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THE EVOLUTION OF INTELLIGENCE

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THE EVOLUTION OF INTELLIGENCE

It has been assumed that the intelligence of animals on various rungs of the evolutionary ladder differs only in degree. New experiments on animals from fish to monkey show that the differences are qualitative,

by M. E. Bitterman

Suppose an animal is given a choice between two alternative courses of action, one of which is rewarded consistently and the other never. If the alternatives are readily discriminable, the animal will, after a number of trials, develop the habit of choosing the rewarded one. By plotting trials against errors, the experimental psychologist constructs a curve called a learning function that summarizes the course of the animal's mastery of the problem.

It has been known for some time that learning functions based on such simple problems do not differ significantly among diverse animals; the curves for a monkey and a fish, for example, have a similar shape. This fact, implying some intellectual continuity throughout the evolutionary hierarchy of animals, tended to corroborate a theory of animal intelligence that prevailed during the first half of the 20th century.

According to this theory, an animal is born with tendencies to react in certain ways to certain stimuli—tendencies based on inherited neural connections between sensory and motor systems. The animal's ability to learn is simply its ability to modify these connections (to break some and to form others) as needs and circumstances dictate. Differences in intelligence from species to species are differences only of degree. The higher animals can form more connections than the lower animals because of better sensory and motor development and because their nervous systems afford more elements for this purpose. Hence the evolution of intelligence merely entails refining old processes and replicating old neural equipment.

Since learning was thought to involve qualitatively similar processes throughout the evolutionary hierarchy it seemed that there was nothing to be gained

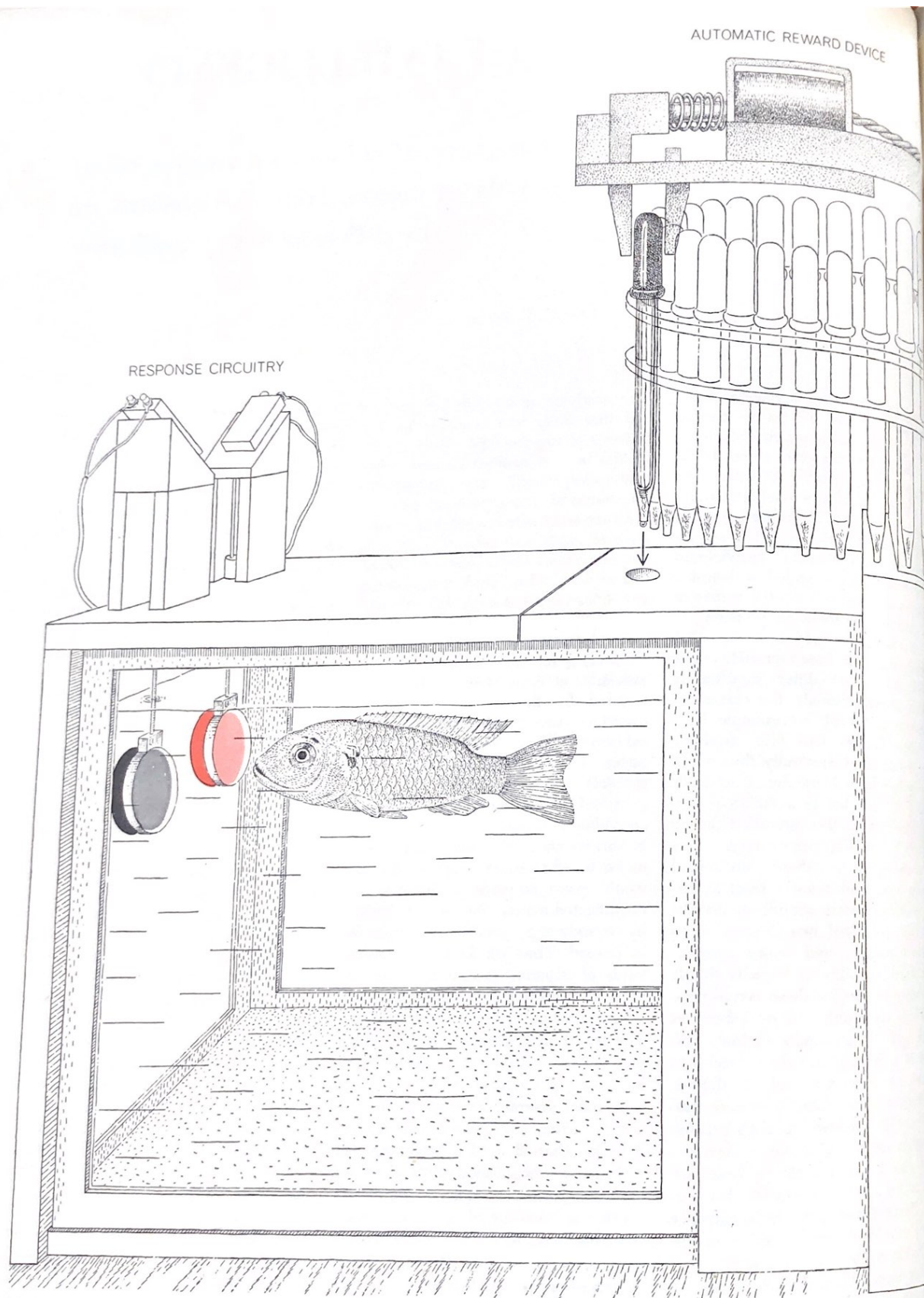
from studying many different species, and that there was much to be lost in terms of experimental efficiency. Attention became concentrated on a few mammals—primarily the rat—selected for reasons of laboratory custom or convenience and treated as being representative of animals in general. The number of animals under study narrowed, and so did the likelihood of discovering any differences that might in fact exist.

