Learning in honeybees as a function of amount of reward: Tests of the equal-asymptote assumption

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In Experiments 1 and 2, honeybee foragers visiting the laboratory were fed on targets of two different colors, one containing 5 μ l and the other containing 20 μ l of 50% sucrose solution. The targets were presented singly in quasi-random sequences on the training visits, after which preference was measured in an unrewarded choice test. In Experiment 1, 16 differentially rewarded training trials with each color were followed by the same number of trials with the color-amount relation reversed; no preference for either color was found in the subsequent choice test. In Experiment 2, 20 differentially rewarded training trials with each color—enough to produce a clear preference for the 20- μ l color when given directly after pretraining—were given after 10 feedings to repletion on each color that were calculated to generate near-asymptotic associative strength; no preference for either color was found in the subsequent choice test. In Experiment 3, there were 12 feedings to repletion on one color and, on the other, 12 feedings to repletion followed by 15 trials with a small (5 μ l) reward; no preference was found in a subsequent choice test. The results of all three experiments support a nonrepresentational interpretation of the role of amount of reward in the learning of honeybees.

In a continuing series of experiments on learning in honeybees as compared with learning in vertebrates (Bitterman, 1988), we began recently to study amount of reward (Buchanan & Bitterman, 1988), an important parameter of learning in vertebrates (Mackintosh, 1974). Some previous work had suggested that learning in honeybees might be independent of amount of reward (Menzel & Erber, 1972), but the method employed in that work seemed inadequate for a variety of reasons which need not be considered again here. Our own method was to train honeybees with two targets of different colors that were presented successively in quasi-random sequences, one target always containing 5 μ l of a 50% sucrose solution, the other containing 20 μ l of the same solution, and then to measure persistence of response to the targets in an extinction test, that is, when they no longer contained sucrose. If the number of training trials with the two targets was the same, the animals responded more in extinction to the 20- μ l target than to the 5- μ l target, but the difference in amount of reward could be offset by a difference in frequency. If the number of 5- μ l training trials was at least three times the number of 20- μ l trials, the animals responded more in extinction to the 5- μ l target; if the number of 5- μ l training trials was twice the number of 20- μ l trials, the animals responded equally often to the two targets in extinction.

Although the sucrose solution presented on a target is technically a "reward" because access to it is contingent upon response, the conditioned tendency to approach a target on which sucrose has been found may well be understood as classical rather than instrumental—that is, in terms of an association between target and reward (cf. Grossmann, 1970). In trying to develop such an account of our data on amount of reward (Buchanan & Bitterman, 1988), we considered two possibilities suggested in the vertebrate literature (Spence, 1956). One theory, characterized as *representational*, is that animals learn about amount of reward as such—that training with different amounts of reward produces different memories or expectancies (Tolman, 1932), which is to say, associations having different second terms or significates. The second theory, characterized as *nonrepresentational*, is that the significates are the same (sucrose or sweetness in each case), but that the associations differ in strength, either asymptotically (Hull, 1943), or in rate of approach to a common asymptote (the *equal-asymptote assumption*), or both (Rescorla & Wagner, 1972). All of our 1988 data could be simulated accurately without reference to representation on the equal-asymptote assumption, although the assumption probably was not severely constrained by those data.

The fact that honeybees show successive negative incentive contrast when trained with sucrose rewards of different concentrations (Couvillon & Bitterman, 1984) may be thought to call for a representational account; it was, of course, the discovery of successive contrast in rats (Elliott, 1928) and monkeys (Tinklepaugh, 1928) that first gave substance to representational theory. Whether

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honeybees would also show the effect in training with rewards differing in amount remains, however, to be determined, since sweetness may be "represented," but not amount. That the results for amount and concentration of sucrose need not be the same is clearly suggested by runway experiments with rats, although in those experiments successive contrast was found for amount but not for concentration (Flaherty, 1982). In any case, a contrast experiment with amount of reward, which might be regarded as the obvious next step in our work with honeybees, did not seem feasible, and we decided, therefore, to approach the problem from the other end, setting out in the present experiments to test some unique implications of the nonrepresentational equal-asymptote assumption. Disconfirmation of that assumption would bring us to the more difficult task of choosing between representational theory and unequal-asymptote nonrepresentational theory, with the disconfirming data themselves hopefully providing some clues as to how to proceed.

