

This behavioral change to a light stimulus in *Hermisenda* was retained for several days following training, gradually returning to baseline levels after several days of testing for behavioral retention. The subsequent reacquisition suggests that acquisition was more rapid following original training. The significant differences between the paired group and controls at the end of acquisition and retention demonstrates that the behavioral change was dependent on the temporal association of light and rotation. Therefore, this change in behavior exhibited some of the defining characteristics of associative learning (17). An examination within well-defined neural networks of the cellular mechanisms underlying this associative behavioral change in *Hermisenda* may provide a basis for studying operationally similar processes in more complex neural systems.

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7. *Hermisenda* were provided by M. Morris of the Sea Life Supply Co., Sand City, Calif.
8. The intensity of the training and testing lights (7.2×10^3 ergs $\text{cm}^{-2} \text{sec}^{-1}$ and 5.2×10^3 ergs $\text{cm}^{-2} \text{sec}^{-1}$, respectively) was measured with a radiometer (Yellow Springs 65A).
9. The subjects received a rotational stimulus during the acquisition phase equivalent to 2.24g at 93.6 revolutions per minute. The near maximum velocity of the turntable followed the onset of the light stimulus with a 250 msec delay, reaching maximum velocity in 5 seconds.
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11. The light and rotation were independently programmed to occur an equal number of times on a random schedule over the same time periods as the training session for the experimental group.

The unpaired control group received stimuli programmed on a random schedule of interstimulus intervals with the restrictions that the stimuli could not overlap in time and could not occur more than once without being followed by the second stimulus.

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13. Z. Annau and L. J. Kamin, *J. Comp. Physiol. Psychol.* **54**, 428 (1961). Cutoff scores of 180 minutes were used for all groups during the acquisition and reacquisition tests, and scores of 90 minutes for all groups during the retention tests. During initial baseline measurements, fewer than 10 percent of the animals did not respond to the test light within 90 minutes. These animals were not used in the study.
14. M. Hollander and D. A. Wolfe, *Nonparametric Statistical Methods* (Wiley, New York, 1973), p. 125. Mann-Whitney U tests were used for independent two-group comparisons of reacquisition data and Wilcoxon matched-pairs signed-ranks tests for related two-group comparisons.

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16. The saving method typically compares original performance with relearning performance by retraining subjects to the original criterion. Comparing reacquisition of the experimental group with acquisition of groups which had originally received control procedures may have overestimated group differences because of inhibition resulting from preacquisition experience with the stimuli.
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Modification of Attention in Honey Bees

Abstract. *Honey bees were trained in two consecutive two-dimensional (color-position) problems with one dimension (color or position) relevant and the other irrelevant in each problem. As in analogous experiments on dimensional transfer in rats and monkeys, performance in the second problem was more accurate when the relevant and irrelevant dimensions were the same as in the first problem than when they were interchanged. The results of further experiments suggest that the transfer is mediated by different modes of responding that develop in color and position problems rather than by some special process of dimensional selection, such as has been assumed to operate in vertebrates.*

Transfer experiments with rats and monkeys (1) suggest that discriminative training may alter attention not only to the stimuli encountered in training but also to novel stimuli varying in the same dimensions (2). The procedure is to train animals in consecutive two-dimensional problems with one relevant and one irrelevant dimension in each problem and with a different set of stimuli in each. For one group of subjects (the intradimensional group), the relevant and irrelevant dimensions remain the same from one problem to the next; for another (extradimensional) group, the relevant and irrelevant dimensions are interchanged. If attention to the relevant dimension tends to be increased by differentially reinforced experience with stimuli varying in that dimension and attention to the irrelevant dimension tends to be reduced by nondifferential reinforcement, intradimensional performance should be more accurate than extradimensional performance. Although such results have been obtained in experiments with rats and monkeys, the results for pigeons are inconclusive (3, 4) and those for carp and goldfish entirely negative (4, 5). It is particularly interesting, therefore, to find results like those for rats and monkeys in honey bees.