The investigations I have been conducting for several years with my associates at Bryn Mawr College were inspired by the conviction that the traditional theory called for more critical scrutiny than it had received. We began with the knowledge that the simplest problems would not serve to reveal distinct modes of intelligence and different neural mechanisms at work in various animals. Hoping that experiments based on more complex problems would point to such differences, we complicated matters for our test animals by introducing certain inconsistencies in reward. Thus we developed several kinds of experiment on which our diverse subjects (monkey, rat, pigeon, turtle and fish) gave diverse performances. The two I shall describe in this article are habit-reversal and probability-learning experiments.

In habit-reversal experiments animals are rewarded for choosing alternative A rather than B until a preference for A has been established, then B rather than A is rewarded. When a preference for B has been established, A is again rewarded, and so forth. Trained in this way, a rat or monkey shows a steady improvement in performance. It may make many errors in mastering early reversals, persisting in the choice of previously rewarded alternatives, but as

training continues it shifts its preference more and more readily. A fish, in contrast, shows no improvement at all; later reversals are accomplished no more readily than earlier ones.

Although the various sensory, motor and motivational characteristics of the five species we have been studying call for different experimental environments, we have been able to keep certain elements of the test apparatus analogous. In each case the animal is confronted with a pair of translucent Plexiglas panels on which various colors and patterns are projected from behind, and it makes a choice by pressing against one or the other of the panels in its own way: the fish strikes or bites, the pigeon pecks, the monkey pushes with its hand, the turtle or the rat presses with its head or forefoot or both. A correct choice is rewarded with food (a *Tubifex* worm for the fish, a bit of fish for the turtle, some grain for the pigeon, a pellet of sucrose for the rat, a peanut for the monkey), after which there is a brief interval of darkness and then the next choice is offered. If the animal makes an incorrect choice, there is a six-second interval of darkness (called a "time-out"), after which the correct panel alone is illuminated (a procedure called "guidance") and the animal is rewarded for responding to it. Guidance after error guarantees that the animal will not stop responding altogether in the course of a reversal before it has had a chance to learn that the previously unrewarded alternative now is rewarded. The time-out between error and guidance delays access to the reward and thus penalizes precipitous, indiscriminating choice. Without the time-out it would not matter much to the animal whether its choices were correct or not.



FISH IN A DISCRIMINATION TANK is presented with a visual problem in which the lights projected on two stimulus disks are differently colored. By pressing its head against the proper disk

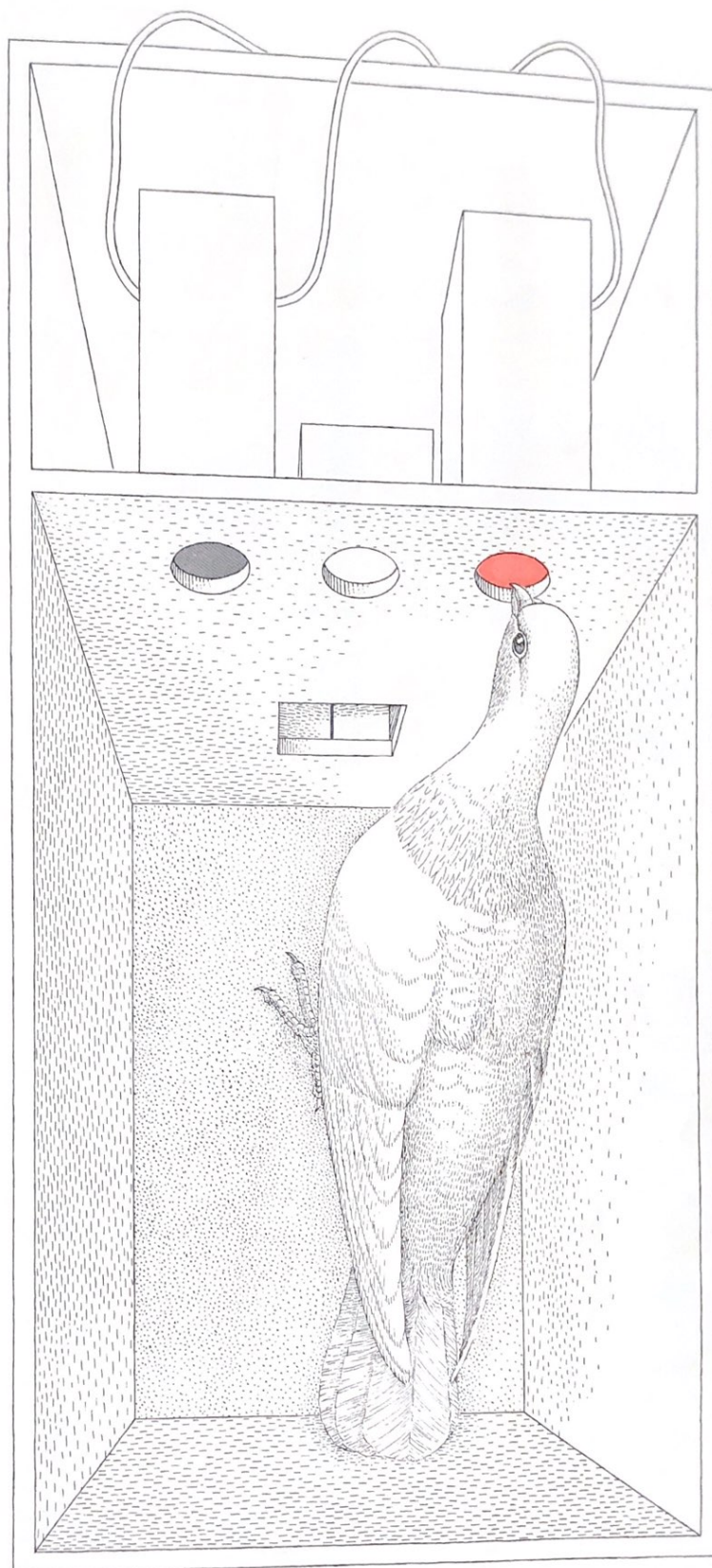
the fish triggers an automatic reward device: the pincers above eyedropper (top right) close, squirting a *Tubifex* worm into tank. The experimental apparatus was designed by the author.