As has been noted before (Buchanan & Bitterman, 1988), we are handicapped in this work by the lack of a good within-subjects measure of acquisition. Latency of response to a single target is unreliable, and so also is choice between two simultaneously presented targets. Although choice is extremely useful when there is a single self-correction trial with feeding to repletion as the reward on each visit (Couvillion & Bitterman, 1988), animals given a series of small-reward trials on each visit often seem to respond precipitously, without the hesitant inspection of both alternatives that characteristically precedes choice when the reward is feeding to repletion. We have found it necessary, therefore, to rely on resistance to extinction, which has the decided disadvantage that multiple groups of animals are required to follow the course of acquisition over trials. In properly designed experiments, it does, however, prove to be an efficient measure.

EXPERIMENT 1

In this experiment, each animal was trained concurrently with targets of two different colors, one always containing 20 μ l of sucrose solution and the other always containing 5 μ l of the same solution. There were 32 trials, 16 with each color, which are enough to produce a marked preference for the large-reward color when given after the usual pretraining (Buchanan & Bitterman, 1988). Then there were 32 additional trials with the color-amount relation reversed, after which preference was measured in an extinction test. The prediction from equal-asymptote nonrepresentational theory was that there would be no preference for either of the colors because their associative strengths at the end of training would be exactly the same.

The terminal values can be computed easily from the simple linear equation

$$\Delta V = \beta(1 - V),$$

with V representing associative strength; ΔV , the change in strength produced by each reinforcement; β , the learning rate; and the asymptote taken as 1. If, for example, we assume that the associative strength established in pretraining is .3 for each color (Couvillion & Bitterman, 1988), and that the learning rates are .04 for the larger reward and .02 for the smaller (Buchanan & Bitterman, 1988), the associative strength of the small-to-large-reward color will be .49 after 16 trials and .74 after 32 trials, whereas the corresponding values for the large-to-small-reward color will be .64 and .74. It should be noted that the predicted outcome does not depend either on the learning rates chosen or on how many trials are given with each amount of reward; the terminal associative strengths of the two colors will always be the same if the number of large-reward trials is the same for each and if the number of small-reward trials also is the same. It can be shown in general that

$$V_{m+n} = V_{n+m} = 1 - (1 - V_0)(1 - \beta_1)^m(1 - \beta_2)^n,$$

where V_0 is the initial associative strength of each color, V_{n+m} and V_{m+n} are their terminal associative strengths, m and n are the numbers of trials with the two amounts of reward, and β_1 and β_2 are the learning rates.

The alternative theories (representational theory and unequal-asymptote nonrepresentational theory) afford no precise predictions, although it follows from both of them that exactly equal response to the two colors in the test would be rather unlikely. If no preference were found, it would be necessary in both cases to assume that the reversal training had been carried just far enough to eliminate the preference established initially but not to reverse it.

In rats, between-groups comparisons of runway performance have shown clear differences in the effects of training with large followed by small reward and training with small followed by large reward (e.g., Capaldi, 1970; Capaldi & Lynch, 1967), the differences generally being taken as evidence of representation. The runway seems a reasonably good analogue of our honeybee situation in that runway performance, although nominally instrumental, yields in the simplest case to analysis in terms of classically conditioned approach.

Method

Subjects. The subjects were 12 honeybees (*Apis mellifera*) from our own hives situated near the laboratory. All were experimentally naive.

Procedure. Individual honeybees were pretrained to fly from hive to laboratory and drink from a large drop (about 100 μ l) of 50% sucrose solution on a target that was set on the sill of an open laboratory window. The target was a plastic disk, 5 cm in diameter and 1 mm thick, that was (nominally) half-blue and half-orange (180° of each color). An animal selected at random from a group of foragers at a feeding station equipped with a jar of 10%–15% sucrose solution was captured in a match box, carried to the sill, and placed on the target. There it was permitted to drink its fill (during which time it was marked with a spot of lacquer) and then to fly back

to the hive. Typically, the animal would return to the laboratory in a few minutes, continuing to shuttle back and forth between the hive and the sill as long as food was available there. If the marked bee did not return to the sill after its first placement, it was picked up at the feeding station (where it usually could be found) and placed again on the target. The pretraining ended with the animal's second return to the sill of its own accord.

