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20. Supported in part by NIH grant MM-19322 and a grant from the Institutional Scientific Research Pool of Columbia University. We thank Drs. N. Graham and B. Schneider for their helpful comments and Dr. E. Galanter for making available the facilities of his laboratory, which are supported in part by a contract with the Office of Naval Research.

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Learning by Following a Food Source

Abstract. *Hungry pigeons first learned to eat grain from the experimenter's hand. When the hand approached and "pecked" a small disk to produce grain in a food hopper, the pigeons followed the hand and rapidly learned to peck the disk. Birds given operant conditioning training took significantly longer to learn the same response. Under natural conditions, young animals may learn to behave like their parents simply by following parental sources of food.*

Although some behaviors are transmitted from one generation to the next by genetic mechanisms, others, acquired during the lifetime of the parents, must be transmitted differently. In the research described here, we examined a simple, but possibly important, means by which learned behaviors are transmitted. Young animals follow their parents—notably during weaning, after imprinting, or when part of a social group (*1*). However, there have been few experimental studies of what and how the young learn by following. Church (*2*) showed that rats learned to approach food in the lighted arm of a maze by following previously taught leader rats. Galef and Clark (*3*) showed that a learned preference for one of two food sources was transmitted from adult rats to pups; the pups learned by following their parents to the preferred source. Galef and others suggest that rats may be subject to peculiar selective pressures because of human attempts to eradicate colonies of wild rats through poisoning. Rats may have evolved the learning-through-following mechanism, thereby avoiding poisoned foods. In this present research, we extend the Church and Galef demonstrations by showing that members of a different species, pigeons, rapidly learned an operant response, pecking a disk, by following an arbitrary source of food, grain held in a human hand. Learning through following is not specific to rats in the presence of conspecifics, nor specific to a given type of response or mode of feeding. "Following" may be a general means by which some behaviors are socially transmitted from one organism to another.

Twenty experimentally naive White Carneaux pigeons, 2 months old at the start, were maintained at approximately 85 percent of their normal body weights The experimental chamber, a box 76 by 51 by 36 cm, had an opening of 31 by 11 cm to permit the experimenter's hand to move freely within it. The front wall contained a Gerbrands response disk and a hopper in which mixed grain could be presented. The response disk was similar in color to the surrounding metal panel and was never transilluminated. Two overhead white 7-watt bulbs provided continuous illumination of the chamber, and four overhead red 7-watt bulbs served as a stimulus signal.

In the first of four experimental conditions, five pigeons were taught to eat grain from the experimenter's hand and to follow the hand about the chamber. When red stimulus lights then flashed, the hand slowly moved to the disk and "pecked" it, thereby causing grain to appear in the hopper. The main question was whether the pigeons would learn to peck the disk. This method of training was then compared with three control conditions.

For the first 7 days in condition 1, each pigeon was fed mixed grain in its living cubicle from a small cup, about 3.8 cm in diameter and 3.8 cm high, held in the experimenter's hand. Then, during nine sessions in the experimental chamber, each bird learned to follow and eat grain from the handheld cup. Sessions averaged 18 minutes, during which the birds each ate about 12 g of grain. The experimenter intermittently covered the cup with her palm so that during the last few sessions grain was accessible for only a few seconds; nevertheless, all pigeons followed the hand through most of each session.

After these preliminary sessions of following a food source, training to peck the disk was begun. At the start of the first session, the hopper was operated until the bird ate for 10 seconds; at the beginning of all subsequent sessions the bird was permitted to eat grain in the handheld cup for 10 seconds. During the remainder of each session, the cup was covered by the experimenter's palm so that the grain could not be seen. The experimenter occasionally "pecked" at grain in the cup with her index finger to maintain the bird's attention but covered the cup before the bird could eat. The procedure consisted of S+ trials with red lights flashing (1.5 flashes per second) alternated with S− intertrial periods with the red lights dark. S+ lasted a maximum of 15 seconds, during which a peck to the disk shut off the flashing red lights and produced 6 seconds of access to grain in the hopper. After grain presentation or 15 seconds without a response, S− began. Thus, grain presentation was possible only once per S+ period. Programmed S− periods varied between 8 and 36 seconds, with an average of 15 seconds. In addition, each response during S− delayed the onset of S+ for an additional 7 seconds; the pigeons therefore had to learn to not respond in S−.