The entire experimental sequence is programmed by some simple relay circuitry and the responses are graphically recorded. With this introduction of automatic control and the removal of the experimenter there is a gain in objectivity: the animals can no longer be influenced by features of the experimenter's behavior. The task of data collection also becomes less arduous and can be entrusted to a co-worker of limited training, who can take data from several subjects concurrently.

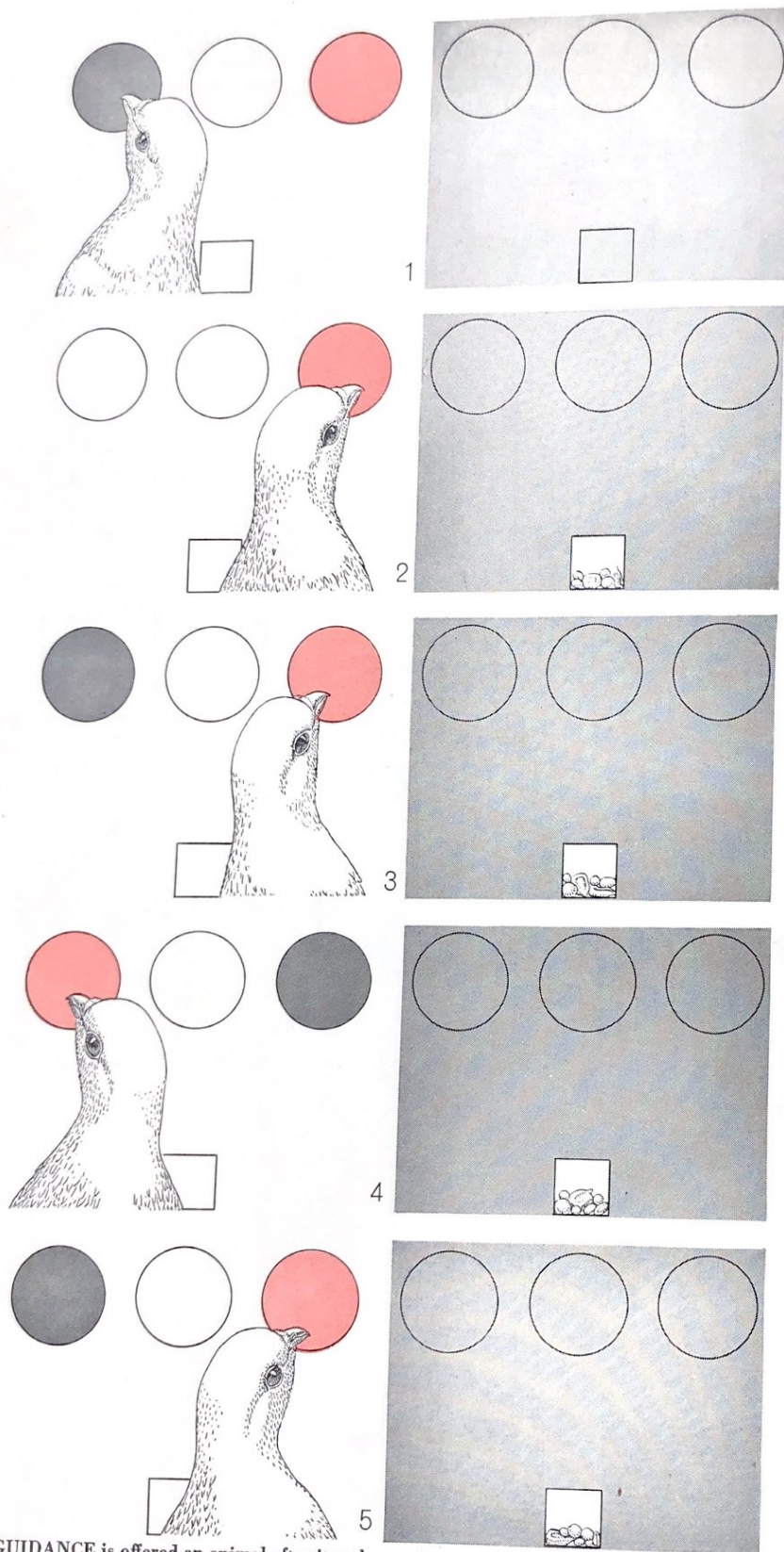
In our experiments we employ both spatial and visual problems. A spatial problem is one in which the alternatives are identical to the eye (that is, the stimuli projected on the two Plexiglas panels are the same) and reward is correlated with the position of the panel. A visual problem is one in which the alternatives look different—blue light and green light, for example, or a triangle and a circle—and reward is correlated with appearance, regardless of position. The results of experiments based on spatial and visual problems can be plotted in comparable fashion, as the two graphs on page 7 indicate.