One of the dimensions used in our experiment was color. On each trial, two square targets of plastic, each 4.5 cm on a side, were presented, one yellow and the other orange or one green and the

other blue. These pairs of colors provided equal discriminability and negligible generalization from pair to pair. The targets were laid on a square white background, 40 cm on a side, which was fixed to the top of a rectangular table in a small laboratory room just before a door opening to the outside.

The second dimension used was position. On each trial, the two targets were arranged either latitudinally (one to the right and one to the left of the entrance) or longitudinally (one to the front and one to the rear), 15 cm apart edge to edge. The spatial dimension was chosen on the basis of earlier research (6) and after pilot experiments had shown that the animals could readily learn to go to position (right rather than left or front rather than rear) independently of color in both spatial arrangements.

The 32 subjects were trained in each of two consecutive 20-trial problems, the first with one of the two pairs of colors in one of the two spatial arrangements and the second with the alternative pair of colors in the alternative spatial arrangement. Within each problem, each color appeared equally often in each of the two positions. For example, in the longitudinal yellow-orange problems, yellow was half the time at front and half the time at rear in quasi-random order (7). Half the subjects were trained first with yellow and orange targets and half with green and blue targets; half were trained first with the latitudinal arrangement of the

targets and half with the longitudinal arrangement; half were trained first with color relevant and half with position relevant. There were four main experimental groups—two intradimensional and two extradimensional—of eight subjects each. For one of the intradimensional groups color was relevant in both problems (C-C), and for the other, position was relevant in both (P-P). For one of the extradimensional groups, color was relevant in the first problem and position in the second (C-P); for the other, position was relevant in the first problem and color in the second (P-C). Rewarded colors and positions were balanced over groups in a Latin-square design.

The bees were trained individually to fly from the hive and drink their fill from a large drop of 35 percent sucrose solution on a multicolored pretraining target (equal parts of yellow, orange, green, and blue surrounding a central black area) placed in the middle of the white ground. The method was a conventional one. A young bee was picked up in a small matchbox from a feeding platform several meters away from the laboratory at which a 10 percent sucrose solution was available, carried into the laboratory, and set down at the drop of 35 percent sucrose solution on the preliminary training target. As the animal drank, it was marked with a spot of colored lac-

quer, after which it was free to return to the hive. After the animal had made five visits to the preliminary training target, discriminative training began. On each choice trial, the positive target contained a drop of 35 percent sucrose solution and the negative target a drop of fresh water. The first contact (if any) with the negative target during a trial was counted as an "initial" error, and any further contacts with the negative target during the same trial were counted as "repetitive" errors. The trial ended when the animal settled on the positive target, drank to repletion, and returned to the hive. In the 4 to 6 minutes between the animal's successive visits to the laboratory, both targets were washed, set down again in the appropriate arrangement, and rebaited. Between trials 20 and 21, the stimuli used in the first problem were replaced with those used in the second. Occasional intruders were captured and killed.

In Fig. 1, the performance of the four groups is plotted in terms of mean initial errors per block of five trials in each of the two problems. As the learning curves for the first problem suggest, the color and position tasks were equally difficult ($F < 1$), and the intradimensional and extradimensional groups were well matched ($F < 1$). As the learning curves for the second problem suggest, performance was more accurate in the intradimensional groups than in the extradimensional groups [$F(1, 28) = 40.50$, $P = .0001$]. The color tasks were not significantly easier here than the position tasks [$F(1, 28) = 2.03$, $P = .16$], and the influence of dimension on the magnitude of the intradimensional-extradimensional difference was negligible (F for the interaction < 1). Comparison of the first and second problems shows a statistically unreliable improvement in the performance of the intradimensional groups ($F < 1$), perhaps because learning was already so rapid in the first problem as to leave little room for improvement. There was, however, a substantial decrement from the first to the second problem in the performance of the extradimensional groups [$F(1, 14) = 25.00$, $P = .0002$]. Analysis of repetitive errors yields no new information; curves based on total (initial plus repetitive) errors show the same pattern as the curves based on initial errors alone. This experiment provides clear evidence, then, of better intradimensional than extradimensional transfer in honey bees.

