stimuli consisting of straight lines differing both in color and in angular orientation (say, red and yellow horizontals and verticals), and suppose that color is the "relevant" dimension and angle the "irrelevant" dimension—for example, responses to red lines are rewarded and responses to green lines are not rewarded, irrespective of orientation. After having mastered this problem, the animals are trained with a new set of stimuli differing in the same two dimensions (say, green and blue diagonals), color being relevant again for some and angle now being relevant for others. In experiments with monkeys, rats, and perhaps also pigeons, animals for which the relevant dimension of the first problem is kept relevant in the second perform better than do animals for which the relevant dimension of the first problem is made the irrelevant dimension of the second—that is, intradimensional transfer is better than extradimensional transfer (*36*). This effect fails, however, to appear in carp and in goldfish (*37, 38*). Some sample results with those species are plotted in Fig. 9.

Methodological Problems

The fact that a phenomenon known in one animal fails to appear in a few experiments with a second animal does not prove, of course, that it does not occur at all in the second animal. Laboratory rats do not always show the depression effect; negative results are obtained with low drive, with magnitude of reward defined in terms of amount and concentration of sucrose, or with a long time interval between the training with large reward and with small (*39*). Nor do goldfish and pigeons always show random probability matching; the phenomenon may come and go with seemingly minor variations in training procedure (*31, 40*). The failure of the depression effect to appear in goldfish or of random probability matching to appear in rats is significant only on the assumption that the conditions under which the animals have been compared are indeed equivalent, an assumption which is difficult to justify. How, for example, are rats and fishes to be made equally hungry? Or how is the incentive value of food pellets for rats to be compared with that of *Tubifex* worms for goldfish?

An alternative to equating the experimental conditions for different animals (which we as yet have no way to do) is to vary them systematically (*41*). Consider,



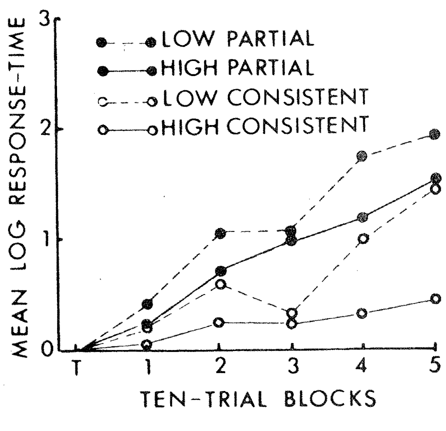


Fig. 10 (left). Runway performance of two groups of rats on the last day of training (*T*) with consistent or partial reward and in subsequent trials without reward (*25*). Fig. 11 (right). Target-striking performance of four groups of African mouthbreeders on the last block of training trials (*T*) with consistent or partial reward and in subsequent trials without reward. One consistently rewarded and one partially rewarded group were maintained throughout at a low level of hunger and the other groups at a substantially higher level (*43*).

for example, the so-called partial reinforcement effect: in rats, "partial" or intermittent reward during training (say, on a random 50 percent of trials) typically produces greater resistance to extinction than does consistent reward during training (*42*). Sample data are plotted in Fig. 10. Two groups of rats were trained in a runway with spaced trials and large reward, one group partially and the other consistently rewarded. The two groups were responding with equal promptness at the end of training, but the consistently rewarded group showed much less resistance to response extinction (*25*). Plotted in Fig. 11 are the results of a spaced-trial partial reinforcement experiment with African mouthbreeders maintained on two different feeding schedules, one designed to produce only moderate hunger and the other to produce a much stronger drive (*43*). At each level of drive, resistance to extinction was greater after consistent than after partial reward—an outcome quite opposite to that of rat experiments—and the invariance of the outcome with drive level makes it unlikely that the difference is the product of a difference in strength of drive. The possibility that the experimental conditions for the two species were not equivalent in other potentially important respects, such as sensory demand, attractiveness of reward, or effortfulness of response, may be examined in like manner.

