$< .9$). Figure 2 gives information concerning the number of attacks and the mean latencies for attacks by snakes that attacked both extracts at least once. If the attack frequency data alone are considered more closely, no differences are noted, except that overall the fish-fed group was slightly less responsive (for total number of attacks, $\chi^2 = 0.03$; d.f. $= 1$; $.8 < P < .9$). More effective extracts generally lead to more attacks and shorter latencies (as well as higher tongue-flick frequencies) (*9*), and this finding is repeated here. Earthworms were more effective than fish throughout (maternal diet worms: all subjects, $P < .002$, binomial test, two-tailed; attackers only, $P < .002$; maternal diet fish: all subjects, $P < .02$; attackers only, $P < .001$).

This experiment shows that maternal chemical-feeding experience has no significant effect on the chemical preferences of young snakes if this experience is given as long as 9 weeks before parturition. Feeding of the mother was controlled from about the gastrulation stage of embryonic development (*10*), which would seem to encompass any conceivable prenatal critical period. While the lifelong feeding experience of the mother may be involved, it would seem more profitable to focus study on the genetic-developmental processes involved. In addition, an explanation based on maternal feeding must deal with possible differences between adult and neonatal diets.

The combined results of this and the postnatal experiments show that the process of being born seems to radically change the ability of the animal to make use of chemical experience, although the very nature of the differences between the pre- and postnatal environments make experimental equivalence impossible. Indeed, whether the newborn snake can even perceive chemicals from its mother's diet is unknown, yet remains so far the only possible normal path for a nongenetic shaping of the differences seen at birth in chemical-cue preference. In oviparous species which evidence similar selective perception upon hatching, it would appear that even this channel of information would have severe limitations (*11*). Prenatal processes are certainly important, but clearly they cannot be considered the source of all the specific perceptual information possessed by neonates.

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References and Notes

1. P. R. Marler and W. J. Hamilton, III, *Mechanisms of Animal Behavior* (Wiley, New York, 1966), pp. 228–315.
2. G. M. Burghardt, *Psychon. Sci.* **4**, 37 (1966).
3. W. S. Wilde, *J. Exp. Zool.* **77**, 445 (1938).
4. G. M. Burghardt and E. H. Hess, *J. Comp. Physiol. Psychol.* **66**, 289 (1968).
5. G. M. Burghardt, *Science* **157**, 718 (1967); *Copeia* **1968**, 732 (1968); *Behaviour* **33**, 77 (1969).
6. J. L. Fuchs and G. M. Burghardt, *Learning and Motivation*, in press. A litter of newborn *T. sirtalis* were divided into two groups. One group was fed fish and the other worms for eight feedings at 4-day intervals. Before any feedings and after every second feeding, the snakes were tested with surface extracts prepared from the fish and worm species. By the second meal the snakes were more responsive to the extract from the prey being fed, and the difference increased until the foods given the snakes were reversed for eight feedings, whereupon the chemical extract differences largely disappeared.
7. G. M. Burghardt, *Amer. Zool.* **8**(4), 56 (1968), and in preparation. In these experiments equal numbers of newborn *T. sirtalis* were exposed briefly to three swab presentations of either earthworm or fish extract. The following day, still without ever being fed, all snakes were tested on the worm and fish extracts. It was found that snakes which attacked an extract the previous day and did not habituate showed more responsiveness to that extract, while snakes in which attack behavior was not released during the final presentation on the preceding day were more responsive to the unexperienced extract.
8. W. Schleidt, *Z. Tierpsychol.* **19**, 697 (1962).
9. G. M. Burghardt, *Behaviour* **36**, 246 (1970).
10. D. R. Zehr, *Copeia* **1962**, 322 (1962).
11. G. M. Burghardt, in *Communication by Chemical Signals*, J. W. Johnson, Jr., D. G. Moulton, A. Turk, Eds. (Appleton-Century-Crofts, New York, 1970), p. 241.
12. Assisted by NIMH grant MH 15707. I thank the naturalists at the Palos Division, Cook County Forest Preserve (Ill.), for providing the gravid snakes.