The experiment that provided the data plotted in the top graph was conducted with rats. Each animal was given 40 trials per day and was reversed whenever it made no more than six errors on any given day. The curve traces the average number of errors made in accomplishing each reversal by the group of rats tested. It reveals that the original problem (Reversal 0) was mastered with few errors, that the first reversal was mastered with difficulty and that adjustment to succeeding reversals was progressively less difficult. The bottom graph shows a similar progressive improvement in habit reversal made by pigeons as they were confronted with a visual problem. The plot of average errors per reversal points to a stage of increasing difficulty followed by a stage of steady improvement. Both for the pigeon and for the rat the first reversal is usually the point of maximum difficulty in spatial problems; the point of maximum difficulty tends to occur later in visual problems.

The fish follows a markedly different pattern. Neither of the two types of fish used in our experiments has shown progressive improvement in habit reversal. In two representative experiments fish were tested on spatial and visual problems, and each animal was reversed whenever it made six or fewer errors on a given 40-trial day. When



PIGEON MAKING A CHOICE is offered two visually distinct stimuli. (The center light is used in another type of test.) If the correct choice is made, some grain is presented in the rectangular opening. The experimental sequence is programmed by relay circuitry.



GUIDANCE is offered an animal after it makes an incorrect choice, as the pigeon has done on its first trial (top left). No reward is given and the lights go out in the box for six seconds (top right). Then the correct panel alone is lighted and the pigeon is rewarded for pecking at it (2). Thereafter the pigeon is shown selecting the proper panel even when faced with the wrong alternative (3) or a change in the position of the correct panel (4 and 5).

we plot the results in terms of average errors per reversal, both curves diverge from the original problem to the first reversal but then fail to decline with continued training [see upper illustrations on page 8].

Before we can conclude that the fish is incapable of improvement in habit reversal, two other possibilities must be considered. The first is that the fish is in fact capable of progressive improvement, but only after more reversals than higher animals require. This possibility seems unlikely; in experiments with fish as many as 150 reversals have failed to yield evidence of improvement. Another possibility is that the conditions under which the fish has been tested are to blame for its poor showing, that the difference in performance is to be traced not to a difference in capability but to an inequality in some contextual variable such as sensory demand, motivational demand, degree of hunger or attractiveness of reward.

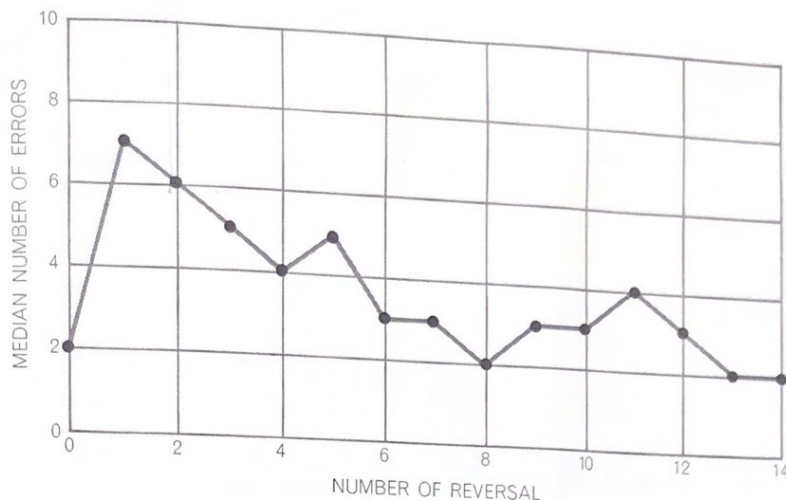
Although the environments we construct for the various animals are roughly analogous, there is no way of equating them exactly with respect to such variables. Do a fish and a pigeon distinguish between a pair of red and green lamps with equal ease? Probably not. Does a *Tubifex* worm have the same reward value for a fish that a sucrose pellet has for a rat? Probably not. We do not know how to select stimuli that will be equally discriminable or rewards that will be equally attractive. Can we ever, then, rule out the possibility that a difference in performance of two different animals in such an experiment stems from a difference in some confounded contextual variable?