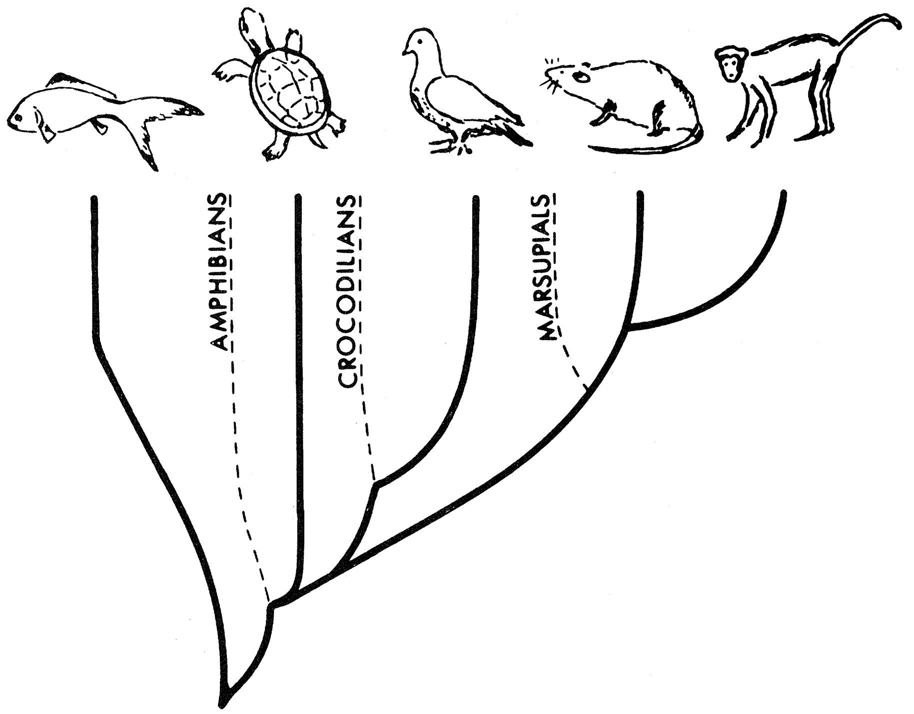


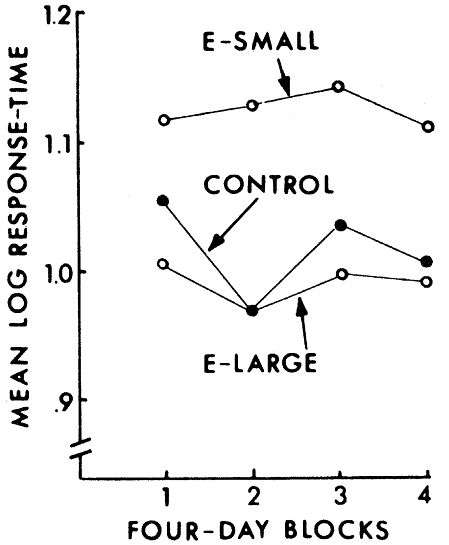
Fig. 12. Rough sketch of the evolutionary relationships among the species studied in these experiments. The broken lines show other lineages that might profitably be represented.

Unfortunately, systematic variation is a rather expensive control procedure. The number of variables that conceivably may determine the appearance of even the simplest phenomenon of learning is quite large, and if their interactions also are considered (as they must be), a factorial study of tremendous proportions is called for. It is tempting, therefore, not to examine each cell, but simply to sample the factorial space, with emphasis perhaps on any variables which may have been found to be of importance for animals that do show the phenomenon. There is always the danger, however, that the sample will not be large enough. In general, the wider the range of circumstances under which a given phenomenon appears in one animal and fails to appear in a second animal, the more plausible is the assumption that it is not to be found at all in the second. Both conditions are important. Consider, for example, the "overlearning-reversal effect": rats trained to discriminate between two stimuli and then to reverse the discrimination may not accomplish the reversal as readily as do rats that have been overtrained extensively in the original discrimination. This effect is found often enough to suggest that it is a genuine one, but since it fails more often than not to appear in rats (*44*) little significance can be attached to the fact that it has failed to appear in two experiments with fishes (*45*).

The scope of parametric variation may be restricted, too, on the basis of certain internal consistencies in the data. For example, confidence in the negative results obtained with one animal may be strengthened by negative results with another. We may be guided also by considerations of functional consistency [compare (*46*)]. If the analysis of two phenomena, both of which appear, say, in rats, suggests that they are functionally related, and if one of them fails in the course of extensive research to appear in goldfish, then less work will be required to convince us that the other also is absent in goldfish. It is useful as well to consider what may be called consistency with evolutionary relationships. Sketched in Fig. 12 is a simplified phyletic tree on whose topmost branchings are arrayed the widely divergent extant species used in these comparative studies. Now suppose that some phenomenon which is characteristic of rats and rhesus monkeys has failed in the course of intensive research to appear in either goldfish or pigeons; less work then will be required to convince us that it is not to be found in painted turtles. If, however, a phenomenon appeared both in goldfish and in pigeons, we should certainly not be easily convinced of its absence in painted turtles.

The problem of interpretation is by no means so simple, of course, as the foregoing treatment may suggest. The common ancestor of fishes and reptiles may have possessed some behavioral property which was selectively lost in the turtles. The possibility of convergence also must be considered—teleost fishes and birds may have developed quite independently some behavioral property which was not present in their common ancestor—although it may be argued that convergence to the point of identity or even of seriously confusing similarity is rather unlikely in "elaborately polygenic" behavioral systems (*47*). It is interesting to note in any case that all the patterns of difference which have been considered here are directly understandable in terms of the evolutionary history of the species compared, with no assumptions either of selective loss or of independent development being required. For example, experiments on probability learning distinguish goldfish, painted turtles, and pigeons from rats and monkeys, whereas experiments on the inverse relation between amount of reward and resistance to extinction distinguish goldfish and painted turtles from pigeons and rats. What will happen when the range of animals and the range of phenomena studied are extended remains, of course, to be seen. The broken lines in Fig. 12 show some other lineages that might well be represented in these studies.