During the first ten trials in each session, the experimenter demonstrated the correct response: When the red lights flashed, her hand slowly moved to the disk and "pecked" it and then "pecked" the grain in the hopper. At the end of the hopper operation, her hand moved away from the disk and was motionless during S−. She withdrew her hand after ten demonstration trials, and the pigeon was given 20 test trials to determine whether it would peck the disk when alone in the chamber. Except for the absence of the hand, test trials were identical with demonstration trials. Generally two sessions were given per day, with an interval of about 10 minutes.

The criterion for learning to peck was three pecks to the response disk during three successive S+ periods. This criterion was reached in a median of 20 demonstration trials (Table 1). The birds followed the hand to the disk and often pecked softly at the hand, peeped, and flapped their wings, gestures observed when young birds feed from their parents (*4*). Three of the five birds first pecked the disk while pecking at and around the hand during demonstration trials. The other two birds responded first during test trials; both had been pecking at the finger as it "pecked" the disk during the preceding demonstration period. After a pigeon pecked once or twice during S+, responses were thereafter emitted reliably (Fig. 1). The birds also rapidly learned not to peck in S−, although initially a large number of S− responses, or errors, were made (Fig. 1).

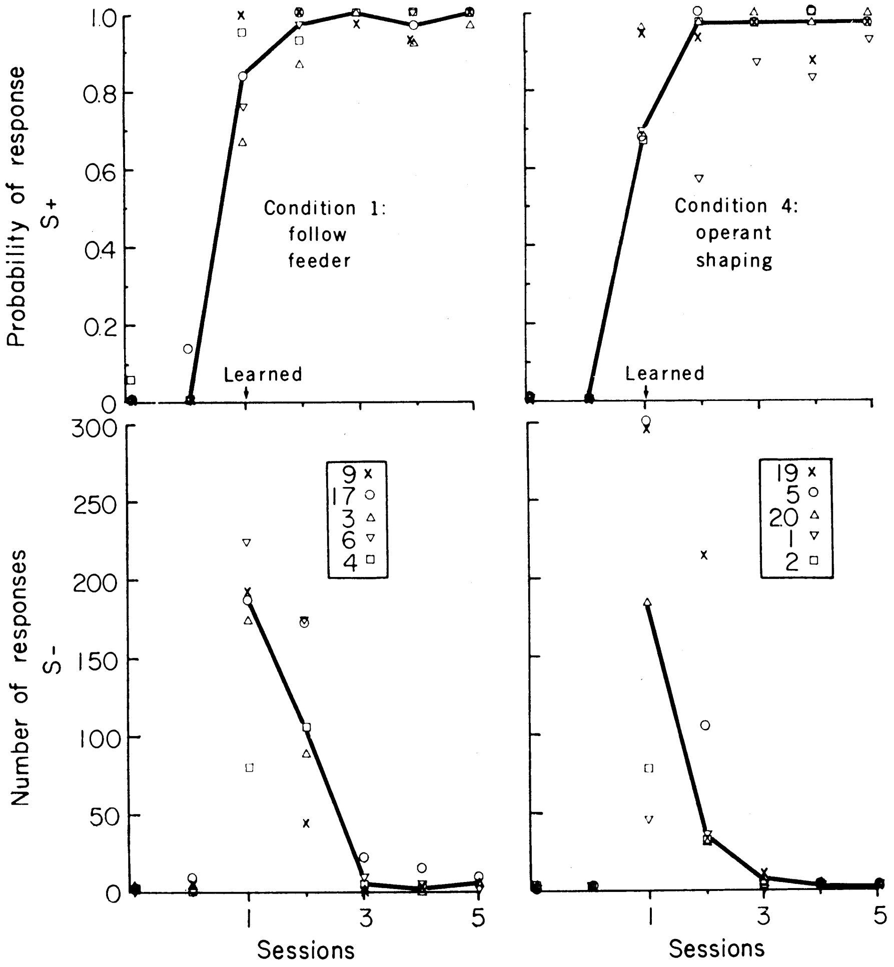

Fig. 1. Formation of the discrimination between S+ trials (red lights flashing) and S− trials (red lights off). The upper graphs show S+ response probabilities, or the proportion of S+ trials per session in which a disk-peck response occurred; the lower graphs show the number of S− responses per session. The left graphs are from the "following" procedure in condition 1, and the right graphs are from the operant shaping procedure in condition 4. Session 1 is the session in which each bird learned to peck the disk (see text for criterion of learning); the points to the left are from the last two sessions before learning. The lines connect group medians.

Did learning to peck depend on the hand moving toward and "pecking" the response disk? In condition 2, five birds received the same training as in condition 1 except that during demonstration trials the hand remained in the rear of the chamber; during each S+ period the hopper was activated automatically and independently of the bird's behavior. Birds in this condition were given grain in the hopper at the same frequency as the birds in condition 1, but now the hand did not "peck" the disk to produce the hopper operation. Subjects received 12 sessions. Four of five birds never learned to peck the disk (Table 1). The birds generally stayed close to the hand during demonstration trials, and two birds did not eat grain in the hopper when it was presented. After 12 sessions, the birds were given additional sessions in which the hand "pecked" the disk and grain in the hopper during S+, as in condition 1. The four birds then learned after a median of 20 demonstration trials (Table 1).