Although bees trained to discriminate color continue to exhibit considerable apparently indecisive hovering over the targets even after the probability of an

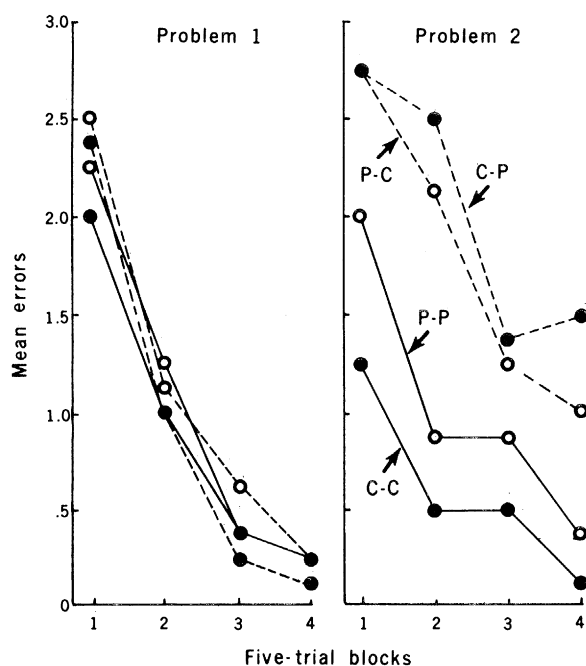


Fig. 1. The performance of two intradimensional groups (C-C, color-to-color; P-P, position-to-position) and two extradimensional groups (C-P, color-to-position; P-C, position-to-color) in each of the two consecutive two-dimensional (color and position) problems.

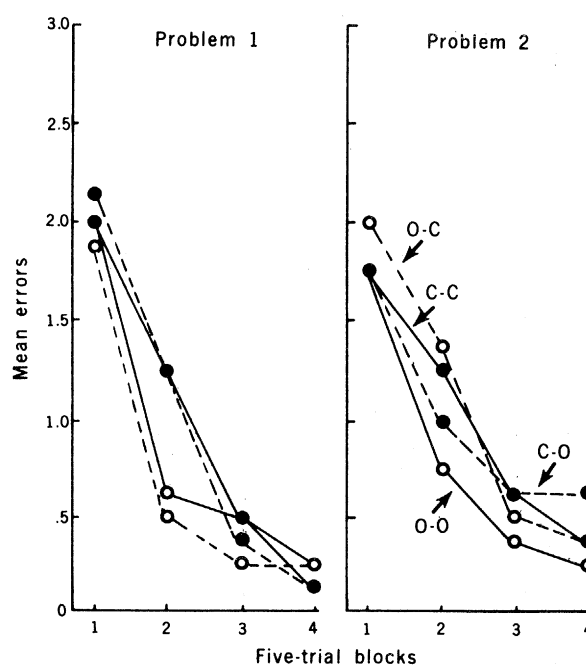


Fig. 2. The performance of two intradimensional groups (C-C, color-to-color; O-O, odor-to-odor) and two extradimensional groups (C-O, color-to-odor; O-C, odor-to-color) in each of two consecutive two-dimensional (color and odor) problems.

