Performance of honeybees in reversal and ambiguous-cue problems: Tests of a choice model

P. A. COUVILLON and M. E. BITTERMAN
University of Hawaii, Honolulu, Hawaii

Individual honeybees visiting the laboratory regularly for food were trained in a variety of discrimination-reversal and ambiguous-cue problems to choose between two differently scented targets, of which one or the other contained sucrose solution. The training was simulated with a set of equations for predicting choice on the basis of associative strength, and the accuracy of prediction was indexed by the root-mean-square deviation of simulated data from obtained data. Developed earlier on the basis of performance in other problems (Couvillon & Bitterman, 1985), the model proved adequate for the new problems as well.

In recent experiments designed to analyze the process of choice in honeybees (Couvillon & Bitterman, 1985), individual foragers shuttling back and forth between the hive and the sill of an open laboratory window were presented on each visit with two targets that were discriminably different in odor. One of the targets contained a drop of water (which was unacceptable), and the other contained a drop of 50% sucrose solution from which the animal fed to repletion; if the animal went first to the target containing water, it was free at once to correct its choice. With position balanced, the location of the sucrose was for some animals perfectly predictable on the basis of odor, but for others less so, and for yet others not at all (each of the targets contained the sucrose on half the visits in quasi-random order). The various training schedules then were simulated quantitatively, always with the same simple linear equations for computing change produced by reinforcement or nonreinforcement in the strength of association between each target and sucrose, but with a diverse array of functions for predicting choice on the basis of relative strength. The purpose was to find a choice function that would maximize the accuracy of prediction as indexed by the root-mean-square (RMS) deviation of simulated performance from real performance.

Change in associative strength is expressed in the model by a linear equation (Bush & Mosteller, 1951) in the familiar notation of Rescorla and Wagner (1972):

$$\Delta V_A = \beta(\lambda - V_A)$$

with V_A representing the associative strength of alternative A, ΔV_A the change in strength produced by reinforcement or nonreinforcement,

λ the asymptotic associative strength, and β the learning-rate parameter. Rescorla and Wagner's salience parameter, α , does not appear in the equation, on the assumption that the odors used are equally salient; whatever the actual value of α , which is assumed to influence associative strength, the prediction of choice, based as will be explained in a moment on relative strength, is the same. The value of λ is taken as 1 when there is reinforcement (on the assumption that the magnitude of reinforcement is maximal) and as 0 when there is no reinforcement, and provision is made in the model for the possibility that the value of β is different for reinforcement and nonreinforcement ($U\beta =$ incremental or up β , $D\beta =$ decremental or down β). The associative strength of A relative to that of B is designated as r_A and is expressed by the equation

$$r_A = V_A / (V_A + V_B),$$

where V_B is the associative strength of B. A simple computer program evaluates r on the basis of assumed initial values of V_A and V_B , dictates a choice, and then calculates the resulting changes in associative strength. When A is the reinforced alternative on a given visit, V_A alone is changed (incremented) if A is chosen initially; if B is chosen initially, V_B is decremented and then V_A is incremented (correction method). Choice is dictated by any one of a family of power functions that may be incorporated in the model, that is, functions relating P_A , the probability of choosing A, to r_A .

To generate the choice functions, we used the scaling equations

$$P = .5 + s(2r - 1)^\kappa$$

for $r \geq .5$, and

$$P = .5 - s(1 - 2r)^\kappa$$

for $r < .5$, which, with $s = .5$, yield a set of sigmoid curves passing through the points (0,0), (.5,.5), and (1,1).

This research was supported by Grant No. BNS 85-11647 from the National Science Foundation. Helpful advice from William T. Woodard is gratefully acknowledged, as is the assistance of Diane Baird, Celestino Palacio, Philip Okamoto, and Mei Yee Wong in collecting the data. Requests for reprints should be addressed to the authors at the Békésy Laboratory of Neurobiology, 1993 East-West Road, Honolulu, HI 96822.

When $K > 1$, P changes slowly in the region of $r = .5$ and progressively faster at the extremes; when $K < 1$, the opposite is true; and when $K = 1$, the relation between P and r is linear, as shown in Figure 1 where the curve for $K = 1$, $s = .5$ is included to provide a frame of reference. (The curves of Figure 1 are plotted only for $r \geq .5$, because all the functions are perfectly symmetrical for $r < .5$.) When $s > .5$, with P truncated to $0 \leq P \leq 1$, the curves are steeper, as may be seen by comparing $K = 1$, $s = .833$ with $K = 1$, $s = .5$ in Figure 1, or by comparing $K = .75$, $s = .833$ with $K = .75$, $s = .625$. The truncation of P , of course, implies a performance ceiling—insensitivity of the choice measure to differences between extreme values of r .

