CONTINUOUS, FIXED-RATIO, AND FIXED-INTERVAL REINFORCEMENT IN HONEY BEES

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Bees learned to enter a Plexiglas tube and to suck small portions of sugar solution; every entry or every fifth entry was reinforced. During an extinction phase, the bees on the fixed-ratio schedule emitted twice as many responses as did those given continuous reinforcement. Bees on a fixed-interval schedule of reinforcement emitted lower response rates than did those given fixed-ratio reinforcement. By extending the conditioning procedure for several days, it was possible to maintain responding with fixed-ratio schedules requiring 30 responses per reinforcement and with fixed-interval values up to 90 sec. Under fixed-interval schedules, response rates did not increase toward the end of the reinforcement intervals.

Learning in insects has been explored in various ways (Markl and Lindauer, 1965). The learning ability of honey bees, in particular, has been the subject of a number of learning experiments (von Frisch, 1965; Ribbands, 1953; Wenner and Johnson, 1966).

Only one study involving intermittent reinforcement with insects is known to the present author. Pessotti (1969) scheduled reinforcement for meliponies for a color discrimination on fixed-ratio schedules as high as FR 12 and found that behavior was maintained.

The present study presents data on the effects of continuous reinforcement (CRF), fixed-ratio (FR) reinforcement, and fixed-interval (FI) reinforcement on the acquisition and extinction performance of honey bees (*Apis mellifera*). Extinction data were examined for evidence of an increased resistance to extinction resulting from intermittent reinforcement, a relationship that has been demonstrated for vertebrates (Bitterman and Schoel, 1970).

METHOD

Subjects

Honey bees (*Apis mellifera*: Hym., Apidae) that came from a bee-house located about 30 m away from the ground-floor experimental

room were used. They were lured to a window feeding station that provided a 10% sucrose solution. Enough bees were always at the feeding station to provide a supply of experimental subjects.

Apparatus

Figure 1 presents a diagram of the apparatus. The experimental chamber consisted of a 5 mm inside diameter Plexiglas tube that contained a small reinforcement cup located 8 mm from the entrance end of the tube. A solenoid driven pump, calibrated to deliver 1.92 μ l of 50% sucrose solution per reinforcement, was connected to the reinforcement cup by a tube. A 3.8 cm (1.5-in.) diameter Plexiglas disc, with a hole drilled in the center to allow insertion of the chamber, was affixed to the entrance end of the chamber to provide a landing platform. The chamber and landing platform were surrounded by a plastic cylinder, not shown in Figure 1, 11 cm in diameter and 10 cm high (4.25 by 4 in.). It supported an infrared light source and a photocell located on opposite sides of the cylinder so that light to the photocell would be interrupted when a subject entered the chamber. A response was counted for each interruption of the light beam. Thus, after entering the chamber, a subject had to withdraw from the chamber and then reenter it for another response to be counted. Subjects remained on the platform with their middle and hind legs, and entered the chamber with their heads, thorax, and front legs; they remained in the chamber only long enough to suck the sucrose solution (ap-

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proximately 1.5 to 3 sec). The entire sequence of diving into the chamber, sucking the sucrose solution, and getting out of the chamber lasted approximately 5 sec.

Procedure

Individual bees were carefully carried from the feeding station to the apparatus by their wings with a pair of tweezers. They immediately began sucking a 50% sucrose solution that was placed on the upper part of the chamber. When a subject was filled, it returned to the hive, emptied its social stomach, and, in most cases, returned to the apparatus. Shaping procedures were used to train the subjects to enter the chamber with their heads. Initially, small amounts of sucrose solution were put at the entrance of the Plexiglas tube. Next, these drops were located deeper inside the chamber. Finally, the solution was pumped by hand into the reinforcement cup. After several reinforcements, the bee was marked with a small color dot (powered paint and shellac) on its thorax, a procedure described by von Frisch (1965). When the subject returned, it was identified by the color dot and the apparatus was switched on.

Each new arrival and subsequent working period at the apparatus was called a "visit". During each visit, individual subjects sucked between 50 and 80 μ l, i.e., they received 25 to 40 reinforcements, which is close to the body weight of a bee. The number of reinforcements per visit was highly consistent for individual subjects.

After the general training procedure described above was accomplished, the following investigations were conducted.