It has been argued that comparisons of such diverse animals as goldfish, turtles, pigeons, rats, and monkeys can tell us nothing at all about the evolution of behavior



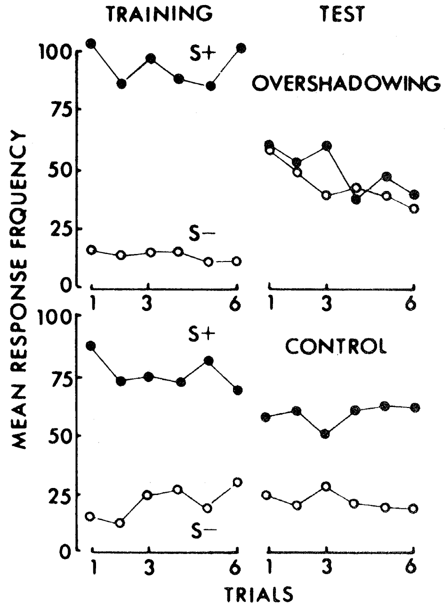


Fig. 13 (left). Asymptotic target-striking performance of two groups of goldfish, an experimental group (*E*) trained with small reward for response to one color and large reward for response to a second color, and a control group trained with small reward for response to both colors (*54*). Fig. 14 (right). Response of two groups of carp to positive (*S*+) and negative (*S*−) stimuli on the last day of training and in subsequent test with response to neither stimulus rewarded. The training stimuli were 30° and 60° lines, one red and the other green for the experimental ("overshadowing") group, and both red or both green for the control group. In the test, both lines were yellow for both groups (*38*).

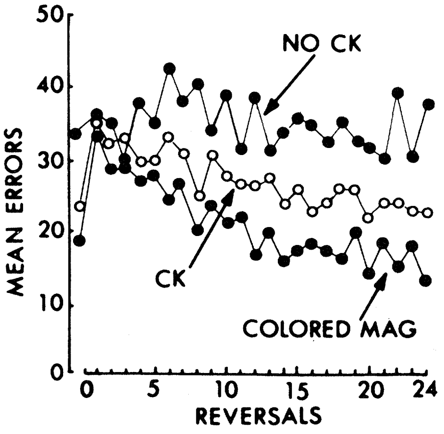
since the animals do not constitute an evolutionary series, and that there is no meaningful way of ordering living animals in relation to lines of descent—that "the sequence of animals from left to right" in a diagram such as that shown in Fig. 12 "is completely arbitrary" (*1*, p. 339). In fact, however, trees drawn with random sequences may be hopelessly complex; one simplifying dimensional principle is recency of common ancestry with man (*48*). As to the evolution of behavior, I see no reason why the behavioral properties of extinct animals cannot, like their morphological properties, be inferred from those of living descendants on the principle that (barring convergence) properties common to a set of animals are attributable to their common ancestor. The more distantly related the animals compared, the more remote the common ancestor about whose functional properties we are informed, and the more likely we are to come upon any functional divergences that may have occurred. The discovery of different learning processes in any two species whatever would permit at least the conclusion that there has been divergence, which is by no means so trivial as it might appear to one unacquainted with the history of thought on the subject. Comparisons of more closely related animals certainly are not without interest; as I have noted before, unique results obtained with goldfish or pigeons immediately suggest the question of generality over order or class (*49*). It should be evident, however, that comparisons of distantly related animals, although not much more costly than comparisons of closely related animals, provide a much broader picture of the evolution of behavior.

Learning Phenomena and Learning Processes

Although similarities and differences in the performance of diverse animals in a variety of learning situations are interesting in themselves, their principal importance lies in what they tell us about underlying processes. Learning processes are not, of course, given directly in the data of learning experiments but are inferred from those data, and the relation may be rather complex (*50*). Different phenomena may be produced by the same processes, and what appear to be identical phenomena may be produced by different processes. Consider, for example, the depression effect and the inverse relation between amount of reward and resistance to extinction. Given the finding that the depression effect increases with the difference in size between present and past rewards (*51*), and treating nonreward as a point on the amount-of-reward continuum, we may understand both effects as reactions to discrepancy between anticipated and actual amounts of reward. Evidence compatible with this interpretation comes from the comparative studies already reviewed: rats show both effects, whereas goldfish and painted turtles show neither. If the processes responsible for two phenomena are the same, then we may expect that any animal which shows one will show the other also. If, however, an animal can be found that shows one phenomenon but not the other, we may suspect that the processes are different (*52*).

A phenomenon found in rats and pigeons that may seem at first to be closely related to the depression effect is "simultaneous incentive contrast" (*53*). As in the depression effect, performance for a smaller reward is impaired by experience with a larger reward, but in this case the two rewards are encountered concurrently rather than successively. Plotted in Fig. 13 is the asymptotic performance of a group of goldfish rewarded with about ten times as much liquid food for response to one color as for response to another color, along with the performance of a control group rewarded with the smaller amount of food for response to either color (*54*). The experimental animals responded to the small-reward color more slowly than did the controls. Despite the intuitive similarity of this effect to the depression effect, then, the fact that goldfish show one but not the other suggests that the underlying processes are not entirely the same.