Fortunately, yes, thanks to a technique known as systematic variation. Consider, for example, the hypothesis that a fish fails to show progressive improvement in a given experiment because it is far less hungry (or far more hungry) than a rat that does show improvement. This hypothesis implies that at some level of hunger the fish will show progressive improvement. Therefore we can test it—although we cannot produce in the fish the precise degree of hunger in a given rat—by repeating the experiment with subjects of widely different degrees of hunger. Hypotheses about other contextual variables have been tested by similar systematic variation. Progressive improvement in habit reversal has been sought without success in the fish under a wide variety of conditions, whereas the

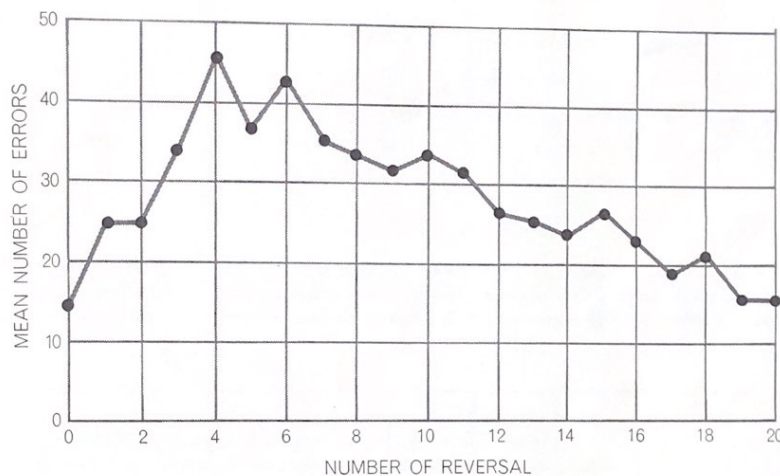
and the pigeon do progress under an equally wide range of conditions. Indeed, it is difficult to find a set of conditions under which the pigeon and the turtle fail to show improvement. The results of experiments on habit reversal in the painted turtle are in a sense intermediate between those for the fish on the one hand and those for the pigeon and the rat on the other. In spatial problems the turtle shows progressive improvement; in visual problems it does not. The data from two recent experiments with turtles, one group trained in a spatial problem and the other trained in a visual problem, are plotted at the bottom of page 8. Both curves give the average number of errors made per reversal. The curves rise from the initial presentation of the problem to the first reversal; then the spatial curve declines but the visual curve does not. We conclude simply that experiments on habit reversal tap an intellectual capability of higher animals that is not at all developed in the fish and is manifested by the turtle only in a restricted class of problems.

Other intellectual differences between our test animals appear when the rewarded alternative is changed within a given trial session (not from session to session). Experiments involving this technique are called probability-learning experiments. In a typical probability-learning experiment alternative A would be rewarded on, say, a random 70 percent of the trials and B would be rewarded the other 30 percent. As in experiments on habit reversal, we confront the animal with either a visual task or a spatial one. We can employ either the guidance method (in which an incorrect choice is followed by a time-out, presentation of only the correct alternative and finally a reward) or the noncorrection method (in which the trial ends whether the rewarded or the unrewarded alternative is chosen). Trained without guidance, subjects of all species tend to "maximize," choosing the 70 percent alternative on all the trials. (An occasional subject comes to the situation with a preference for the 30 percent alternative and persists in choosing it.) If guidance is used, however, striking differences appear among the various species.

Some representative results for the rat and the fish are presented in the two graphs on page 9. During the first stage of the experiments reflected in the graphs the animals were trained on a visual problem—horizontal



PROGRESSIVE IMPROVEMENT of a group of rats tested on spatial problems that required habit changes is plotted. In solving the original problem (*Reversal 0*) the group made a median number of two errors. When the rewarded alternative was switched (*Reversal 1*), many errors were made before the rats mastered the problem and the rewarded alternative could be switched again. The rats then made fewer errors in achieving reversals.



HABIT-REVERSAL EXPERIMENT involving a group of pigeons trained on visual problems yielded the results summarized in this graph. The birds were given 40 trials per day. They made a mean number of 15 errors in mastering the original problem. Difficulty in coping with reversals continued past the first one, reaching a maximum on the fourth reversal, when most animals had to be trained for six days before achieving reversal.

v. vertical stripes—by the guidance method. The choice of horizontal stripes was rewarded in 70 percent of the trials for the first 30 days and in 100 percent of the trials for the next 10 days. The rat tended to maximize under these conditions: after several days it began to choose the 70 percent alternative much more than 70 percent of the time; with the shift in the reward ratio to 100 percent the trend toward absolute preference continued as it might have even without the shift. In contrast, the fish showed a choice pattern we characterize as "matching." It began to choose the 70 percent alternative about 70 percent of the time after a few days of training,

and when the reward ratio was shifted to 100 percent, it rapidly began choosing the rewarded alternative in every instance. In other words, the fish produced a choice ratio that tended to match the reward ratio. We found that in spatial problems too the rat maximizes and the fish matches as long as guidance is used (although without guidance both species tend to maximize).

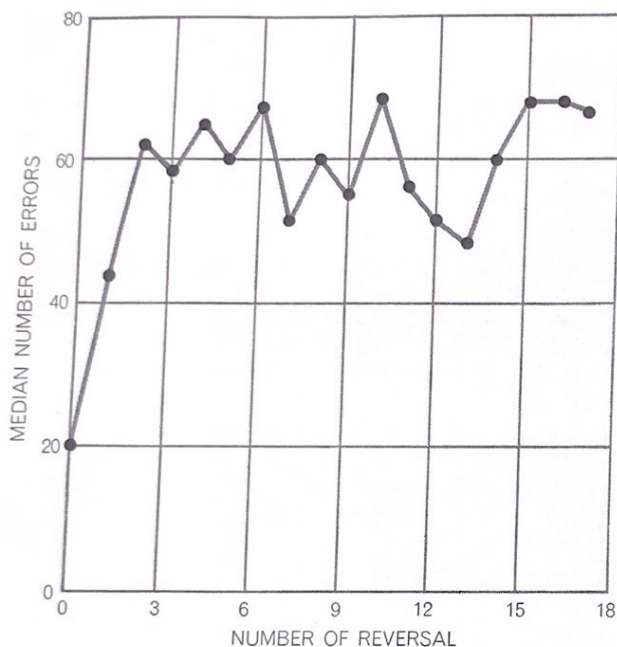
Whereas the rat and the monkey usually maximize in experiments on probability learning even when guidance is used, they sometimes show a correspondence between choice ratio and reward ratio of a rather different kind from that