Is preliminary training to follow a hand necessary for learning from hands? In condition 3, five birds were never trained to eat grain from the hand and the hand was not in the chamber during preliminary sessions; however, during demonstration trials, the hand "pecked" the disk as in condition 1. So that the birds in this condition would spend the same time in the chamber and eat approximately the same amount of grain as the birds in the previous conditions, about 13 g of grain were scattered on the floor of the chamber during each of nine preliminary sessions. After this preliminary training, the procedure was the same as in condition 1; that is, the hand "pecked" the disk to produce grain in the hopper during each of 10 demonstration trials per session and was absent from the chamber during the 20 test trials which followed. Although the birds watched the hand "peck" the disk, none learned to peck within the 12 sessions given (Table 1). During

Table 1. Number of demonstration trials before each pigeon learned to peck the disk.

Condition	Procedure	Individual scores	Median
1	Fed from hand; hand "pecked" disk	10, 16, 20, 41, 60	20
2a	Fed from hand; hopper activated automatically*	110, 120, 120, 120, 120	+120†
2b	Hand "pecked" disk	10, 20, 20, 41	20
3	Fed on floor of chamber; hand "pecked" disk*	120, 120, 120, 120, 120	+120†
4	Fed on floor of chamber; operant shaping	61, 170, 185, 251, 647	185†

* Training was stopped after 120 trials without a response. † Significantly different from condition 1 ($P = .004$, Mann-Whitney U test, one-tailed).

demonstrations, all birds remained in the rear of the chamber, away from the hand, and consequently none ate from the hopper. During test periods, the birds occasionally pecked at the inoperative hopper and, for some subjects, this occurred more frequently during S+ than S−, which perhaps indicates some learning through observation.

The speed of learning with an operant conditioning procedure was assessed to condition 4. As in condition 3, grain was scattered on the floor during nine preliminary sessions. As in all conditions, the hopper was activated at the beginning of the first training session until each bird ate for 10 seconds. The experimenter then operantly conditioned, or "shaped," each of five birds by observing it through a peephole and reinforcing successive approximations to the disk-peck response with access to grain in the hopper. At no time was the experimenter's hand in the chamber. To make the situation analogous to condition 1, only one reinforcement was given per 15-second S+ period. Again, 10 demonstration trials, in this case shaping trials, were followed by 20 test trials.