The point is important enough, perhaps, to warrant another example. Consider the fact that learning about A, a component of the compound stimulus AB, may be impaired by the presence of B, a phenomenon known as overshadowing. Plotted in Fig. 14 is the performance of two groups of carp trained to discriminate between straight lines with orientations of 30 and 60 degrees from the vertical (*38*). For the experimental ("overshadowing") group the lines differed also in color, one red and the other green; for the control group the lines were of the same color, either red or green. After the animals had mastered the discrimination they were tested with yellow lines differing only in orientation. The experimental group had learned little about orientation, evidently having dealt with the original problem primarily in terms of the more salient color cues. Although it has been proposed that overshadowing and the dimensional transfer effect may have a common attentional basis (*46*), the fact that carp show overshadowing but not dimensional transfer (see Fig. 9) suggests that different processes may be involved. Much more serious consideration now must be given to a recently proposed nonattentional theory of overshadowing which, because it does not handle the dimensional transfer effect, might otherwise seem superfluous (*55*). Another phenomenon which has been reported in fishes (*56*) as well as in a number of other vertebrates and which usually is interpreted in attentional terms is transfer along a continuum. For example, rats trained to choose the lighter of two quite different grays and then trained to choose the lighter of two rather similar grays do better than rats trained from the outset with the more similar grays (*57*). Unfortunately, proper controls for general transfer are lacking in the fish experiments. The importance of such controls is demonstrated by a recent study in which goldfish shifted to a difficult tonal frequency discrimination after training on an easy color discrimination did better than goldfish trained from the outset with the tones (*58*). There is now no good evidence of attention in fishes.



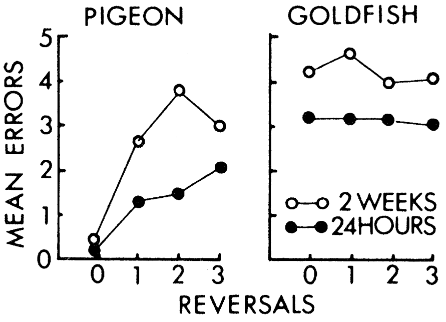


Fig. 15 (left). Target-striking performance of three groups of goldfish trained in a series of reversals of a red-green discrimination. For the group designated *No CK* each trial began with the presentation of the red and green alternatives. For both the other groups each trial began with the presentation of a center key, response to which was required for presentation of the red and green alternatives, but during presentation of reward for correct choice the *Colored Mag* group was exposed to a light of the positive color while the *CK* group was exposed to a white light (*71*). Fig. 16 (right). Performance of pigeons and goldfish in tests of retention given 1 day or 2 weeks after mastery of an original red-green discrimination and each of three subsequent reversals (*73*).

Even what seems to be the same phenomenon in two different animals, or in the same animal studied under two different conditions, may in fact be produced by different processes. For a good many years unsuccessful attempts have been made to develop a common explanation of "the" partial reinforcement effect found in rats. According to the sensory carry-over theory, resistance to extinction is greater in partially rewarded animals because whenever a rewarded training trial follows one or more unrewarded trials the animals are rewarded for responding to the sensory aftereffects of nonreward (such as feedback from an emotional reaction to nonreward)—aftereffects that will be met again in extinction (*59, 60*). To account for the fact that rats show the partial reinforcement effect even in widely spaced trials (which should permit dissipation of aftereffects in the intertrial intervals), the notion of sensory carry-over has been broadened by vague reference to "memory" (*61*), but sequential influences cannot be detected over intertrial intervals as long as those that yield the partial reinforcement effect (*25, 62*). According to a rival theory, an emotional reaction to nonreward is conditioned to situational cues on unrewarded trials and evoked again by those cues on subsequent trials, both rewarded and unrewarded, independently of the intertrial interval and of the sequence of rewarded and unrewarded trials [(*63*); see also (*59*)]. A large body of data on the performance of partially rewarded animals as a function of the pattern of partial reinforcement (the sequence of reward and nonreward) in massed trials cannot, however, be accounted for in these terms (*42*).

That no satisfactory common explanation of the partial reinforcement effect in massed and spaced trials has yet been found is not surprising in the light of comparative studies. Although pigeons, like rats, show the partial reinforcement effect both in massed and in spaced trials (*64*), fishes (*43, 65*) and turtles (*22, 66*) show the effect only in massed trials, a pattern of results that suggests the operation of different processes. One of these processes seems to be sensory carry-over, effective only in massed trials and assumed to operate in all of the animals studied. Another process—effective both in massed and in spaced trials and assumed to operate only in animals which show the partial reinforcement effect in spaced trials—may be the same as that which produces both the depression effect and the inverse relation between amount of reward and resistance to extinction. It should be noted that rats show the partial reinforcement effect in spaced trials only with large reward, which serves primarily to reduce resistance in the consistently rewarded animals (*24, 25*).

The work on partial reinforcement has an interesting strategic implication. One might be willing to assume, as was Thorndike, that the processes of learning in two animals are the same if the phenomena of learning shown by them are the same. From this point of view, only a qualitative difference in performance as already defined—the failure of a phenomenon of learning known in one animal to appear in another—can provide any basis for suspecting the operation of different processes, but now it seems that such an approach is too conservative, and that grounds for suspecting the operation of different processes are provided also by a striking difference in the conditions under which some phenomenon occurs in two animals (*67*). The difficulty of determining when physically different conditions are functionally equivalent for different animals (to which reference already has been made) does, of course, create something of a dilemma; it may seem reasonable in certain cases to use the occurrence of the phenomenon to define the equivalence of the conditions under which it appears in different animals, assuming that the learning processes are the same. Which alternative is more plausible will depend in part on the nature of the differences in the conditions under which the phenomenon appears and in part on the fine grain of the data, which those differences may impel us to scrutinize carefully.