revealed by the fish. The mammals produce a pattern of systematic matching. Occasionally, for example, a group of rats will choose the rewarded alternative of the preceding trial. This tendency toward reward-following produces a 70 percent choice of the 70 percent

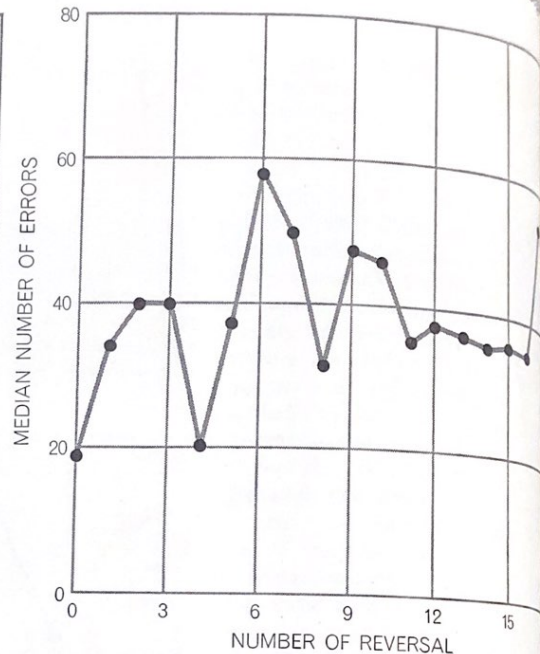
alternative when the reward ratio is 70 to 30, and a 50 percent choice of each alternative in a problem in which the ratio is 50 to 50. An opposite strategy—to avoid the rewarded alternative of the preceding trial—sometimes has been used by the monkey. No such systematic

tendencies are reflected in the matching of the fish, which can be characterized as random.

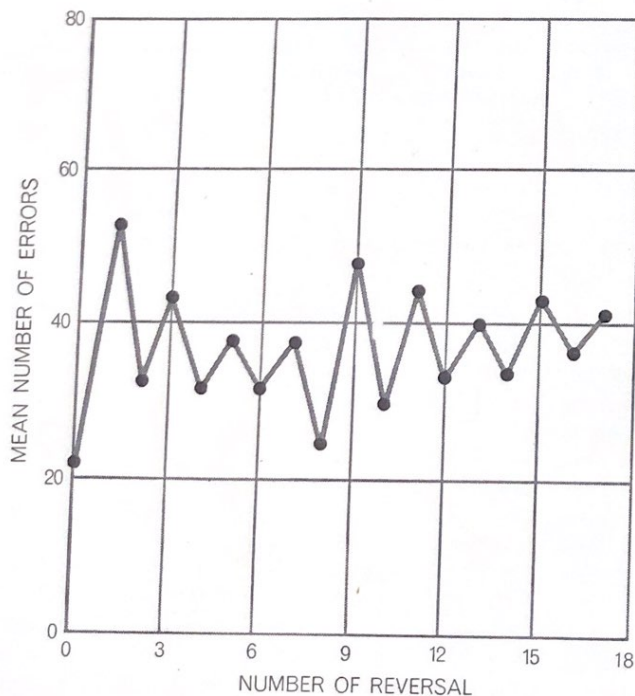
A pattern of random matching is produced by the pigeon when it is tested on a visual problem. Since the pigeon maximizes in such cases or



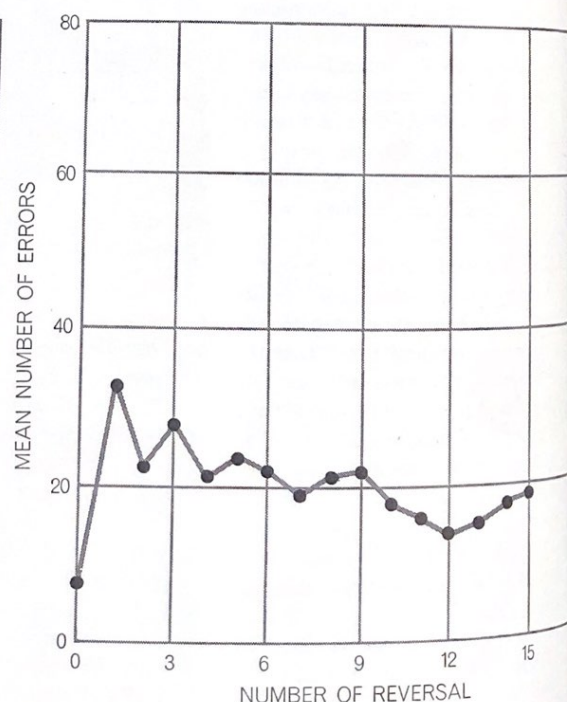
FISH TESTED ON SPATIAL PROBLEM yielded data for this graph, which reveals no progressive improvement in habit reversal. The curve remains approximately level after the first reversal.