Arriving from the hive on each of the first eight training visits, the animal found a target like the pretraining target, but either all blue or all orange, containing either a 5- μ l or a 20- μ l droplet of 50% sucrose solution. After taking the sucrose, the animal would fly up from the target, hovering over the sill while the target was quickly removed and replaced with another target, again either blue or orange and containing either 5 or 20 μ l of the sucrose solution. The second target was quickly replaced by a third, and so on, until the animal left of its own accord for the hive. For 6 of the 12 subjects, the blue targets always contained 20 μ l of sucrose and the orange targets 5 μ l, with the opposite true for the remaining subjects. The two targets were presented in balanced quasi-random sequences over these visits, during which each animal could be expected to have about 16 trials with each target (an average of two trials with each target on each visit, with the expected average intake of about 50 μ l). The procedure was such, of course, that the number of training trials with each target for each animal could not be fixed exactly, since it depended on the behavior of the animal, but the approximation was very close; the average number of trials was 16.0 with the 20- μ l color and 16.5 with the 5- μ l color. On the next eight visits, the procedure was exactly the same except that the color-amount relationship was opposite to that on the first eight visits; the color which before had been paired with the larger amount was now paired with the smaller (the large-to-small or LS color), and the color which before had been paired with the smaller amount was now paired with the larger (the small-to-large or SL color); the average number of trials was 16.0 with the 20- μ l color and 16.2 with the 5- μ l color.

After the last training visit, each animal returned from the hive to find a pair of fresh targets, one blue and the other orange, set 10 cm apart in a lateral arrangement on the window sill. For half the animals, the LS target was on the left; for the remaining animals, the LS target was on the right. Each target now contained 10 μ l of tap water (unacceptable and distinguishable from the sucrose solution only by taste). Upon encountering water on one of the targets, the animal would leave it, then return to it or go to the other target, leave again, return again (often only briefly, with no attempt to drink), and so forth, the interval between successive responses increasing as the test continued. All actual contacts with each target, however brief, during a 10-min extinction period were recorded by the experimenter, who pressed one of two hand-held switches that activated counters programmed to print stored frequencies at 30-sec intervals. The duration of the test was 10 min. (These temporal parameters—the 30-sec cumulation interval and the 10-min test duration—are used routinely in our laboratory.)

Results

The performance of the animals in the extinction test is plotted in Figure 1 in terms of the mean cumulative number of responses to each target over successive 30-sec intervals. The two curves are very much the same. Analysis of variance—based in accordance with our routine practice on uncumulated 30-sec scores in 2.5-min blocks—yielded a significant blocks effect [$F(3,33) = 39.95, p < .0001$], but neither a significant stimulus (LS vs. SL) effect ($F < 1$) nor a significant stimulus $\times$ blocks interaction ($F < 1$). The results are precisely those that were predicted on the basis of the equal-asymptote assumption.

EXPERIMENT 2

This experiment was designed to test another unique implication of equal-asymptote nonrepresentational theory, which is that training with different amounts of reward will have little differential effect when associative strength is already close to the asymptote. We know from our previous work (Buchanan & Bitterman, 1988) that 20 20- μ l trials with one color and 20 5- μ l trials with another will produce a substantial preference for the 20- μ l color when those trials are given after the usual pretraining. If, merely for purposes of illustration, we assume as before that the growth rates (to an asymptote of 1) are .04 for 20 μ l and .02 for 5 μ l, the terminal associative strengths are .69 and .54, respectively, when the differential training is begun after pretraining assumed to give each color an associative strength of .3 (Couvillon & Bitterman, 1988). When, however, the differential training is begun after 10 feedings to repletion on each of the colors, which on the assumption of a growth rate on the order of .2 brings the strength of each color to .92, the terminal values are .97 and .95, respectively. As to the alternative theories, there is nothing in either of them to suggest that differential training with two smaller rewards should fail to produce a preference when it follows training with a very large reward. If there were no preference, it would be necessary in each case to say that not enough training had been given.

The use of feedings to repletion to bring associative strength close to the hypothetical asymptote before beginning differential reinforcement was a convenient substitute for what might be preferred as a more direct test of the equal-asymptote assumption, namely, to use prolonged training with differential reinforcement from the outset. If our estimates of the learning rates for the two amounts of reward are correct, the direct test would require about 150 trials with each color, or about 75 training visits in all, which probably would not be a wise use of our (limited) resources. Not only would the training time for each

Figure 1. Mean cumulative number of responses in extinction to the large-to-small-reward (LS) and small-to-large-reward (SL) colors in Experiment 1.

animal be very much longer, but the number of animals failing to return for the scheduled number of visits would be much greater, and so also would be the variation over time in field and hive conditions.