Consider the phenomenon of progressive improvement in reversal, which has been studied extensively in comparative experiments. After an animal is trained in a discriminative problem, the positive and negative stimuli are reversed, then reversed again, and again, until performance has stabilized. Painted turtles, pigeons, rats, and many other vertebrates show progressive improvement (as measured by errors per reversal) under a wide variety of conditions in such experiments; only rarely does improvement fail to occur [for representative experiments see (*29, 68, 69*)]. In choice experiments with fishes, by contrast, improvement *occurs* only rarely, although it does occur (*29, 70*). Plotted in Fig. 15 is the performance of three groups of goldfish trained under different conditions in a series of 24 red-green reversals (*71*). The top curve shows no improvement—the usual outcome. The middle curve is for animals trained with "center key" (a white target), response to which at the start of each trial earns the opportunity to choose between red and green. The bottom curve is for animals exposed to the positive color of each problem during each presentation of reward for correct choice. The fact that such stratagems are quite unnecessary to produce substantial improvement in choice experiments with other vertebrates leads to the suspicion of difference in process, a suspicion which is strengthened by analysis of the course of improvement.

An important component of improvement in rats and pigeons is a decline in retention, which has been attributed to interference (*72*). At the outset of each early reversal, the animals show a strong preference for the positive stimulus of the immediately preceding problem, but as training continues the preference established in each reversal tends increasingly to be lost in the interval between reversals, until at asymptote the animals may begin each reversal without any retarding preference at all for the previously positive stimulus. No such decline in retention has been found in fishes. Plotted in Fig. 16 are the results of an experiment with pigeons and goldfish trained in an original red-green discrimination followed by three reversals, with a retention test given either 1 day or 2 weeks after each problem (*73*). The retention of the pigeons, almost perfect to begin with, became worse over the series of problems, but the retention of the goldfish, although not so good to begin with as that of the pigeons, did not change. Progressive improvement probably is due in part also to general transfer effects such as are observed when animals are trained in a series of unrelated discriminative problems and which are attributable to common features of the problems apart from the stimuli to be discriminated. In rhesus monkeys and in chimpanzees, training in a series of reversals has been found to facilitate subsequent performance in a series of problems with unrelated objects (*69, 74*), and evidence of general interproblem transfer appears also in experiments with goldfish (*75*).

Since performance in learning situations is determined by a variety of processes other than learning, differences in performance may be due to differences in processes other than learning. This question is not the same as the question about the equivalence of experimental conditions and arises even if that equivalence is stipulated. Consider, for example, the depression effect. To explain the results for goldfish, it may be assumed that their performance is not governed by anticipation of reward—that they are Thorndikian animals in which larger rewards simply produce stronger connections. It is possible also, however, that the difference between goldfish and rats is emotional—that goldfish either do not become upset about a discrepancy between anticipated and actual rewards, or that their emotional response to such a discrepancy does not compete with instrumental behavior as it is assumed to do in rats.

Results compatible with this interpretation have been obtained in a depression experiment with rats tranquilized by injections of amobarbital sodium; like goldfish, the drugged rats discriminated between large and small rewards but were unaffected by the change (*76*). What is required is an experiment designed to provide independent evidence of learning about reward in goldfish, such as a Thorndikian placement experiment (*77*). It is interesting that simultaneous incentive contrast in goldfish might easily have been interpreted in terms of learning about reward if those animals also showed the depression effect, although a perfectly plausible interpretation in terms of sensory contrast can be offered (*78*).

If the Thorndikian explanation of the results for goldfish proves correct, it will be tempting to conclude that the Thorndikian process operates also in rats but is masked in depression (and related) experiments by anticipation of reward and the consequences of unrealized anticipation. (The depression effect does not contradict the S-R reinforcement principle; it calls only its sufficiency into question.) Other evidence of the masking of what may be a phyletically older and perhaps quite general process by one of more recent origin comes from experiments on probability learning. Although random probability matching does not occur in normal rats, it has been found in rats which have been extensively decorticated at an early age (*79*).

The learning processes that we now are able to infer from performance in learning situations are far removed, of course, from learning mechanisms. They are at best a series of functional principles (like the S-R reinforcement principle) from which the observed phenomena of learning can be deduced and which may be expected to guide the search for mechanisms (*80*). At the

