Signals for Food: Reinforcers or Informants?

Abstract. *Ring doves pecked one of two keys for food. Pecks at the chosen key then stopped being reinforced, and the signals that normally preceded food were either present or absent. In the presence of signals for food, the dove switched to the second key more quickly. When only one key was used, the same signals acted, as expected, to keep the bird pecking the extinguished key.*

Conditioned reinforcers are previously neutral stimuli that have acquired the power to modify an animal's behavior. They have been invoked to account for several phenomena that cannot be understood on the basis of primary reinforcers alone (*1*), and there has been much discussion of their properties and how they acquire them (*1*-*4*). Regardless of the theoretical account one adheres to, it is clear that stimuli habitually associated with, say, food can to a certain extent maintain the behavioral responses that normally procure food delivery even in the absence of food. I now present evidence that, if a choice of feeding sites is available, the presence of conditioned reinforcers, which normally signal food, facilitates switching to the alternative site when food is not available at the preferred site.

Subjects were four adult ring doves (*Streptopelia risoria*) maintained at 85 percent of their free-feeding weight. They had previously experienced 130 sessions in a two-key operant conditioning apparatus. The two keys were some 35 cm apart on opposite walls of a box; food was delivered by a food cup set in the rim of a large wheel and was accessible through a hole below and beside the key (*5*, *6*). Each reinforced response was accompanied by the whir of the motor that rotated the wheel to bring the next food cup into position and by the sight of the turning wheel and approaching food cup. Each subject had experienced this sequence some 4000 times, and on every occasion the food cup contained a single crumb of commercial chicken food (Purina Master Breeder).

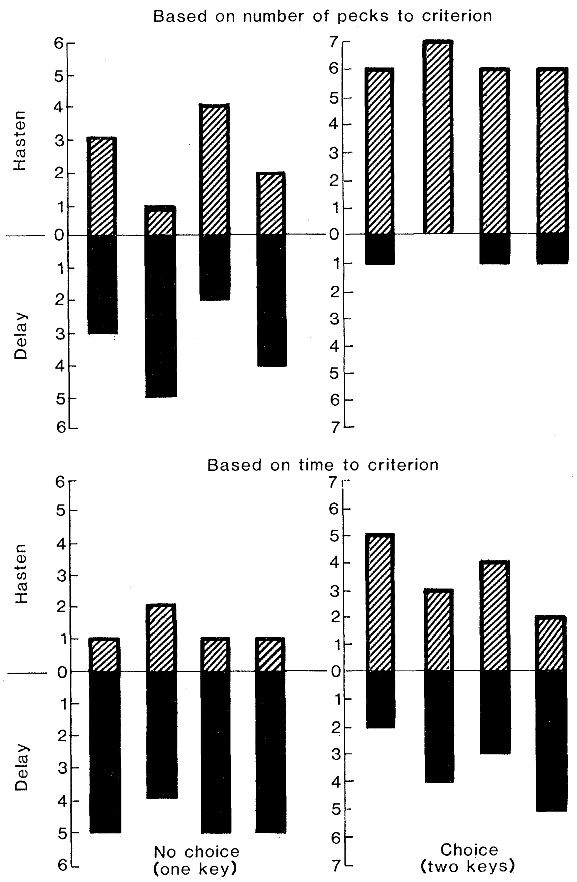

Fig. 1. Effect of signals for food on behavior during extinction. For each bird, the two sessions that constituted each day's trial were compared. If the bird reached criterion sooner in the presence of signals for food than in their absence, the signals hastened departure (hatched bars). If the bird took longer to reach criterion with signals present, the signals delayed departure (solid bars). When there was only one operational key (no choice), signals for food delayed the attainment of criterion (60 seconds without pecking the key). The median of the difference between time to criterion without and with signals for food for birds 1, 2, 3, and 4 was −271.5, 51, −79.5, and −226 seconds, respectively (Wilcoxon test, $T = 2, 8, 2$, and 0, respectively; $P < .05$ for bird 4 only). The signals are acting as conditioned reinforcers. When the bird had a choice between two operational keys, the bird could abandon the extinguished key in favor of the other key, which still provided food. In these circumstances, signals for food hastened attainment of criterion (100 consecutive pecks at the alternative key). The median of the difference between pecks to criterion without and with signals for food for birds 1, 2, 3, and 4 was 116, 41, 102, and 102, respectively (Wilcoxon test, $P < .05$ in each case). The signals are not acting as conditioned reinforcers. The ordinates are scaled so that they are equivalent for the no choice and choice conditions.

The behavior of a bird upon being placed in the apparatus can best be described as "explore and exploit" (*5*, *7*). After some exploration of the two keys, the bird exploited one (almost always the more profitable, richer food site) more or less exclusively (*8*). The present experiment was done under two different conditions to see how the bird would respond to a sudden decrease in the profitability of the food site it was currently exploiting. In one condition, pecks on the key no longer turned the wheel and no food appeared. In the other condition, pecks continued to turn the wheel and produce the food cups, but the cups were empty. In both conditions, food could still be obtained at the other food site by pecking that key. Would the presence of a signal for the arrival of food—movement of the wheel and the empty food cups—affect the readiness of the bird to switch from one food site to the other?