FISH TESTED ON A VISUAL PROBLEM show no progressive improvement in habit-reversal experiments. Even graphs of experiments involving 150 reversals do not reveal any downward



TURTLES TESTED VISUALLY failed to show any progressive improvement in habit reversal. Occasional drops between reversals have no significant statistical effect on the slope of the curve.



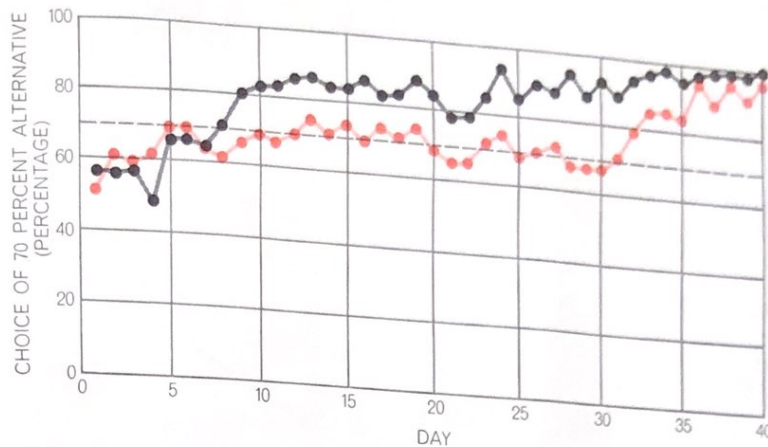
TURTLES SOLVING SPATIAL PROBLEMS do show progressive improvement when the results of a habit-reversal experiment are plotted. In this graph improvement follows the initial reversal

ward-following, the experiments on probability learning have provided us with a clear functional difference between the rat and the pigeon. Experiments on probability learning yielded results for the turtle that are reminiscent of the result of experiments on habit reversal. The efforts of the turtle can be described as random matching on visual problems but maximizing or reward-following in spatial problems. In both kinds of experiment, then, its behavior is ratlike in spatial problems but fishlike in visual problems.

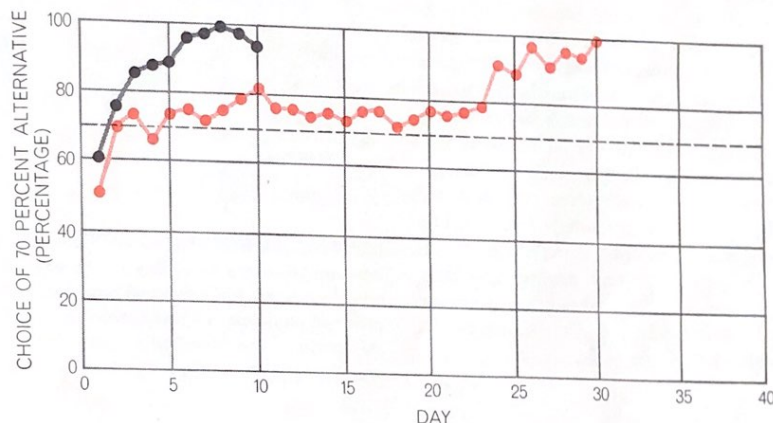
We can use such categories of intellectual behavior (ratlike or fishlike) to tabulate the results of our experiments on habit reversal and probability learning. Such a table [see bottom illustration on page 10] suggests the following generalizations: As we ascend the evolutionary scale we do not find a pattern of intellectual continuity but one of discontinuity. Moreover, the modes of adjustment evolved by the higher animals appear earlier in spatial than in visual contexts.

The monkey and the rat are not differentiated by the criteria used to construct our table. The two mammals do, however, show differences in their styles of probability learning, with the reward-following of the rat giving way in the monkey to the opposite strategy (avoiding the rewarded alternative of the preceding trial). It is notable that this strategy of the monkey has been observed so far only in spatial problems, providing support for the generalization that as we go up the evolutionary scale new modes of adjustment appear earlier in spatial than in visual settings.

The idea of advance has long been implicit in the idea of evolution. We are thus led to ask if the ratlike modes of adjustment are really effective in the sense that they help the animal to cope with its environment. Do they actually represent a higher intelligence? In general the answer is yes. Progressive improvement in habit reversal represents a flexibility that cannot help but be of value in an animal's adaptation to changing circumstances. As for probability learning, the ability to maximize produces a higher percentage of correct choices than does matching. In a problem where the reward ratio is 70 to 30, for example, the probability of correct choice is 70 percent if the subject is maximizing but only 58 percent— $(.70 \times .70) + (.30 \times .30)$ —for an animal that is matching. Systematic matching is no more successful than random matching



PROBABILITY LEARNING is the subject of experiments such as the one summarized in this graph. The graph compares results for a group of rats (black curve) and fish (colored curve) tested on visual problems. One alternative was rewarded on 70 percent of the trials for 30 days and on 100 percent of the trials thereafter. Almost from the outset the rat "maximized," tending to make the advantageous choice on 100 percent of the trials. The fish "matched," keeping its choice ratio equal to the reward ratio throughout the experiment.