incorrect choice has fallen almost to zero, bees trained to discriminate position tend at asymptote to approach the correct target directly. The results of a second experiment suggest that performance in the second problem is related to the mode of responding adopted in the first. The 20 subjects were trained in two consecutive problems, the first with one or the other of the two pairs of colored targets presented in the latitudinal arrangement for 25 trials. Color was relevant and position irrelevant for ten of the animals in this first problem, each color appearing equally often in each position. For the remaining animals, color and position were confounded, which is to say that the positive color appeared in only one of the two possible positions (for example, yellow at left reinforced, orange at right unreinforced). The two tasks proved to be equal in difficulty ($F < 1$), and both learning curves looked much like those for problem 1 of experiment 1 (Fig. 1). There was a difference, however, in the mode of responding; whereas the animals in the color group showed the familiar color mode, those in the confounded condition showed the position mode even more clearly (it was our impression) than did the position animals of experiment 1. In the second problem, there were 15 trials with the alternative pair of colored targets in the longitudinal arrangement, color relevant and position irrelevant for both groups. Here the former color animals performed well (much like the intradimensional animals in Fig. 1), but the former confounded animals performed poorly (much like the extradimensional animals of experiment 1); the difference between the groups was highly reliable [$F(1, 18) = 34.31$, $P = .00001$]. If the mode of flight developed in the confounded task is taken as evidence of a set to respond in terms of position, these results suggest again that a dimensional bias established in training with one set of stimuli may affect the performance of bees in a subsequent problem with a new set of stimuli.

While the conclusion of one recent reviewer (8) that the phenomena of learning in honey bees are not qualitatively different from those in rats seems premature, we have come here upon another striking similarity in the performance of the two species. Just how far the similarity goes, however, is open to question. The mode of responding developed by the bees in position and in confounded tasks may in fact reflect the operation of some central process of dimensional selection analogous to that suggested by the data for rats and monkeys; but it is possible also that the ori-

enting response is itself the vehicle of selection, mediating interproblem transfer as the postural orientation of rats has been found to do in certain position-relevant tasks (9). The orientation hypothesis is supported by the results of a third experiment identical in procedure and design to experiment 1 except that odor was substituted for position. On each trial, two 4-cm colored squares (yellow and orange, or green and blue) were presented in the latitudinal arrangement, not directly on the white background, but on glass cylinders 4 cm high and 4.5 cm in inside diameter, leaving narrow openings at the edges of the squares. Inside the cylinders were balls of cotton impregnated with scented oils (lemon and orange, or jasmine and violet). The pairs of odors, like the pairs of colors, provided equal discriminability and negligible generalization from pair to pair. Color and odor were varied independently. For example, the first problem for a given animal might consist of trials with green-jasmine versus blue-violet and green-violet versus blue-jasmine, each pair presented equally often with, say, green rewarded independently of odor where color was relevant, or jasmine rewarded independently of color where odor was relevant. The various stimuli were balanced over problems as in experiment 1. The two color-odor compounds in each pair were presented equally often in each spatial arrangement, position being irrelevant throughout.

The performance of the four groups (C-C, O-O, C-O, and O-C) was plotted in terms of mean initial errors per block of five trials in each of the two consecutive problems (Fig. 2). Analysis of variance confirms the suggestion in the curves for the first problem that the groups trained with odor relevant learned somewhat more rapidly than those trained with color relevant; while the overall difference in error is not significant [$F(1, 28) = 2.40$, $P = .13$], the interaction with blocks of trials is significant [$F(3, 84) = 3.51$, $P = .0187$]. The analysis proves also that the intradimensional and extradimensional groups were well matched ($F < 1$). In the data for the second problem, group variances (color versus odor and intradimensional versus extradimensional) are negligible ($F < 1$), and so also are all the interactions ($F < 1$). These null results support the conclusion that the pattern of interproblem transfer found in experiment 1 was mediated by overt modes of orientation, strikingly different in color and position problems but very much the same in color and odor problems. We should predict that a repetition of the first exper-

iment with odor substituted for color (rather than for position) again would show better intradimensional than extradimensional transfer.

It is interesting in this connection that the results of experiments on discriminative learning in octopus, the only other invertebrate studied in any detail, closely resemble those for rats; the opinion has been offered that a common attentional model will fit the data for both animals (10). Convergence to the point of identity or even of seriously confusing similarity is unlikely, however, in "elaborately polygenic" behavioral systems (11). We expect, therefore, that further work with octopuses, like our work with bees, will point to important functional differences between vertebrate and invertebrate learning (12). Quite apart from questions about evolution, of course, our work is significant for the information it provides about learning in bees. Many other diagnostic experiments devised for the study of vertebrates promise to be useful in the analysis of learning in this small-brained animal.

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