For each of a substantial variety of choice functions, we set out to find the initial value of $V_A = V_B$ (assumed to be > 0 in consequence of pretraining with the two stimuli) and the values of $U\beta$ and $D\beta$ that would yield the minimal RMS deviation (square root of the mean of the squared deviations) of predicted from obtained choices, and the functions were compared in terms of minimal RMS deviations. The best fit to the data previously reported (RMS deviation about .10) was achieved with $K = .75$, $s = .625$, for $V_A = V_B = .3$ and $U\beta = D\beta = .25$. The high initial value of $V_A = V_B$ and the high learning-rate parameters reflect the fact that the performance of the bees is strongly influenced by the pattern of reinforcement. Some readers have found the equality of $U\beta$ and $D\beta$ disturbing on the assumption that acquisition with partial reinforcement requires $U\beta > D\beta$, but that assumption is incorrect; given $U\beta = D\beta = .25$, for example, V rapidly approaches an average value of about .50 with 50% reinforcement.

Figure 1. Five choice functions yielding good fits to the data presented here and in a previous paper (Couvillon & Bitterman, 1985), with $K = 1$, $s = .5$ included for reference.

Our purpose in the present work was to determine how well the same choice function ($K = .75$, $s = .625$), together with the same assumption about the effect of pretraining on the initial associative strength of the alternatives ($V_A = V_B = .3$) and the same learning-rate parameters ($U\beta = D\beta = .25$), would predict performance in a series of problems quite different from, and somewhat more complicated than, the problems used in the development of the model. One of the old problems required reversal of a preference (there were 10 visits with B+ after 10 visits with A+). Here we used two other such problems, both extending over 32 visits, with reversal after every 8 visits in the first problem and after every 4 visits in the second. We also used three problems involving three stimuli (A, B, and C), which were presented in pairs. The first was the so-called ambiguous cue or positive-ambiguous-negative (PAN) problem, in which A is paired with B, and B is paired with C; B (the ambiguous cue) is reinforced when paired with C, but not when paired with A (Leary, 1958; Thompson, 1954). The second was a modification of the PAN problem, A always reinforced when paired with B, but B and C equally often reinforced when paired with each other. In the third problem, all three possible pairings of the three stimuli were presented, with probabilities of reinforcement of .75 for A, .50 for B, and .25 for C. These five problems were selected, not for the purpose of challenging the obviously oversimplified associative features of the model (which would come later), but simply to cross-validate the first results—that is, to get some idea of the extent to which they capitalize on chance.

METHOD

Subjects

The subjects were honeybees (*Apis mellifera*) that were foraging for nectar. They came from our own hives, situated in the vicinity of the laboratory. Five separate groups of subjects, all experimentally naive, were trained in the five problems.

Procedure

Individual bees were pretrained to fly from their hives to the laboratory and to drink to repletion from a large drop (about 100 μ l) of 50% sucrose solution on a single target that was set on the sill of an open window. An animal was selected at random from a group of foragers at a feeding platform equipped with a large jar of 10%–15% sucrose solution, carried in a small matchbox to the laboratory, and placed on the target. There it was permitted to drink its fill of 50% solution (during which time it was marked with a spot of colored lacquer) and then to fly to the hive. Typically, the animal returned to the laboratory of its own accord in 3 or 4 min, continuing thereafter to shuttle back and forth between the hive and the laboratory as long as food was available. If the marked bee did not return to the laboratory after the first placement, it was picked up again at the feeding platform (where it usually could be found), carried back to the laboratory in the matchbox, and set down on the target once more. The pretraining ended with the bee's second return to the laboratory of its own accord.

The targets were covered petri dishes of clear plastic, 5.5 cm in diameter. In each cover, which was sprayed with flat gray paint, eight equally spaced holes, .5 cm in diameter, were drilled at the outer circumference. Three sets of targets were used in the train-

ing. The dishes of one set contained wads of cotton that were impregnated with a jasmine scent, the dishes of the second set were scented in the same way with peppermint, and the dishes of the third set were scented with geraniol. The covers used on each visit were washed and exchanged for others in the same set after the visit in order to balance extraneous stimuli. For purposes of pretraining only, there were targets labeled with both jasmine and peppermint (the scents used in the two-stimulus reversal problems) and targets labeled with all three scents (for the three-stimulus problems).