MAXIMIZING is illustrated for rats (black curve) and fish (colored curve). The animals were trained on spatial problems in which one alternative was rewarded on 70 percent of the trials. The rat, after 10 days, chose the advantageous alternative almost invariably. The fish matched its choice ratio with the reward ratio for 20 days, at which time guidance was discontinued and it tended to choose the advantageous alternative on almost every trial.

by this criterion, and yet we know that human subjects employ systematic matching in trying to find a principle that will enable them to make the correct choice 100 percent of the time. If the use of systematic matching by lower animals is based on some crude, strategic capability, it represents a considerable functional advance over random matching.

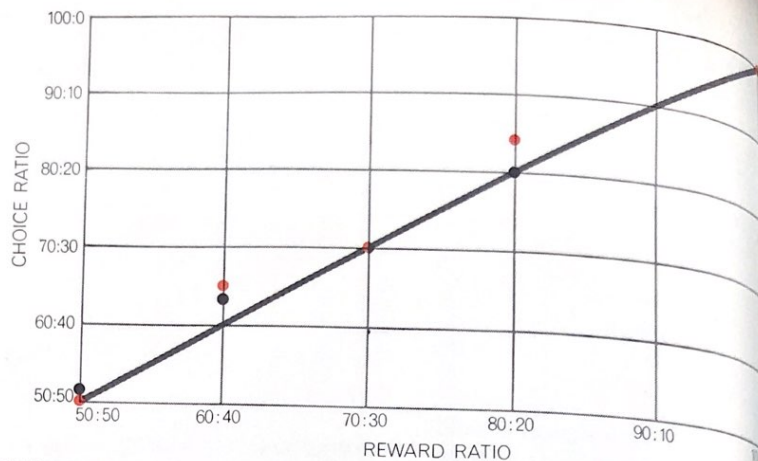
Having found behavioral differences among the various types of animal, we are now trying to trace them to physiological differences. My colleague R. C. Gonzales has lately been conducting experiments on habit reversal and probability learning with adult rats lacking extensive portions of the cerebral cortex, a prominent feature of the

mammalian brain that is absent from the brain of the fish and first appears in the reptilian brain. The decorticated rats showed progressive improvement in habit reversal on spatial but not on visual problems. In experiments on probability learning they maximized on spatial problems but took to random matching on visual problems. The intellectual behavior of these decorticated rats was exactly like that of the turtle, an animal with little cortex.

Summarizing the meaning of these experiments calls for sketching the origins of the study of animal intelligence. A century ago, as Charles Darwin developed his theory of evolution, he denied not only the physical uniqueness of man but also the intellectual uniqueness. In

doing so he used the only evidence available to him: episodes described by naturalists, hunters, pet-owners and zoo-keepers. It was not until the start of the 20th century that the study of animal intelligence was brought from the realm of the anecdote into the laboratory by Edward L. Thorndike, who was then working at Harvard University. Thorndike's experiments led him to deny the existence of intellectual uniqueness anywhere in the evolutionary hierarchy of animals. It was he who set forth the theory that differences from species to species are only differences of degree, and that the evolution of intelligence involves only the improvement of old processes and the development of more neural elements.

Our studies of habit reversal and probability learning in the lower animals suggest that brain structures evolved by higher animals do not serve merely to replicate old functions and modes of intellectual adjustment but to mediate new ones (a contradiction of the Thorndike hypothesis). Work with decorticated rats points to the same conclusion. Yet it should be observed that these recent studies represent a new turn in the investigative path founded by Thorndike himself. Clearly bringing the study into the laboratory was the real first step toward replacing guesses with facts about the evolution of intelligence and its relation to the evolution of the brain.



MATCHING of choice ratio (vertical axis) with reward ratio (horizontal axis) approaches a linear relation for both the pigeon (colored dots) and the fish (black dots). The graph is based on studies of fish given visual and spatial problems and pigeons given visual ones.

TEST ANIMAL	SPATIAL PROBLEMS		VISUAL PROBLEMS	
	REVERSAL	PROBABILITY	REVERSAL	PROBABILITY
MONKEY	RAT	RAT	RAT	RAT
RAT	RAT	RAT	RAT	RAT
PIGEON	RAT	RAT	RAT	FISH
TURTLE	RAT	RAT	FISH	FISH
FISH	FISH	FISH	FISH	FISH

DIFFERENCE IN INTELLIGENCE of the five animals studied by the author (columns left) are tabulated according to the subject's response to spatial and visual problems in experiments on habit reversal and probability learning. The behavior of each animal in each test situation is characterized as ratlike (progressive improvement in habit reversal and maximizing or nonrandom matching on probability-learning tests) or fishlike (no improvement in habit reversal and random matching on probability-learning tests).

The Author

M. E. BITTERMAN is professor of psychology and chairman of the department of psychology at Bryn Mawr College. He is a native New Yorker who was graduated from New York University in 1941; the following year he obtained an M.A. from Columbia University and in 1945 he received a Ph.D. at Cornell University. During World War II he was involved in the training of specialized military personnel. Subsequently he taught at Cornell and the University of Texas. He spent a year as a visiting professor at the University of California at Berkeley and two years as a member of the Institute for Advanced Study before going to Bryn Mawr in 1957. Since 1955 he has been coeditor

of the *American Journal of Psychology*. He conceived the general plan of his present work in the comparative intelligence of animals as an undergraduate but has pursued it intensively only in the past few years.

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