Birds received two sessions daily for 7 days. At the start of each session, the two keys provided food on variable ratio (VR)10 and VR20 schedules, but the bird could not predict the more profitable key. As expected (*8*), the bird sampled both keys initially and then quickly settled down to exploit the more profitable VR10 key. A "decision to exploit" was recorded at the start of a run of 100 consecutive pecks on one key. Food was withdrawn after 20 food deliveries on the VR10 key; one of the daily sessions consisted of straightforward extinction (no food cups and no conditioned reinforcers) and the other of empty food cups on a VR10 schedule (conditioned reinforcers—signals for food—presumed to be present). Order of presentation of the two sessions was randomized each day.

The bird continued to peck at the VR10 key for some time after the start of extinction, but eventually switched to the VR20 key and, sometimes after repeated switching between the two keys, made a new decision (100 consecutive pecks) to exploit that key. Sessions ended after 1000 pecks unless a potential decision-criterion run was in progress, in which case the session ended as soon as the criterion had been reached. All birds made a decision to exploit the VR20 key within 1000 pecks in every session. I recorded the number of pecks to the extinguished key and the time elapsed before the second decision.

Each bird switched sides more quickly, and after fewer pecks, when signals for food (empty food cups) were present than when they were absent (Fig. 1). If the signals for food are indeed condi-

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tioned reinforcers, this result is contrary to all theories of conditioned reinforcers.

Other studies (*4, 9*) have shown that stimuli associated with food strengthen performance during extinction. In this experiment, however, these stimuli eased the animal's transfer to another food site. The main difference in procedure is that an alternative key was present in the box. It may be that signals hastened the bird's transfer because the other key was available. Alternatively, the whir of the motors and associated stimuli may not, in fact, be conditioned reinforcers. To investigate these possibilities I repeated the experiment with only one key available during each session.

There were six daily pairs of sessions; the order of the sessions with and without conditioned reinforcers and the key to be used were decided randomly. Sessions began with 25 food deliveries on the VR10 schedule, after which the key no longer produced food. Sessions ended when 60 seconds had elapsed without a single response, a criterion chosen because it never occurred in a normal nonextinction session but was judged to be not so severe as to extinguish responses at the start of the next session.

If only one key was available, the bird generally took longer to reach the criterion of extinction when its pecks produced stimuli that had been associated with food than when they produced nothing (Fig. 1).

If an alternative feeding site is available, signals for food allow the dove to abandon the no-longer-profitable site more quickly. When no alternative site is present, the same signals keep the dove working on the only available site, despite its unprofitability. This being the case, how may one account for the more rapid switch seen in the presence of signals for food when an alternative key is available?

Foraging consists of a chain of responses, each leading to the next until the final act of consuming the food (*10*). Responses early in the chain are performed more often than responses late in the chain and are rewarded correspondingly less often. Estimates of the profitability of a patch are updated largely with the outcome of responses very late in the chain, rather than with every act in the chain. When no food is obtained because only early elements in the chain are completed, the profitability estimate drifts slowly down until the patch no longer fulfills the animal's expectations and is abandoned (*11*). But when the whole chain save the consumatory act is completed, the estimate of profitability is revised every time the consumatory act is reached but not performed. If the dove averages profitability over a short period of feeding, under the latter conditions its estimate of patch profitability will decline sharply.

Krebs *et al.* (*8*) have shown that the great tit (*Parus major*) efficiently gathers information about resource profitability. This report extends their findings to encompass a change in profitability during the feeding session. The signals that accompany food provide usable information (*2*) more rapidly than the nonarrival of both signals and food. They also interrupt the repeated pecking of the key and so provide both the information and opportunities needed for the bird to transfer its attention to the other key. In this way, signals for food during extinction allow the doves to obtain more food than simple extinction without signals (*12*).

Much recent work on foraging has stressed the qualitatively good fit between observed behavior and models of optimal behavior (*7, 13*). Deviations from predicted results are usually seen in terms of the deficiencies of simple foraging models (*8, 14*), rather than as reflections of the mathematical complexities of even simple models. Real psychological mechanisms must underlie real foraging behavior, but in very few cases (*15*) has understanding gone beyond the simple fact of near-optimal foraging to the mechanisms that govern the acquisition and use of information. I have demonstrated that one psychological mechanism, that of the conditioned reinforcer, may be used by the animal to aid its decision-making in a way that is counterintuitive; almost obtaining food is as important as actually obtaining it because both provide more information than does obtaining nothing at all.

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12. Total pecks delivered to both keys for each food crumb actually obtained in choice trials were calculated. Birds pecked significantly less when empty food cups appeared during extinction of the VR10 key. In other words,the total feeding session was more profitable, in terms of pecks expended for each food item gained, when empty food cups provided the doves with information that the patch was exhausted.

Median pecks per food delivery in choice trials; N.S., not significant.

Bird	Condition		Statistics*		
	Empty cups	No cups	*T*	*N*	*P*
1	24.3	42.1	2	7	<.05
2	22.0	28.0	0	6	<.05
3	25.0	32.8	3	7	N.S.
4	24.0	30.6	2	7	<.05

*Wilcoxon matched-pairs signed-ranks test.

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Protein Secretion by the Pancreas

Isenman and Rothman report that ligation of the exocrine duct does not increase the concentration of amylase in pancreatic juice (*1*). In spite of studies demonstrating increased permeability of the entire network of exocrine ducts after the main duct is obstructed, they propose that their finding supports the view that diffusion (as opposed to exocytosis) is the chief mechanism directing secretion of protein into pancreatic juice. However, the entire exocrine duct system is permeable to large molecules even at low pressures (*2*), and excess fluid containing large amounts of pancreatic enzyme activity begins to leak from the confines of this system and, within 10 to 30 minutes of ligation of the main duct,