On each training visit, the animal found two targets set 10 cm apart on a line parallel to the outer edge of the window sill, with position balanced over visits in accordance with selected Gellermann orders. One of the targets contained a large drop of 50% sucrose solution, and the other a large drop of tap water that was distinguishable from the sucrose only by taste. The target first chosen by the subject on each visit was recorded, and the trial ended when the animal had found the correct target, fed to repletion, and gone back to the hive.

Eight-visit reversals. Each of 12 bees was permitted 32 visits to a pair of targets, one scented with jasmine, the other with peppermint. One of the scents was reinforced on visits 1-8 and 17-24, the alternative on visits 9-16 and 25-32. Of the 12 animals, 6 began with peppermint reinforced and 6 with jasmine reinforced. The position of the reinforced scent was balanced over visits in a sequence that was the same for all animals.

Four-visit reversals The training of 20 bees was the same as in the 8-visit reversals except that positive and negative stimuli were reversed after every 4 visits in the series of 32 visits. Again, half the animals began with jasmine reinforced and half with peppermint reinforced.

PAN 1 Each of 12 bees was trained in 32 visits with three scents designated A, B, and C. The actual scents were jasmine, peppermint, and geraniol, and their roles in the experiment were balanced (e.g., jasmine was A for 4 animals, B for 4, and C for 4). On 16 visits, A and B were presented with A reinforced, and on the remaining visits, B and C were presented with B reinforced, which meant that the probabilities of reinforcement were 1.0 for A, .50 for B, and 0 for C. The visits of the two kinds (A+B- and B+C-) were scheduled in a balanced order that was the same for all animals. Position also was balanced over visits, with the positive member of each pair appearing equally often on the right and on the left in a sequence that was the same for all animals.

PAN 2. The training of 12 bees was exactly the same as in PAN 1 except that B and C were equally often reinforced (in a balanced order that was the same for all animals) on BC visits, which meant that the probabilities of reinforcement were 1.0 for A, .25 for B, and .50 for C. In this problem, both B and C were "ambiguous."

Three pairs. The training of 12 bees was with the same three scents as in the PAN problems except that all three pairs of the scents were presented. There were 12 visits to AB, 12 to AC, and 12 to BC, with the roles of the three scents balanced over animals. A was reinforced on nine of the AB visits and on nine of the AC visits, and B was reinforced on nine of the BC visits, which meant that the probabilities of reinforcement were .75 for A, .50 for B, and .25 for C—all three stimuli were "ambiguous." The sequence of A+B-, B+A-, A+C-, C+A-, B+C-, and C+B- visits was the same for all animals, and the probability of reinforcement for each stimulus was the same whether it was on the left or on the right.

RESULTS

Performance in the eight-visit reversals is plotted in Figure 2 in terms of the proportion of animals that chose A (the scent initially reinforced) on each visit. The preference was quickly established and then quickly reversed, again and again. The agreement between the real perfor-

mance and the simulated performance of 50 stat bees, also plotted in Figure 2, is substantial (RMS deviation about .15). The largest single discrepancy is for visit 10, at which point the obtained proportion of animals choosing A seems spuriously low.

Performance in the four-visit reversals is plotted in Figure 3 in terms of the proportion of animals that chose A (the scent initially reinforced) on each visit. Agreement with the simulated performance of 50 stat bees, which also is plotted in Figure 3, again is quite good (RMS about .13). Both the obtained and the simulated performance show what seems to be a progressive deterioration that, given the nature of the data, is difficult to evaluate statistically. The effect was observed in the performance of the first 10 subjects in the group, and it was for the purpose of confirmation that the size of the group was increased to 20. It is interesting to note that a simulation of 20 four-visit reversals shows no further deterioration of performance, which remains like that in visits 25-32. A diverse assortment of previous reversal and quasi-reversal experiments with honeybees (Meineke, 1978; Menzel, 1969; Schmetter, 1979; Sigurdson, 1981) has yielded some quite inconsistent results—progressive improvement in certain cases and progressive deterioration in others—which have yet to be understood.

Performance in the PAN 1 training is plotted in Figure 4 in terms of the proportion of the animals that chose A (the consistently reinforced scent) on each AB visit, and the proportion of animals that chose B (the "ambiguous" scent) on each BC visit. The agreement between

8 - VISIT REVERSALS

Figure 2. Proportion of A choices (A = the originally reinforced alternative) on each visit in the eight-visit reversal training. The large circles are for the obtained data. The small circles are for data simulated with $K = .75$, $s = .625$, initial $V_A = V_B = .3$, and $U_B = D_B = .25$.