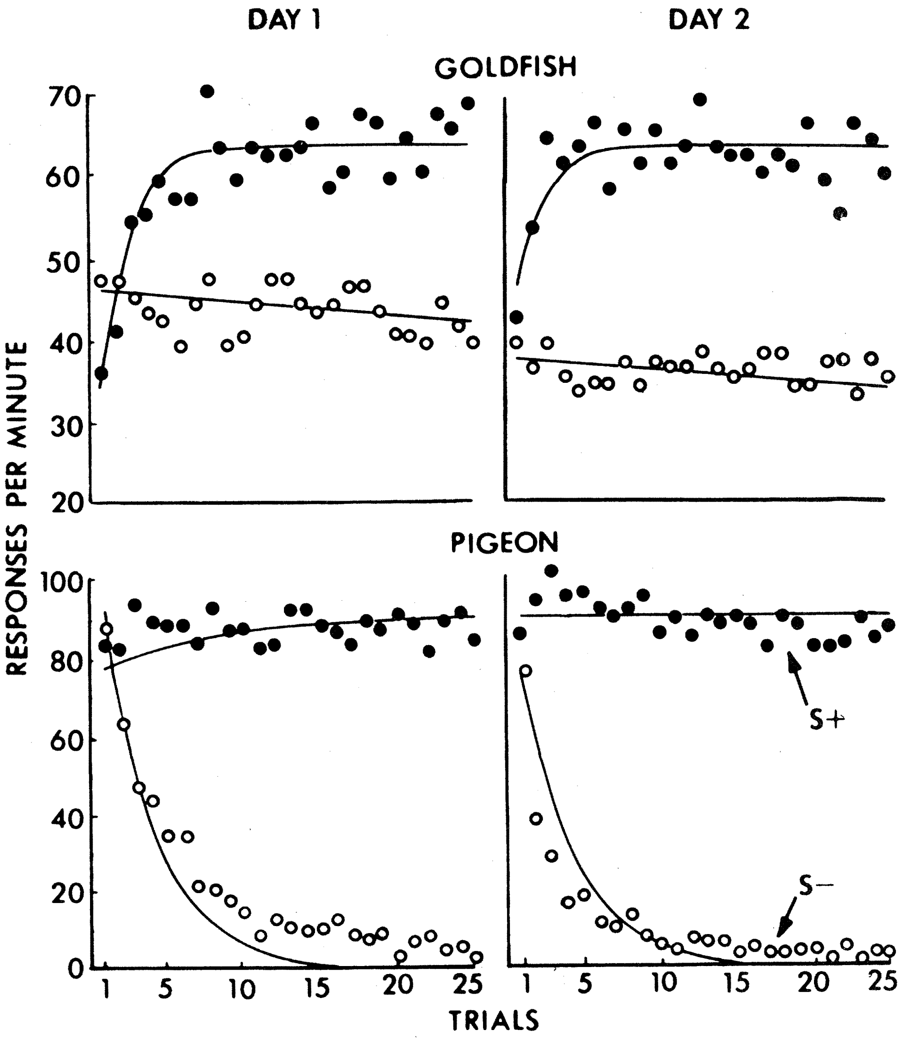


Fig. 17. Asymptotic performance of pigeons and goldfish trained in a series of 2-day red-green reversals (positive and negative stimuli reversed every 2 days). The smoothed curves are predictions from a model, developed on the basis of a variety of pigeon data, which differs for the two species only with respect to the values of five free parameters (*82*).

present stage of the inquiry, the question whether the processes of learning are the same in all animals reduces to the question whether the performance of all animals can be deduced from a common set of principles or whether different principles are necessary. It should be evident that the answer to this question must come not from casual work with a large assortment of animals but from intensive work with a small number of widely divergent forms. Thousands of learning experiments with rats have not yet yielded a set of principles from which the performance of rats can be derived satisfactorily, although a great deal of progress has been made in the 75 years or so since the first rat was introduced into the first maze (*81*). By comparison, the quantity of data from which a set of principles for goldfish or painted turtles might be derived is small indeed. There should, of course, be considerable transfer from work with one animal to work with another. Long experience in the analysis of learning in rats should help us to get more quickly at the principles of learning in goldfish, and (as already has been noted) similarities and differences which appear in analogous experiments with goldfish should contribute to the analysis of learning in rats.

It may be well to emphasize that qualitative differences in performance do not necessarily imply the operation of different processes but perhaps may be explained in terms of purely quantitative variations in the operation of common processes. Consider the rather striking contrast afforded by the asymptotic red-green reversal performance of goldfish and pigeons plotted in Fig. 17. At this point in the experiment, there were 25 20-second presentations of each stimulus on each day in balanced quasi-random orders, with positive and negative colors reversed every 2 days. The patterns of change in the performance of the two animals are quite opposite in direction: the principal change in goldfish is in rate of response to the positive stimulus, which increases within sessions and decreases between sessions, while the principal change in pigeons is in rate of response to the negative stimulus, which decreases within sessions and increases between sessions. Nevertheless, the data for both animals can be derived (as the fitted curves show) from a set of five principles stated in mathematical terms and differing for the two animals only in the values of five free parameters which have to do with learning rate, forgetting rate, and the like (*82*).

What we have here is not just a simple exercise in curve fitting. The principles, which have clear functional meaning, along with the parametric values for the pigeons were worked out on the basis of the performance of the pigeons over the entire course of reversal learning and a substantial range of asymptotic conditions varying in number of trials per session, number of sessions per reversal, amount of reward, intertrial interval, intersession interval, and point of reversal (within or between sessions). These variations suggested that the simplest Pavlovian theory of performance as some algebraic function of independent excitatory and inhibitory processes generated by reinforcement and nonreinforcement (*7*) cannot deal with reversal learning. If excitatory and inhibitory growth is asymptotic, reversal must eventually become impossible unless there is some weakening in one or both processes. Pavlov assumed temporal decay, but the rates of decay estimated from data on intertrial and intersession intervals are far too low to account for the precipitous within-sessions reversal of which sophisticated pigeons are capable. An alternative assumption (incorporated in the present model) is that nonreinforcement produces not an independent, countervailing inhibitory process but a decrease in excitation. Whatever the correctness of this assumption or of the entire model, the same equations with altered parametric values fit the goldfish data.