The results of runway experiments with rats have pointed for a good many years to a positive correlation between asymptotic performance and amount of reward (e.g., Crespi, 1942; Zeaman, 1949), and like results have been obtained in runway experiments with vertebrates of other classes (e.g., Gonzalez, Potts, Pitcoff, & Bitterman, 1972; Pert & Bitterman, 1970), although there have been some reports that asymptotic differences disappear in the course of prolonged training (e.g., Campbell, Batsche, & Batsche, 1972). The difficulty in such experiments is that, when there is a difference in asymptotic performance, the training may not have been carried far enough, and when there is not, an underlying difference in associative strength may have been masked by a performance ceiling. Evidence of an asymptotic effect comes also from within-subjects experiments (e.g., Davenport, 1970; Hill & Spear, 1963) in which rats and monkeys choosing between stimuli paired with different amounts of reward persistently prefer the alternative paired with the larger amount.

Method

Subjects. The subjects were 12 foragers from our own hives. All were experimentally naive.

Procedure. The animals were pretrained in the same way as in Experiment 1. In the first stage of training, there were 20 visits on each of which the animal found a single target (like the training targets of the previous experiment) that contained a large drop of 50% sucrose solution from which feeding to repletion was permitted. On 10 of the visits, in quasi-random balanced order, the target was orange, and on the remaining 10 visits it was blue. In the second stage of training, there were 10 visits exactly like the training visits in Experiment 1, with 20 μ l of sucrose on targets of one color—the repletion-to-large or RL color—and 5 μ l of sucrose on targets of the other color—the repletion-to-small or RS color. Again, an average of two trials with each color on each visit, or 20 trials with each color in all, could be expected; the actual values were 20.0 trials with the 20- μ l color and 19.8 trials with the 5- μ l color. After the last training visit, each animal returned from the hive to find (just as in Experiment 1) a pair of fresh targets, one blue and the other orange, set 10 cm apart in a lateral arrangement on the window sill. The RL color was on the left for half the animals and on the right for the rest. The targets now contained 10 μ l of tap water, and all contacts with each during a 10-min period were recorded.

Results

The performance of the animals in the extinction test is plotted in Figure 2 in terms of the mean cumulative number of responses to each target over successive 30-sec intervals. The curves show no substantial preference for the RL color. Analysis of variance yielded a significant effect of 2.5-min blocks [$F(3,33) = 26.11, p < .0001$], but neither a significant stimulus (RL vs. RS) effect ($F < 1$) nor a significant stimulus $\times$ blocks interaction

($F < 1$). These results support the equal-asymptote assumption.

EXPERIMENT 3

Considered in this experiment was the implication of the equal-asymptote assumption that training with a small reward after training with a large reward can only increase the associative strength of a stimulus, although the increase may not be substantial when associative strength is already near its asymptote. If, for example, we assume as before that the associative strength produced by pre-training is .3 and the growth rate for feeding to repletion is .2, the associative strength of a target on which there have been 12 such feedings is .95. The associative strength of a target on which there have been 12 feedings to repletion followed by 15 5- μ l trials, for which the growth rate is .02, is .96. Representational theory predicts that asymptotic performance, once achieved in training with a large reward, will be reduced by a shift to a small reward, because the old expectation ultimately will be replaced by a new one. Decrement in performance with a downshift in amount of reward is predicted also by at least one version of unequal-asymptote nonrepresentational theory (Rescorla & Wagner, 1972), according to which the change in associative strength on a given trial is negative when the preexisting strength is greater than that which the reinforcer will support.

It has been found repeatedly since Crespi (1942) that the runway performance of rats shifted from a large to a small reward may decline to a level even below that of control animals trained from the outset with the small reward, although successive contrast, which has been widely interpreted in representational terms, seems not to be a general phenomenon of vertebrate learning (Bitterman, 1987). Some puzzling experiments with goldfish have been reported in which performance was entirely unaffected by a shift from a large to a small reward (e.g., Gonzalez et al., 1972) but the superior performance of unshifted control animals trained with a large as compared

Figure 2. Mean cumulative number of responses in extinction to the repletion-to-large-reward (RL) and repletion-to-small-reward (RS) colors in Experiment 2.

with a small reward contradicted the equal-asymptote assumption.

Method

Subjects. The subjects were 16 foragers from our own hives. All were experimentally naive.