Figure 3. Proportion of A choices (A = the originally reinforced alternative) on each visit in the four-visit reversal training. The large circles are for the obtained data. The small circles are for data simulated with $K = .75$, $s = .625$, initial $V_A = V_B = .3$, and $U\beta = D\beta = .25$.

the obtained and simulated (50 stat bees) performance again is quite good (RMS deviation about .13), and is somewhat better for BC visits than for the later AB visits (where the obtained proportions of A choices tend to exceed the simulated proportions). It is interesting to note that both the obtained and the simulated asymptotic choice levels are better for BC than for AB visits, a result familiar from work with monkeys (Boyer & Polidora, 1972) and pigeons (Hall, 1980). The bees chose B on BC trials significantly more often than they chose A on AB trials ($p < .01$ by Wilcoxon's test for paired replicates).

Performance in the PAN 2 training is plotted in Figure 5 in terms of the proportion of animals that chose A (consistently reinforced) rather than B (reinforced with a probability of .25) on each AB visit, and the proportion of animals that chose B rather than C (reinforced with a probability of .50) on each BC visit. The agreement between obtained and simulated (50 stat bees) data again is quite good (RMS deviation about .18). With the A:B reinforcement ratio now 100:25, instead of 100:50 as in the PAN 1 problem, the simulated proportions of A choices on AB visits are clearly greater than in PAN 1, but the obtained proportions are not, perhaps because the obtained PAN 1 proportions are spuriously high (see Figure 4). The curves for the BC (25:50) visits show no strong overall preference, either real or simulated, for B. The marked fluctuations in obtained proportions, which are tracked for the most part by the simulated proportions,

can be understood in terms of schedule effects to which the model is sensitive. The principal discrepancies—for BC visits 2 and 3—are due at least in part to random error in the simulation. A repetition of the simulation for 50 stat bees gave values of .46, .26, .50, .29, and .47 for the first five BC visits, a pattern closer to that shown by the real bees. The question of simulation reliability will be considered again later.

Performance in training with all three pairs of the three scents is plotted in Figure 6 in terms of the proportion of animals that chose A on each AB (75:50) visit and on each AC (75:25) visit, and the proportion of animals that chose B on each BC (50:25) visit. Here again are what seem to be schedule-related fluctuations in the obtained proportions which are tracked by the simulated proportions (50 stat bees) with a few marked exceptions on AC visits. The RMS deviation for this problem is about .17.

DISCUSSION

The model developed on the basis of our earlier data (Couvillon & Bitterman, 1985) seems in general to fit the new data rather well. For $K = .75$, $s = .625$, initial $V_A = V_B = .3$, and $U\beta = D\beta = .25$ —the parameters that had yielded the best fit to the earlier data—the RMS deviation based on the entire set of data (new and old combined) is about .14. This deviation is considerably larger than the deviation of about .10 computed earlier on the

Figure 4. Proportion of A choices on each AB visit and proportion of B choices on each BC visit in the PAN 1 training. The large circles are for the obtained data. The small circles are for data simulated with $K = .75$, $s = .625$, initial $V_A = V_B = .3$, and $U\beta = D\beta = .25$.

basis of the old data alone, but inspection of Figures 2–6—with the possible exception of the upper (AB) panel of Figure 4—gives no hint of systematic error. There is good reason, in fact, to suppose, not that the new value reflects limitations of the model which are highlighted by the new problems, but that the old value is unrealistically low. In the first of the four old problems that were studied (100:0 → 75:25), choice of A was computed in four-visit blocks rather than on individual visits, which meant reduced random error both in the obtained and in the simulated data. In another of the old problems (100:0 → 0:100), the obtained data were smoothed for fitting purposes on the stated ground that none of the choice functions being compared could predict the irregularities, but here only the obtained proportions were used. Furthermore, random error tends to be greater in the region of $P_A = .5$ than at the more extreme values of P ; for the only old problem (50:50) in which the choice proportions centered on .5, the RMS deviation was about .15.