A median of 185 shaping trials was required before the birds in condition 4 learned to peck the disk (Table 1), significantly more than the 20 training trials required in condition 1 ($P = .004$, Mann-Whitney U test). However, the birds in condition 4 did not eat from the hopper until after a median of 158 shaping trials as compared with a median of only five demonstration trials in condition 1 ($P = .004$, Mann-Whitney U test). The 10 seconds of access to grain in the hopper during the first session was clearly insufficient for the birds to eat reliably from the hopper. The loud noise produced by hopper activation often inhibits approach to the hopper during initial training (*5*). Following the hand in condition 1 apparently facilitated approach to the hopper. If conditions 1 and 4 are compared with respect to trials after each bird was eating from the hopper, following the hand still engendered significantly more rapid learning—median of 11 demonstration trials versus 52 trials in operant conditioning ($P = .048$, Mann-Whitney U test). After the first one or two pecks were emitted, however, the birds in the two conditions behaved similarly (Fig. 1).

Birds trained to follow a hand approached and pecked a disk in significantly fewer trials than birds given operant conditioning training; but after the birds had pecked the disk once, learning was equally rapid in both conditions. Thus, following a source of food changed the "operant level" of pecking a disk, that is, the likelihood that a peck would occur before it was explicitly reinforced. To learn an operant response, an organism must first make contact with relevant aspects of the environment, in this case the operant manipulandum. Anything that increases the likelihood of such contact will increase the probability of learning. When training a pigeon to peck a disk, experimenters often scatter grain on the floor in front of the disk, or paste grain on the disk itself, to increase the operant level of pecking (*5*). The present research suggests a social means by which operant levels are changed. For example, in natural environments, if parent pigeons approached a specific area where food was regularly available and young birds followed the parents, the young too would be fed and might thereby rapidly learn to approach the same area by themselves. Pigeon squabs have been observed to follow their parents closely during weaning (*4*), thereby permitting extensive learning through following.

A number of questions remain. First, what is the potential extent of learning by following a source of food? We do not yet know whether responses more complex than the disk-peck, or responses of different topographies, could be learned through "following." Church's research (*2*) indicated that somewhat more complex learning is possible: By following a leader, rats learned incidentally to approach the correctly lighted arm of a maze. In the present case, on the other hand, the overhead lights did not acquire discriminative control without many errors. The procedures differed: Learning not to peck in S− may be more difficult than learning to approach a lighted or dark alley, learning from a human hand may be more difficult than learning from a conspecific, or the different results may be caused by phylogenetic differences.

Second, what is the relation between learning by following and learning under other contingencies such as autoshaping and observational learning? When a disk is illuminated for a few seconds before presentation of grain, experimentally naive pigeons rapidly learn—autoshape—to peck the disk (*6*). In condition 1, the correlation between the hand "pecking" the disk and grain presentation was similar to the correlation between disk illumination and grain under autoshaping conditions. Since the birds in condition 3 did not eat from the hopper after the hand "pecked" the disk, they did not experience this autoshaping contingency. We and others (*4*) have observed contingencies similar to autoshaping in a more natural environment: When followed by a squab, a parent often pecks repeatedly at a piece of grain without eating it and then occasionally regurgitates food into the squab's mouth. These parental behaviors may facilitate the squab's learning to peck at grain. Simply observing the hand "peck" may also have facilitated learning. However, the birds in condition 3 did not learn after observing the hand "peck" at the disk and at grain in the hopper —conditions similar to those under which observational learning occurs (*7*). Previous training to eat from the hand might promote such learning through observing.

Third, does learning through following occur in species other than altricial, which feed their young? In precocial species, in which the young are not fed by their parents, other mechanisms serve to ensure following, such as imprinting in ducks and schooling in fish

(*1*). When the young follow adults for any reason, the chances increase that they will experience the same environmental contingencies as the adults. Thus, behaviors may be socially transmitted and the young learn to behave like their elders.