Fig. 1. Diagram of the conditioning apparatus. The bees enter the tube while standing on the platform on the middle and hind legs. During the experiment, the landing plane was located in the center of a round disc that covered a cylinder (see text for explanation).

Experiment 1: continuous reinforcement and fixed-ratio schedules. Eleven subjects received the sugar solution for each response (CRF), 10 for 45 visits and 1 for 30 visits and then responses had no scheduled effect (extinction). Twelve additional subjects received the solution for every fifth response (FR 5 schedule) and extinction was begun after 31 to 48 visits. Behavior during extinction was recorded for 30 min.

Experiment 2: fixed-ratio and fixed-interval schedules. Two identical apparatuses were used so that an FR subject and a paired FI subject could be run on the same day. Paired subjects also came from the same hive in order to ensure that rate of response, if different, would not have been a function of the food supply within the bee hive or due to different quantities and qualities of nectar and other supplies available on different days (see von Frisch, 1965). Eight of the subjects were brought to the terminal fixed-ratio schedule as follows: 15 visits CRF, five visits FR 2, five visits FR 3, 10 visits FR 4, and 10 visits FR 5. Eight additional subjects were brought to a schedule in which the first response occurring after 20 sec produced the sugar solution (FI 20-sec schedule) as follows: 15 visits CRF, five visits FI 6-sec, five visits FI 9-sec, five visits FI 12-sec, five visits FI 15-sec, and 10 visits FI 20-sec. For all 16 subjects, a 30-min extinction session began on the forty-sixth visit.

For another group of eight subjects, four FR 5 subjects and four FI 20-sec subjects, a 30-min extinction session began 7 hr after the first visit, independently of the actual number of visits. The four FR subjects made 45, 57, 60, and 37 visits before extinction was begun and the four FI subjects made 35, 40, 43, and 35 visits; the FR subjects made more visits than the FI subjects because they worked faster (see Table 1).

Experiment 3: extended training sessions. Pairs of subjects were maintained on fixed-ratio schedules and fixed-interval schedules respectively for several days. Ratio schedules eventually reached a value of 30 responses for every reinforcement, interval schedules were extended to 90 sec.

RESULTS

Experiment 1

The mean number of responses during the 30-min extinction period for the 11 CRF sub-

Table 1

Differences in response rates of honey bees on either CRF-FR 5 or CRF-FI 20-sec schedules of reinforcement (mean values, standard deviations, and p-values for eight bees for each condition).

Visits 11-15	CRF Phase				Difference
	Future FR 5 Bees		Future FI 20-sec Bees		
	Mean	SD	Mean	SD	
Min Present per Visit	2.71	0.64	3.00	0.80	t = 0.76, n.s.
Operants per Visit	34.20	2.49	32.80	4.79	t = 0.58, n.s.
Responses per Minute	13.17	3.11	11.57	2.76	t = 0.64, n.s.
Visits 41-45	FR 5		FI 20		
Min Present per Visit	7.14	1.60	9.54	1.39	t = 3.00, p < .01
Number of Responses per Visit	139.90	21.40	85.90	54.20	t = 5.10, p < .01
Number of Reinforcements per Visits	27.60	4.27	22.35	4.68	t = 2.23, p < .05
Responses per Min	21.90	6.27	9.00	2.09	t = 5.22, p < .01
Extinction Phase					
Number of Responses	187.75	61.30	66.63	15.54	X = 5.61*, p < .01

*X-test (Van der Waerden and Nievergelt, 1956)

jects and the 12 FR 5 subjects were 73.0 (SD = 25.3) and 156.6 (SD = 54.3) respectively. The standard deviations indicate wide ranges: 32 to 116 responses for the CRF subjects and 48 to 222 for the FR 5 subjects, however, the differences between the two groups were statistically significant ($t = 2.78, df = 21, 0.01 < p < 0.02$).

Experiment 2

Cumulative records of four of the eight pairs of subjects exposed to FR 5 and FI 20-sec schedules of reinforcement and started on extinction after 45 visits are presented in Figure 2. The FR 5 subjects (Figure 2, upper part) emitted markedly higher response rates than the FI 20-sec subjects (Figure 2, lower part). Table 1 shows the complete data as well as statistical analyses. The fixed-ratio schedules resulted in pauses after every reinforcement and the pauses became longer for higher ratios (see also Figure 3). Figure 2 shows the beginning of pausing after reinforcement. Table 1 indicates that the two groups did not differ at the outset of the experiment (Visits 11 to 15 under CRF), but showed significant differences after sufficient exposure to the FR 5 and

FI 20-sec schedules of reinforcement respectively as well as during the extinction phase.