Procedure. The pretraining procedure was the same as in the preceding experiments, and so were the orange and blue training stimuli employed. In 32 training visits, there were 12 feedings to repletion (of 50% sucrose) on the control color (C)—orange for half the animals, blue for the rest—and, on the other, downshifted color (DS), there were 12 feedings to repletion followed by 15 5- μ l feedings. We did not, however, simply give 12 feedings to repletion on each color in the first 24 visits and then add small-reward visits on the DS color, because that procedure would have produced a confounded difference in recency. Instead, experience with the two colors was spread over all 32 training visits. In the first 19 training visits, there were seven feedings to repletion on C and 12 feedings to repletion on DS. In the next 13 training visits, there were five more feedings to repletion on C interspersed in balanced quasi-random fashion with eight small-reward visits to DS. Each small-reward visit began with one, two, or three presentations of DS containing 5 μ l of sucrose (the number of DS trials on each of these visits varying in quasi-random fashion for a total of 15 over the eight visits), and it ended with the presentation of a (nominally) green target, readily discriminable from the other two, that contained a large drop of sucrose from which feeding to repletion was permitted. The test used in this experiment was exactly the same as in the two preceding experiments. A pair of fresh orange and blue targets, each containing 10 μ l of tap water, was presented, and contacts with each in a 10-min period were recorded.

Results

The performance of the animals in the extinction test is plotted in Figure 3 in terms of the mean cumulative number of responses to each target over successive 30-sec intervals. The two curves are very much the same, and what seems to be a crossover is statistically unreliable. Analysis of variance yielded a significant effect of 2.5-min blocks [$F(3,45) = 33.64$, $p < .0001$], but neither a significant stimulus (C vs. DS) effect ($F < 1$) nor a significant stimulus $\times$ blocks interaction [$F(3,45) = 1.59$, $p < .2039$]. The results again support the equal-asymptote assumption.

DISCUSSION

The results of all three of these experiments yield readily to an equal-asymptote nonrepresentational analysis, which the results for vertebrates—however they may be understood—clearly do not. In Experiment 1, one of two targets contained 20 μ l of sucrose solution on Trials 1–16 and 5 μ l on Trials 17–32, while the opposite was true of the other target. On the equal-asymptote assumption, the terminal associative strengths of the two targets should have been exactly the same and, in fact, no differential response to them was found in a subsequent test. In Experiment 2, 20 differentially rewarded trials with each of two targets were given after 10 feedings to repletion on each that were calculated to bring their associative strengths close to the hypothetical common asymptote, and, in fact, no differential response to them was found

Figure 3. Mean cumulative number of responses in extinction to the downshifted (DS) and control (C) colors in Experiment 3.

in a subsequent test. In Experiment 3, there were 12 feedings to repletion on one target while, on another, there were 12 feedings to repletion followed by 15 5- μ l trials that should not, on the equal-asymptote assumption, have made the animals any less likely to approach it, and, in fact, no differential response to the two targets was found in a subsequent test.

An obvious question, and one that we are inclined to take seriously, is whether such a set of three null outcomes warrants adoption of the equal-asymptote assumption, at least for strategic purposes. Since the only distinctive predictions from the assumption that we are able to test rigorously are of null outcomes, the question reduces to how many such outcomes over how wide a range of experimental conditions would justify the strategy. In evaluating null outcomes, the sensitivity of measurement also must be considered, but the results of our previous experiments (Buchanan & Bitterman, 1988) seem, in our opinion, to leave little room for doubt on that score. In those experiments, small and equal numbers of trials with 5- and 20- μ l rewards produced clear preferences that could be reversed readily by opposing frequency to amount. More recent experiments on overshadowing in honeybees (Couvillon & Bitterman, 1989) showed extinction to be sensitive to small differences in associative strength that were not revealed by transfer tests (reversal or nonreversal) in which correct choice was differentially rewarded with feeding to repletion.

The successive contrast shown by honeybees trained with sucrose solutions differing in concentration (Couvillon & Bitterman, 1984) may suggest that concentration, if not amount, is represented, although both successive contrast and the concentration-dependent overlearning-extinction effect reported in the same paper can be understood without reference to representation—at least in a formal sense. In the model developed by Daly and Daly (1982), it is not unrealized expectation but a negative discrepancy between the strength of a conditioned approach tendency and the strength which the reinforcer will support that is assumed to generate a competing emotional

response. Whether the distinction is more than a verbal one remains, however, to be determined. It would not be surprising, in any case, if the effects of concentration and amount of sucrose were found to be different, since concentration is detected immediately by the taste receptors whereas amount may be detected, if not visually, then only in terms of the duration of feeding. Since representation must depend on perception, it might be useful in trying to understand the difference between our results and those for rats to inquire into the way in which amount of reward is detected by honeybees.

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