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Classical Conditioning of a Complex Skeletal Response

Abstract. *The pigeon's so-called "arbitrary" response of pecking an illuminated disk can be established and maintained by procedures resembling those of classical conditioning. This phenomenon was shown to be independent of the specific signaling relationships between illumination of the pecking disk and presentation of food; it will appear as long as the key is differentially associated with food. When a nondifferential condition is introduced, pecking "extinguishes" even if it has previously been established and even when the new condition involves as much reinforcement as the old one. Reinstating differential conditions reestablishes pecking. The initial conditions determine the speed and apparently the asymptote of pecking rates in the differential condition; initial exposure to a nondifferential procedure retards subsequent acquisition, possibly quite permanently. These findings are discussed in the context of mechanisms of adaptive learning, not involving reward and punishment, which lead to selection of effective behaviors on a nonarbitrary basis.*

Brown and Jenkins (*1*) recently reported that hungry pigeons would spontaneously begin pecking a disk mounted on the wall of an experimental chamber if illumination of the disk signaled the forthcoming presentation of grain. The procedure closely resembled Pavlovian delay conditioning, and its effectiveness with pecking—a complex skeletal act directed outward at the environment—potentially represents a significant extension of the domain of classical conditioning. The delay conditioning procedure exerts such powerful control that birds frequently peck the disk even when conditions are changed so that pecking the disk prevents the opportunity to eat (*2*). Under these artificial laboratory conditions, such behavior appears maladaptive and is difficult to encompass in a biological approach to learning based on the reward value of external events.

In the experiments reported here, we explored the limits of applicability of the classical conditioning paradigm by using a procedure that avoids the specific "pairing" relationship between response key and food, which was characteristic of the earlier procedures. Pairing the response key with food according to the Pavlovian delay paradigm involves the precise signaling of the time of presentation of the unconditioned stimulus (for example, food). By circumventing this intimate signaling relationship, we hoped to determine whether the remarkable stimulus control over the act of pecking was attributable to a peculiarity of the Pavlovian procedures used earlier or whether it represents a more general manifestation of associative learning through classical conditioning.

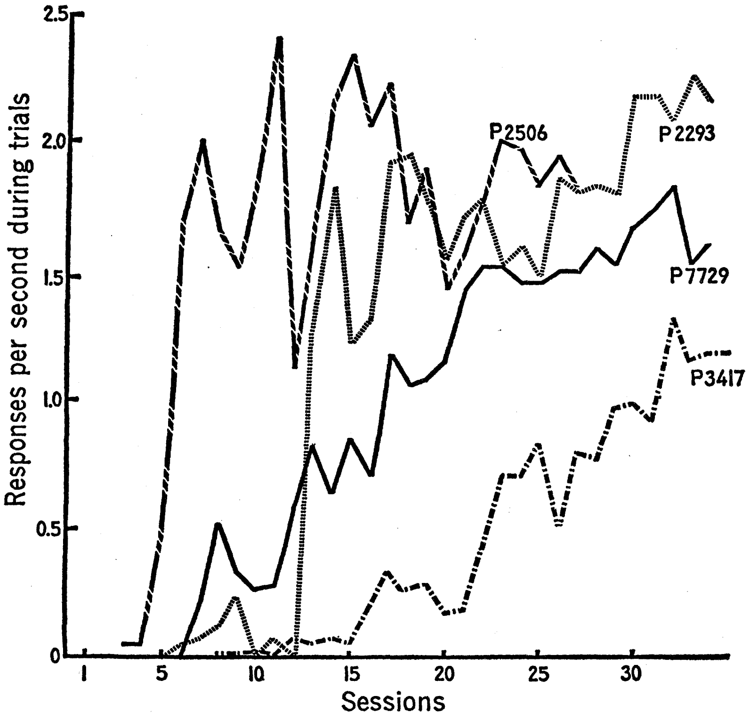
The new procedure that we used was a variant of one introduced by Rescorla (*3*). Throughout the course of these experiments, a pecking disk was illuminated for 8.6-second periods, which were distributed randomly throughout each experimental session with a mean interstimulus interval of 30 seconds. In the presence of the illuminated disk, 4-second periods of access to a grain hopper were provided on a random basis; the probability of initiating such a period of access was .03 at the start of each second of key illumination. We compared pecking to the key under two conditions: a "differential condition," where the probability of access to grain when the disk was not illuminated was zero; and a "nondifferential" procedure, where the probability of grain presentation was the same in the presence and the absence of illumination of the disk. At no point in the experiment did the disk signal the actual time of presentation of reinforcement; it merely accompanied a condition where 4-second access to grain was provided on the average of once every 33 seconds.

Naive adult male Silver King pigeons maintained at 80 percent of their free feeding weight were tested in a standard pigeon chamber measuring 28 by 28 by 26 cm. One wall of the chamber housed a standard pecking disk, which could be transilluminated with white light. The disk was 19 cm above the floor of the compartment, and the grain hopper was centered 11 cm below the pecking disk. At the beginning of the first session, birds were trained to approach rapidly and to eat from the hopper whenever it was presented; they were then immediately exposed to the experimental procedure. A daily session comprised 50 trials of disk illumination, distributed geometrically with a range of 10 to 120 seconds between trials. In the presence of the key, an average of 13 reinforcements were typically presented during 50 daily trials. Grain presentation was always independent of the pigeons' behavior and could be initiated immediately at the onset of a trial or at the start of any other 1-second interval during the trial. Pecking had absolutely no effect on the experimental procedure.