Since the behavior of the eight bees that began extinction 7 hr after the first visit did not differ from that of the 16 bees presented in Table 1, no data are presented for this group.

Experiment 3

The method of both increasing reinforcement ratios and intervals was successful for several individual subjects and several FR-FI pairs. One FR-FI pair was observed for four days, another for seven consecutive days. In each case, both bees came from the same hive. Behavior could be maintained on FR 30 and FI 90-sec. Sample records are shown in Figure 3, upper part for visit 239 on the seventh day of an FR subject, and in Figure 3, lower part for visit 127 on the seventh day of the paired FI subject. The vast majority of the FI records looked like the record of visit 127 in Figure 3. The FR 30 record of Figure 3 is an example of what emerged after increasing the ratio from FR 5 to FR 30. The behavior during the extinction phases looked like a continuation of the behavior patterns produced during ac-

Fig. 2. Selected cumulative curves of four individual bees on fixed-ratio schedules of reinforcement (above), and four paired individual bees on fixed-interval schedules of reinforcement (below). From left to right (above): Visit 15 (CRF); Visit 16 (FR 2); Visit 45 (FR 5); Visit 46, Extinction phase. Below: Visit 15 (CRF); Visit 16 (FI 6-sec); Visit 45 (FI 20-sec); Visit 46, Extinction phase.

quisition, often in a somewhat exaggerated form. Pauses and response bursts were often more pronounced during the early extinction stages than during conditioning proper. Bees on fixed-interval schedule in contrast, continued during the extinction phases with the low response rates acquired during conditioning. They did not, however, develop any noticeable "scallop" as rats, pigeons, and most other vertebrates often have under comparable reinforcement conditions. The FI bees flew around between any two or more responses while the FR bees stayed at the tube and went in and out in rapid succession. They

stood on their four hind legs while the two front legs entered the tube together with the head and the thorax.

DISCUSSION

The present experiments have shown that intermittent reinforcement is possible with honey bees during nectar collection. Furthermore, the procedures were performed with unrestricted bees; they "volunteered" by coming into the experimental room from a beehive 30 m away.

Fig. 3. Representative cumulative curve for bees maintained on intermittent schedules of reinforcement for several days. Upper curve: Visit 239 on Day 7 on FR 30 schedule. Lower curve: Visit 127 on Day 7 on FI 90-sec schedule. The two bees came from the same hive at the same time. See text for explanation.

The behavioral modifications produced by different schedules of reinforcement were effective during acquisition as well as during extinction periods. As with vertebrates, the response frequencies during the extinction phases were greater than after either CRF or FI.

Perhaps the phylogenetic selection of the behavior potential has a certain importance for a successful ontogenetic development of individual organisms and at the same time, of course, for the whole species (see Lorenz, 1961, 1965; Skinner, 1966, for contrasting views on this topic from different scientific positions). For a bee population it is perhaps a matter of survival if its individual members are capable of responding differently to different schedules of nectar presentation. It would be interesting to see if other socially living insects capable of learning would respond in a similar way and if this would be also true for solitary ones. On the other hand, even within vertebrates, the aspects of operant behavior, in general, and intermittent reinforcement, in particular, have not yet been clarified as far as differences between "lower" and "higher" species for different schedules of reinforcement are concerned (Bitterman and Schoel, 1970).

There is yet another possibility from a phylogenetic point of view. The ability of various

systems to adopt to various schedules of reinforcement in a certain manner may not necessarily be a property that has been directly selected during evolution, but may be a property of a system that has evolved because of other advantages and functions.

The author has been puzzled by the problem of whether different schedules of reinforcement provided by natural contingencies may have any impact on the collecting behavior of bees in their natural habitat. It can be clearly seen in natural observation that many a blossom does not contain nectar—it is either empty already or not yet filled again. This would be an obvious prerequisite for intermittent reinforcement of nectar-collecting. In the laboratory, the bees' behavior was clearly influenced by schedules of reinforcement in a predictable manner. Similar behavior effects under natural conditions remain to be demonstrated.

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