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Thermal Inertia versus Thermoregulation in "Warm" Turtles and Tunas

The recent report by Frair *et al.* (*1*) convinces us that large leatherback turtles (*Dermochelys coriacea*), like large pelagic fishes (*2*), can maintain body temperatures several degrees warmer than the environment. However, after cooling one turtle to determine whether the excess body temperature of another could be attributed to experimental manipulation, Frair *et al.* incorrectly computed the coefficient of temperature change, *k*. While Frair *et al.* reached a conclusion that seems substantially correct, their *k* is thermodynamically inconsistent for animals that maintain body temperatures appreciably higher than ambient temperature. Our comment is also directed to reconsideration of presumptive evidence by Carey and colleagues (*2–4*) for thermoregulation in bluefin tuna (*Thunnus thynnus*).

An object that produces no heat changes temperature at a rate proportional to the difference between its temperature (T_b) and that (T_a) of its environment:

$$dT_b/dt = k(T_a - T_b)$$

The term $T_a - T_b$ may be thought of as the driving gradient of temperature. When T_a and T_b are measured in degrees Celsius and *t* in minutes, the units of *k* are degrees Celsius per minute per degree of driving gradient.

For animals that are typically warmer than their environment, the driving gradient of temperature can be redefined to maintain logical consistency in the estimation of *k* (*5*). If a turtle or fish maintains a body temperature 1°C warmer than the water in which it lives, it will not cool at all unless put into water at least 1°C cooler than its body temperature. The body temperature that would ultimately obtain at any given water temperature may be called the equilibrium body temperature (T_e) for that water temperature. The difference, $T_x = T_e - T_a$, between equilibrium body temperature and environmental temperature has been termed the excess body temperature by Stevens and Fry (*6*). If heat production and heat transfer remain constant, the animal will cool or warm only if the environmental temperature falls or rises so that body temperature is no longer at the equilibrium temperature. Moreover, the rate at which the animal cools or warms will be proportional, not to ($T_a - T_b$), but to ($T_e - T_b$):

$$dT_b/dt = k(T_e - T_b)$$

If the animal physiologically regulates body temperature, T_x is not constant with respect to T_a, and the problem of evaluating *k* becomes more difficult. Either *k*, heat production, or both *k* and heat production may change as a function of T_a.

To return to leatherneck turtles, Frair *et al.* (*1*) measured the cooling rate of a 134-kg animal in Florida to establish that the 18°C excess body temperature they had measured from a 417-kg turtle in Nova Scotia was not attributable to warming or cooling during experimental manipulation. The Nova Scotian turtle had a body temperature of 25.5°C after it had been held in seawater at 7.5°C for 24 hours and then kept moist in air at 17° to 26°C for an additional hour. The Florida turtle was held at ambient temperature (?) for 6 days after capture, then cooled in a bath that decreased from 27° to 1°C in about 5 hours. The animal began the cooling experiment with a body temperature of 32°C and was still cooling at 22°C when the bath reached 1°C. The slow rate at which the Florida turtle cooled led Frair *et al.* to conclude that the large excess temperature of the Nova Scotian turtle "must have been due largely to the turtle's having been able to maintain its temperature in the cold water."

The leatherback turtle cooled by Frair *et al.* (*1*) certainly maintained an excess body temperature greater than 0°C and may actually have regulated body temperature. If one assumes that the turtle was at thermal equilibrium when the experiment started and that T_x remained constant at about 5°C throughout the experiment, then the turtle was cooling about 0.035°C per minute with a driving gradient of 16°C at the end of the experiment. Thus, *k* was about 0.0022°C min^{-1} °C^{-1}—not 0.0015°C min^{-1} °C^{-1} as concluded by Frair *et al.* If, on the other hand, this turtle regulated temperature to maintain a potential excess body temperature of 18°C at an ambient of 7.5°C (like the turtle from Nova Scotia), then *k* was about 0.009°C min^{-1} °C^{-1} when the bath was at 7.5°C (*7*). Since the two turtles were of different size and had different thermal histories, true *k* of the Florida turtle was probably nearer 0.002 than 0.009°C min^{-1} °C^{-1}.

Frair *et al.* (*1*) were right to recognize that the slow rate at which a large animal exchanges heat with its environment must be considered in any evaluation of that animal's potential for physiological thermoregulation. Among fishes, such consideration is especially appropriate for tunas (Scombridae), which have countercurrent heat ex-