Figure 1 traces the course of development of pecking for each of four birds studied under the differential procedure. Despite marked differences in rate of acquisition, all birds learned to peck the disk at rates substantially above one per second. Because illumination of the disk accompanied a change in the frequency of reinforcement but did not signal particular occurrences of reinforcement, it is clear that disk illumination need have no precise relationship to specific instances of food presentation. This property of the Pavlovian delay procedure, as such, is not necessary for the development of pecking.

To explore whether the pecking engendered by this procedure was dependent primarily on occasions of feeding in the presence of the disk or whether the differential association was a necessary aspect of the procedure, we began presenting grain in the absence of the illuminated disk at the same frequency as we had previously been presenting it in the presence of the illuminated disk, in sessions that immediately followed those illustrated in Fig. 1. Thus, we changed conditions only during the "intertrial interval" and not during the "trial interval" itself. Results from this nondifferential condition are shown in Fig. 2. Levels of responding to the disk during its periods of illumination fell rapidly to zero. Although a modest "recovery" of rate was observed in one bird over a 4-day period, and in another for a single day, these elevated levels of performance were not sustained. Two other birds showed no tendency to resume responding during the 14-day period. In addition, no bird developed sustained pecking during the interval between trials, when grain was presented but the disk was dark. It is apparent, then, that the presentation of grain in the presence of the illuminated disk is not a sufficient condition to engender pecking: the disk must at least accompany a change in the frequency of grain presentations. Figure 2 also shows that, when the differential condition was reinstated, pecking quickly regained its previous levels. These findings are similar to those of Rescorla, who used a classically conditioned fear response in dogs and rats (*4*).

The failure of the nondifferential condition to sustain pecking indicates that adventitious reward of pecking probably does not play a major role in this phenomenon. The rapid decline of pecking during periods of key illumi-



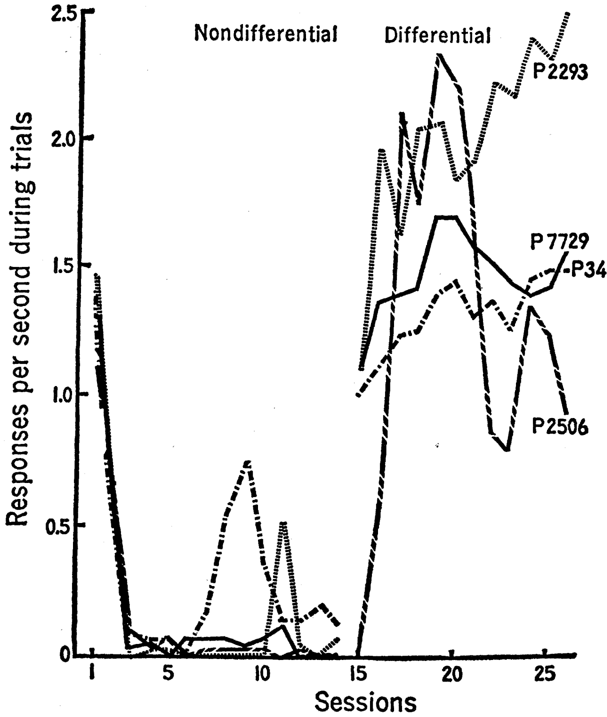


Fig. 1 (left). Individual acquisition curves indicate rate of responding within each session from the outset of the experiment. Fig. 2 (right). Individual rates per session in sessions that immediately followed the sessions of Fig. 1. The rate declined under the nondifferential condition and recovered after reinstatement of the original procedure.

nation took place even though there was no change in response-reinforcer correlations (spurious or otherwise) in the presence of the illuminated disk. If adventitious reward were effective during the differential condition, surely it would continue to be effective in sustaining a high rate of pecking in the nondifferential condition as well.

As a further check on the importance of the differential association of disk illumination with feeding, we studied five new birds on the nondifferential condition. After 14 days of nondifferential exposure to grain presentation, a total of ten pecks had been recorded for all five birds together. All of these occurred during the intertrial interval when the key was not illuminated. Apparently, the decline in responding seen in the first experiment was not an artifact of changing the procedures, nor was it related to prior exposure to a difference in reinforcement density. Acquisition, as well as maintenance of pecking, is dependent on a differential association of key and reinforcer.