Quantitative differences in the performance of his several species led Thorndike to postulate quantitative differences in their learning ability, as, for example, in the extent to which sensory-motor connections in a given animal are strengthened by a given amount of reward (*6*). Many subsequent attempts to find meaningful relations between taxonomic status and purely quantitative features of performance in learning situations have come, however, to nothing (*83*), and the reasons should not be difficult to understand. Learning scores vary widely even in a single species as a function of sensory, motor, and motivational conditions. Consider again, for example, the reversal curves plotted in Fig. 15, which certainly would yield very different estimates of the "learning ability" of goldfish. The idea that animals may be ordered with respect to learning ability or "plasticity" on the basis of interproblem transfer in discriminative learning—the rate of improvement shown or the level of performance ultimately achieved in the course of training in long series of discriminative problems—has been surprisingly persistent (*84*), although variables such as sensory capacity obviously must play an important role. It has been argued that the *best* performance found in a species tested under a variety of conditions affords a useful index of plasticity (*85*), but the argument is unconvincing. Assume that performance in a series of discriminative problems is a function of only two variables—sensory capacity and plasticity—and that the highest score of species A exceeds that of species B. Without an independent measure of sensory capacity, nothing can be said about plasticity, which actually may be greater in species B. It is interesting to contemplate that the only road to the specification of quantitative differences in the operation of learning processes common to diverse species may be the same difficult road as to the discovery of the processes themselves—that meaningful answers to questions about quantitative differences in learning are to be found only in the parameters of the equations which describe the learning processes (*86*).

Thorndike himself worked only with vertebrates, but the early work of others led him to conclude that the same processes of learning operate also in invertebrates (*6*), and contemporary students of learning in honey bees and octopuses have not hesitated to draw the same conclusion on the basis of the performance of their animals in situations patterned after those used for the study of learning in vertebrates (*87*). Behavioral similarity in animals of different ancestry is, of course, to be expected from common selective pressures and may carry with it some similarity of mechanism—given the laws of physics and the properties of available materials, there are only so many ways to build a bridge (*88*). We cannot now say, however, whether the resemblance between vertebrate and invertebrate learning is any more profound than that between the hand of an ape and the claw of a lobster. Although a great deal of effort has been expended in the study of invertebrates, much of the work is faulty in method or design, progressing only rarely beyond the primary question whether the subjects are capable of learning at all (*89*). It is to be hoped that these deficiencies will be remedied as experience in the study of vertebrates is brought to bear on the problem—that we shall have before long some detailed comparative data on what surely must be regarded as independently developed mnemonic solutions to common problems of adjustment.

The Ethological Influence

At a conference in The Hague about 10 years ago, after I had described certain differences in the instrumental performance of albino rats and African mouthbreeders and suggested that they might reflect differences in learning, Lorenz commented that however surprising such a finding might be to a psychologist, it certainly would come as no surprise to an ethologist.

While the strategy of psychologists is to assume that the processes of learning in two animals are the same until proved to be different, he asserted, the strategy of ethologists is to assume that the processes are different until they are proved to be the same. Whatever the merit of the ethological approach as characterized by Lorenz, or the accuracy of the characterization, it should not be thought that psychologists who have been influenced by ethology in their rejection of the more parsimonious Thorndikian view deny all communalities or shirk their just burden of proof. The evidence they offer simply is not persuasive.

The fact that performance in learning situations may be influenced by "species-typical" or "species-specific" responses to reinforcement does not necessarily imply the operation of species-specific learning processes. Consider, for example, the much-cited observation that pigs trained to deposit coins in a food dispenser may persist in dropping the coins to the ground and rooting them (*90*), behavior which is easy to understand in terms of conditioning. Tokens paired with food should be expected to evoke responses like those elicited by the food, and to the extent that those responses are incompatible with the instrumental response the animal will have difficulty; to the extent that they are compatible, of course, there will be much less difficulty. The finding that rats trained to avoid shock acquire certain avoidance responses more readily than others (*91*), which has been explained as due to associative predisposition or "preparedness" (*12*), also can be explained as due to differences in compatibility of the alternative avoidance responses with the unconditioned response to shock. Since the warning stimulus is paired with shock whenever the animal fails to avoid, the response to shock is conditioned to that stimulus and tends, therefore, to interfere with any incompatible response.