It should be emphasized that goodness of fit is limited by random error both in the simulation process and in the data. To estimate the former, we did a second simulation for 50 stat bees trained in the entire set of problems, which yielded an RMS deviation from the real data of .140—close to the value of .141 for the first simulation. On the basis of the RMS deviation of the two simulations from each other, which is .086, the random simulation error, σ_s , may be estimated from the equation

Figure 5. Proportion of A choices on each AB visit and proportion of B choices on each BC visit in the PAN 2 training. The large circles are for the obtained data. The small circles are for data simulated with $K = .75$, $s = .625$, initial $V_A = V_B = .3$, and $U\beta = D\beta = .25$.

Figure 6. Proportion of A choices on each AB and each AC visit and proportion of B choices on each BC visit in the training with all three pairs of stimuli. The large circles are for the obtained data. The small circles are for data simulated with $K = .75$, $s = .625$, initial $V_A = V_B = .3$, and $U\beta = D\beta = .25$.

$$\sigma_s^2 + \sigma_{dm}^2 = (.086)^2$$

as .061, and on the simplifying assumption of independence the random error in the data combined with the systematic model error (σ_{dm}) may be estimated from the equation

$$\sigma_s^2 + \sigma_{dm}^2 = (.14)^2$$

as .126. The reliability of the data is a serious limitation in this work; although the number of stat bees can be increased rather easily, the number of real bees cannot be increased substantially except at great expense.

Good fits to the earlier data (Couvillon & Bitterman, 1985) actually were achieved with several similar choice functions of which $K = .75$, $s = .625$ was only marginally the best. One was $K = 1$, $s = .833$, and another was $K = .5$,

$s = .625$, both of which may be compared with $K = .75$, $s = .625$ in Figure 1. On the chance that the new data might permit a more confident decision among the alternatives, we simulated training in the five new problems with a variety of choice functions, systematically varying initial associative strength and the learning-rate parameters (Couvillon & Bitterman, 1985) in a search for the best fit afforded by each function to the combined data of the old and new problems (220 values in all). The results are shown in Figure 7, which is a plot of minimal RMS deviation against K for three different values of s , and here again we see a cluster of similar functions—five of them—yielding approximately equal goodness of fit. All five are plotted in Figure 1. Among them are the three functions that yielded the best fits to the old data alone: $K = .75$, $s = .625$, with $V_A = V_B = .3$ and $U\beta = D\beta = .25$ as before; $K = 1$, $s = .833$, with $V_A = V_B = .3$ and $U\beta = D\beta = .25$ as before; and $K = .5$, $s = .625$, with $V_A = V_B = .4$ as before, but with $U\beta = .15$ instead of $.10$ (the value that yielded the best fit for this function to the old data alone) and $D\beta = .25$ instead of $.20$. The other two functions did not yield quite such good fits to the old data alone: $K = .75$, $s = .833$, with $V_A = V_B = .4$ and $U\beta = D\beta = .20$; and $K = .5$, $s = .5$, with $V_A = V_B = .4$ and $U\beta = D\beta = .25$.

Since the variance of a proportion decreases with distance from $.5$, it may be argued that RMS computations based on raw values give insufficient weight to small deviations at the extremes of the scale. To remedy this difficulty, we repeated the computations after arcsin transformation of the obtained and the simulated values. Each proportion, P , was replaced by an angle, θ , measured in degrees, according to the equation

$$\theta = (180/\pi) \sin^{-1} P \cdot s.$$

Figure 7. Minimal RMS deviations of simulated data from the combined data of these and previous experiments (Couvillon & Bitterman, 1985) for choice functions varying in the value of the exponent, K , and in steepness, s . Untransformed proportions were used in the calculations.

Figure 8. Minimal RMS deviations (in degrees) of simulated data from the combined data of these and previous experiments (Couvillon & Bitterman, 1985) for choice functions varying in the value of the exponent, K , and in steepness, s . The calculations were made after arcsin transformation of the proportions.

The results are plotted in Figure 8 for comparison with the results based on untransformed proportions, which are plotted in Figure 7. The two sets of curves are not very different; the discrimination is perhaps a bit sharper in Figure 8. Of the five best functions previously selected, which are plotted in Figure 1, all but the linear $K = 1$, $s = .833$ continue to perform well, with best fits for the same initial $V_A = V_B$ values and the same learning-rate parameters as before the transformation in each case. The relative standing of $K = .75$, $s = .833$ has improved considerably, as has that of $K = .5$, $s = .625$, and it may not be accidental that both lie at the upper boundary of the envelope of best-fitting functions plotted in Figure 1, although it is difficult to know how much significance can be assigned to the differences. We note for the record that the arcsin RMS deviation from the obtained data for the second complete simulation with $K = .75$, $s = .625$, $V_A = V_B = .3$, and $U\beta = D\beta = .25$ was 10.3° as compared with 10.4° for the first, and that the arcsin RMS deviation of the two simulations from each other was 5.8° .