When these new birds were shifted to the original differential procedure, all eventually began pecking the disk. Even after 35 days of exposure, however, the mean rate of response was only 20 per minute, and there was no overlap between the rates of pecking of these birds and those of the first group, whose mean terminal rate was 101 responses per minute. Thus, there was a residual effect of nondifferential reinforcement, even after successful acquisition had taken place.

These results demonstrate three important aspects of the autoshaping phenomenon, all of which are consistent with the assumption that classical conditioning is a fundamental factor in the phenomenon. First, we have shown that a specific signaling relationship is not important for acquisition or sustained maintenance of behavior. Second, the necessity for differential pairing in maintenance, as well as acquisition, indicates that informational properties of the stimulus, rather than its mere association with feeding, are responsible for the phenomenon. Third, the phenomenon, although obviously susceptible to analysis by principles of classical conditioning, offers little basis for an account in terms of adventitious reinforcement.

The pecking engendered by autoshaping is directed to a significant part of the environment—that is, a part correlated with the opportunity to eat. The strong and direct control over behavior exerted by this part of the environment indicates the operation of a mechanism in pigeons by which skeletal acts are controlled without the involvement of reward and punishment. The findings of the Brelands (*5*) in a number of nonavian species suggest that such mechanisms are not peculiar to pigeons. Although study of the way in which complex activities are developed and learned has largely excluded effects other than those of reward and punishment, it now seems necessary to include some other factors as well, if the principles of adaptive learning are to provide an adequate account of the development and maintenance of effective but often nonarbitrary behavior. It is apparent that animals do not select behaviors randomly from their repertoire in new situations. The manifestation of associative learning that we have explored in this report may reflect a process by which organisms tailor their behavior nonrandomly to new environments, prior to any "shaping" effect by rewards and punishments.

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References and Notes

→ P. L. Brown and H. M. Jenkins, *J. Exp. Anal. Behav.* **11**, 1 (1968).
2. D. R. Williams and H. Williams, *ibid.* **12**, 511 (1969).
→ R. A. Rescorla, *Psychol. Rev.* **74**, 71 (1967).
4. ———, *J. Comp. Physiol. Psychol.* **66**, 1 (1968); *Psychonom. Sci.* **4**, 383 (1966).
5. K. Breland and M. Breland, *Amer. Psychol.* **16**, 681 (1961).
6. This work was supported by grant G14055 from the National Science Foundation. T. Allaway, B. Schwartz, A. Silberberg, H. Williams, and K. Zonana contributed substantially to our development of this approach.

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Echolocation in Bats: Signal Processing of Echoes for Target Range

Abstract. *Echolocating bats* Eptesicus fuscus *and* Phyllostomus hastatus *can discriminate between the nearer and farther of two targets. Their errors in discrimination are predicted accurately by the autocorrelation functions of their sonar cries. These bats behave as though they have an ideal sonar system which cross correlates the transmitted cry with the returning echo to extract target-range information.*

Bats of the suborder Microchiroptera use a type of active sonar for orientation (*1*). Biologists, psychologists, and physicists have speculated often about the kinds of information available to the bat from echoes and about the nature of the mechanism which processes the echoes from targets in the bat's environment. The possibility of depth perception or target ranging by echolocation has received particular attention (*2–5*). The ease with which bats detect and avoid obstacles and detect, track, and capture airborne targets seems to require some means of determining the distance to targets (*6*).

Three specimens of the North American insectivorous bat, *Eptesicus fuscus*, and three specimens of the neotropical, carnivorous and frugivorous bat, *Phyllostomus hastatus*, learned to discriminate target range in the experiment reported here. The bats were blinded (enucleated) several months prior to the experiment to eliminate the possible use of vision, since the experiment could not be conducted in darkness. Each bat learned to fly from a small, elevated platform to the closer of two other platforms (Fig. 1). A triangular target 10.0 cm wide and 5.0 cm high was mounted at the back of each of the two landing platforms. The platforms were separated by an angle of 40° when viewed from the bat's position on the starting platform.

The landing platforms differed from each other in the distance from the bat on the starting platform to the target. The bat learned to fly to the nearer platform in a straightforward simultaneous discrimination procedure with food as reward (a piece of a mealworm offered in forceps) and without correction of error trials. To make training easier, each bat was deprived of some of its normal food intake until it reached 90 to 95 percent of its weight when captured. The closer platform alternated left to right according to a pseudo-random schedule (*7*).

At first the nearer target appeared at a distance of 50 cm. The farther target was 60 cm from the bat throughout the experiment. After the bat reached a criterion of better