Another much-cited finding is that pigeons come to peck at an illuminated key when illumination of the key is paired repeatedly with the presentation of food (*92*), although it is easy to see in this "autoshaping" (as it is called) another instance of classical conditioning. Not only pigeons but a variety of animals tend to approach, contact, or manipulate localized stimuli paired with reward (*93*). Just as in Pavlov's experiments on salivation in dogs with meat powder or weak acid as the unconditioned stimulus (*7*), so also in experiments on key-pecking in pigeons with grain or water as the unconditioned stimulus (*94*), the properties of the conditioned response are found to reflect the properties of the reinforcement. The fact that autoshaped pigeons continue to peck at the key even when the response prevents presentation of the food (*95*)—although not, of course, with the same frequency as when pecking always is followed by food (*96*)—has suggested the possibility that the extinction functions for "prepared associations" and "unprepared associations" may be different (*12*), but the results are perfectly understandable in terms of general principles of conditioning. The tendency to peck the lighted key, established to begin with by the pairing of key light and food, is weakened by the nonoccurrence of food whenever pecking occurs, but strengthened again by the pairing whenever pecking fails to occur. Comparable results have been obtained in experiments on salivary conditioning in dogs (*97*).

Perhaps the best-known evidence for associative predispositions is provided by an experiment in which rats made ill by x-irradiation after eating a given food developed an aversion to its taste rather than to its visual appearance, while the opposite was true of rats shocked for eating the food (*98*); but here too an alternative interpretation is available. The results for irradiation may be attributed to the fact that gustatory stimuli persisted in the interval between irradiation and illness whereas visual stimuli, of course, did not. The results for shock may be attributed to the fact that the visual stimuli antedated shock by a short interval favorable to conditioning (since the animal saw the food before taking it), whereas the gustatory stimuli were at best simultaneous with shock and may even have followed it (since the animals were shocked immediately upon taking the food). Testing conditions also were confounded with modality; since the visual stimuli antedated the criterion response (eating) and the gustatory stimuli followed the response, it should not be surprising that the visual group hesitated much longer than the taste group before taking the food.

The very fact that taste aversions develop with intervals between ingestion and illness far longer than those which have been found effective in conventional conditioning experiments (*99*) has been taken as evidence of associative predisposition. The possibility that smell and taste receptors are stimulated again at the time of illness by food returned to the mouth from the stomach has not, however, been properly controlled (*100*). I should like to know, for example, whether illness produces aversion to a food introduced into the stomach by fistula. Problems of control abound in these aversion experiments, perhaps because they are not always uppermost in the minds of the investigators. The view actually has been expressed that it "doesn't matter" whether a food aversion is the product of conditioning or pseudoconditioning, that what is important is that "behavior shows astonishingly organismic properties" (*101*).

Even if associative predispositions are assumed, there is no reason to believe that unique processes are required for their realization. Learning often involves the differential strengthening of existing behavioral tendencies rather than the establishment of entirely new ones (*6, 17*). Furthermore, even if it were demonstrated that "prepared" and "unprepared" associations are established by different processes, it might still be true that the same processes are to be found in all animals. A peculiar feature of this new, ethologically oriented comparative psychology is that it leads only rarely to the comparison of different animals, questions of generality within species and generality across species being run together in the criticism of "general process" theory. Evident, too, is a certain lack of interest in functional analysis, for which loose speculation about adaptive significance is substituted. If it is true that quail but not rats are capable of associating visual properties of food and illness (*102*), the explanation must be found not in their differing environments but in their differing structures, which in turn must be understood in terms of their evolutionary histories. The adaptive significance of some capability of an animal in the environment in which we now find it, even if accurately assessed, tells us nothing about the structural basis of the capability or about the evolutionary history either of the structure or of the capability.

Are the laws of learning the same in all animals? Certainly it is safe to assume that there are important communalities at least in the learning of vertebrates. Whether there are important differences as well remains to be determined, but recent evidence suggests that it may be useful now for students of learning to take up again with renewed vigor the line of research begun by Thorndike at the turn of the century.

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5. "The function of the intellect is to provide a means of modifying our reactions to the circumstances of life, so that we may secure pleasure, the symptom of welfare. Its general law is that when in a certain situation an animal acts so that pleasure results, that act is selected from all those performed and associated with that situation, so that, when the situation recurs, the act will be more likely to follow than it was before. . . . The intellectual evolution of the race consists in an in-

crease in the number, delicacy, complexity, permanence and speed of formation of such associations. In man this increase reaches such a point that an apparently new type of mind results, which conceals the real continuity of the process. . . . Amongst the minds of animals that of man leads, not as a demigod from another planet, but as a king from the same race" (*6*, p. 294).

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9. It may be interesting to consider some more recent statements of the same point of view. With reference to almost identical records of the performance of a pigeon, a rat, and a monkey trained under analogous conditions, B. F. Skinner has written: "Pigeon, rat, monkey, which is which? It doesn't matter. Of course, these three species have behavioral repertoires which are as different as their anatomies. But once you have allowed for differences in the ways in which they make contact with the environment, and in the ways in which they act upon the environment, what remains of their behavior shows astonishingly similar properties" [in *Psychology: A Study of a Science*, study 1, S. Koch, Ed. (McGraw-Hill, New York, 1959), vol. 2, p. 374]. According to H. F. Harlow, "it is not unreasonable to hypothesize that the fundamental process of learning has probably remained essentially unchanged for near-countless millions of years. Furthermore, there is nothing relating to the slow, but progressive, evolution of the nervous system to suggest any great master mutation giving rise to any new learning mechanism" (*ibid.*, p. 531).
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