Although the new results provide no more precise definition of the choice function than do the old, they are in accord with the earlier results in limiting the possibilities to much the same fairly narrow range. Since substantially greater precision cannot be hoped for without data from impractically large groups of animals, and since the range of possibilities already seems narrow enough for the purpose, it may be reasonable now to look toward further development of the associative features of the model. As explained at the outset of this project (Couvillon & Bitterman, 1985), our primary interest is in the associative learning of honeybees, which by the nature of the animal can best be studied in choice situations, and we are interested in choice only secondarily, as an expression of that learning. Our strategy was first to look for the rule

of choice in simple experiments requiring only the most primitive assumptions about the effects of experience on the attractiveness of the alternatives, and then to complicate those assumptions, as almost certainly will be necessary to deal with a wide range of challenging phenomena, familiar from work with vertebrates, that are found in honeybees (Couvillon & Bitterman, 1980, 1982, 1984; Couvillon, Klosterhalfen, & Bitterman, 1983; Klosterhalfen, Fischer, & Bitterman, 1978; Sigurdson, 1981). The underlying and perfectly testable assumption is that the choice rule approximated in the simple experiments will continue to apply.

REFERENCES

- BOYER, W. N., & POLIDORA, V. J. (1972). An analysis of the solution of PAN ambiguous-cue problems by rhesus monkeys. *Learning & Motivation*, 3, 325-333.
- BUSH, R. R., & MOSTELLER, F. (1951). A mathematical model for simple learning. *Psychological Review*, 58, 313-323.
- COUVILLON, P. A., & BITTERMAN, M. E. (1980). Some phenomena of associative learning in honeybees. *Journal of Comparative & Physiological Psychology*, 94, 878-885.
- COUVILLON, P. A., & BITTERMAN, M. E. (1982). Compound conditioning in honeybees. *Journal of Comparative & Physiological Psychology*, 96, 192-199.
- COUVILLON, P. A., & BITTERMAN, M. E. (1984). The overlearning-extinction effect and successive negative contrast in honeybees (*Apis mellifera*). *Journal of Comparative Psychology*, 98, 100-109.
- COUVILLON, P. A., & BITTERMAN, M. E. (1985). Analysis of choice in honeybees. *Animal Learning & Behavior*, 13, 246-252.
- COUVILLON, P. A., KLOSTERHALFEN, S., & BITTERMAN, M. E. (1983). Analysis of overshadowing in honeybees. *Journal of Comparative Psychology*, 97, 154-166.
- HALL, G. (1980). An investigation of ambiguous-cue learning in pigeons. *Animal Learning & Behavior*, 8, 282-286.
- KLOSTERHALFEN, S., FISCHER, W., & BITTERMAN, M. E. (1978). Modification of attention in honeybees. *Science*, 201, 1241-1243.
- LEARY, R. W. (1958). The learning of ambiguous cue problems by monkeys. *American Journal of Psychology*, 71, 718-724.
- MEINEKE, H. (1978). Umlernen einer Honigbiene zwischen Gelb- und Blau-Belohnung im Dauerversuch. *Journal of Insect Physiology*, 24, 155-163.
- MENZEL, R. (1969). Das Gedächtnis der Honigbiene für Spektralfarben: II. Umlernen und Merfächlernen. *Zeitschrift für vergleichende Physiologie*, 63, 290-309.
- RESCORLA, R. A., & WAGNER, A. R. (1972). A theory of classical conditioning: Variations in the effectiveness of reinforcement and non-reinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning: II. Current research and theory* (pp. 64-99). New York: Appleton-Century-Crofts.
- SCHNETTER, B. (1979). *Vergleichende Untersuchung zum Lernverhalten der Bienen und Hummeln unter besonderer Berücksichtigung ihrer Blütenstetigkeit*. Habilitationsschrift, Freiburg, BRD.
- SIGURDSON, J. E. (1981). Automated discrete-trials techniques of appetitive conditioning in honey bees. *Behavior Research Methods & Instrumentation*, 13, 1-10.
- THOMPSON, R. (1954). Approach versus avoidance in an ambiguous-cue problem in chimpanzees. *Journal of Comparative & Physiological Psychology*, 47, 133-135.

(Manuscript received January 21, 1986;
revision accepted for publication May 30, 1986.)