Intramodal competition for attention in honeybees

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Honeybees were trained to discriminate between targets varying in color and length, one dimension relevant and the other irrelevant. Performance in acquisition was better when the pairs of targets presented on each trial differed only in the relevant dimension than when they differed in both, suggesting that difference in the irrelevant dimension promoted attention to the irrelevant stimuli at the expense of attention to the relevant stimuli. Subsequent performance in an unreinforced choice test was also better when the targets differed only in the relevant dimension rather than in both dimensions. The results are considered in relation to those of previous experiments with honeybees that point to attentional effects in the conditioning of intramodal but not of intermodal compounds.

The results of a wide variety of experiments on the conditioning of color–odor compounds in honeybees (Couvillon & Bitterman, 1987, 1988, 1989, 1991) give no reason to question the parsimonious independence assumption of traditional continuity theory (Hull, 1929; Spence, 1936), which is that the components of a compound stimulus gain and lose associative strength independently with reinforcement and nonreinforcement of the compound. In the vertebrate literature, the independence assumption has long been rejected in favor of the assumption that the components of a compound stimulus compete for associative strength (Rescorla & Wagner, 1972) or for attention (Mackintosh, 1975; Sutherland & Mackintosh, 1971), and the color–odor results for honeybees are especially interesting because they are almost alone in pointing to a difference in the learning of honeybees and vertebrates (Bitterman, 1988, 1996; Bitterman & Couvillon, 1991). It appears, however, from the results of more recent experiments with other compounds that the difference is less far-reaching than the color–odor results may suggest.

In one set of experiments, learning about the color of a target, but not its odor, was found to be impaired by the presence of a small white dot used to mark the location of reward on the target—that is, there was overshadowing by the dot in dot–color but not dot–odor compounds (Couvillon, Mateo, & Bitterman, 1996). In a second set of experiments, blocking was found in compounds of two colors and of two odors as well as in color–position compounds (Couvillon, Arakaki, & Bitterman, 1997; Smith & Cobey, 1994), but not in color–odor or in odor–position compounds (Couvillon et al., 1997; Funayama, Couvillon, & Bitterman, 1995). If position is given visually (Huber, Couvillon, & Bitterman, 1994), a reasonable in-

ference from these results is that the independence assumption may hold for intermodal compounds but not for intramodal compounds.

The new results also prompt reconsideration of an earlier experiment with honeybees in which better intradimensional than extradimensional transfer—a vertebrate phenomenon understandable in terms of competition for attention (Shepp & Eimas, 1964; Shepp & Schrier, 1969)—was found for color–position compounds but not for color–odor compounds (Klosterhalfen, Fischer, & Bitterman, 1978). Foragers trained first to choose between two color–position compounds with one dimension relevant and the other irrelevant, and then in a second such problem with new colors and positions, performed better in the second problem when the relevant dimension was the same as in the first problem than when it was not. After training in a color–odor problem, performance in a second problem with new colors and odors was the same whether or not the relevant dimension was the same in the two problems. Odor and position might be thought to function differently in compound with color because odor and color are integral properties of a target whereas position is not. Noting the development of a distinctive manner of choice in position-relevant training (the animals tended to approach the positive alternative directly instead of hovering for a time over both alternatives, as in color-relevant and odor-relevant training), Klosterhalfen et al. guessed, in fact, that the color–position transfer might have been mediated by overt orientation rather than by some central process of dimensional selection. Now, however, an interpretation in terms of intramodal competition for attention seems at least as plausible, and our purpose in the somewhat simpler experiment reported here was to look for independent evidence of attentional competition with integral intramodal compounds.

With A and B representing two points on one dimension, and X and Y representing two points on a second dimension, suppose that one group of animals is trained with the compound AX+ paired with BX–, and AY+ paired with BY–; that is, the two members of each pair differ only

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in the relevant dimension. A second group is trained with AX+ paired with BY−, and AY+ paired with BX−, the two members of each pair differing in both dimensions. Poorer performance in the second group than in the first can be taken to mean that within-pairs difference in the irrelevant dimension increases attention to the irrelevant stimuli at the expense of attention to the relevant stimuli. Just such results were reported by Wortz and Bitterman (1953), who trained rats in the Lashley jumping apparatus to choose between equilateral triangles that were either black or white, upright or inverted. In an intermodal experiment of the same design with targets varying in color and odor, Couvillon and Bitterman (1987) found no such effect in honeybees; performance was the same whether the two targets of each training pair differed in both dimensions or whether they differed only in the relevant dimension. The question asked here is whether within-pairs variation in the irrelevant dimension will impair the performance of honeybees trained with targets varying in color and length—trained, that is, with integral compounds that are intramodal.

METHOD

Subjects

The subjects were 64 foraging honeybees (*Apis mellifera*), all experimentally naive, from our own hives situated near the laboratory. They were assigned in balanced order to four experimental groups—C1, L1, C2, and L2—each of which had 16 subjects. Studied individually, each in a single session lasting several hours, the subjects were recruited at a feeding station near the laboratory that provided 10%–12% sucrose solution. A forager newly arrived at the feeding station was picked up in a match box, carried in it to the sill of a laboratory window, and placed at a large drop of 50% sucrose solution on a pretraining target. There the animal was marked with a drop of colored lacquer as it fed to repletion, after which it left for the hive to deposit the sucrose. Typically, the ani-

mal would return to the laboratory after a few minutes, continuing to fly back and forth between the hive and the window as long as sucrose was available there. If the marked animal did not return after its first placement, it would be picked up again at the feeding station (where it could usually be found), placed again on the pretraining target, and permitted to feed to repletion. More than two placements were rarely required. The discriminative training began with the second return of the subject of its own accord to the laboratory window.

Apparatus and Training Procedure

The training situation is diagrammed in the left panel of Figure 1. It was a resined plywood enclosure—56 cm wide, 58 cm high, and 46 cm deep—set on the sill of a laboratory window. The enclosure was open to the outside, and it was fitted with a pair of sliding Plexiglas doors through which the experimenter had access to the enclosure from the inside. The training targets were wooden blocks, half of them painted blue and the rest white. The width of each block was 4 cm, and so also was the height, but half the blocks of each color were 14.5 cm in length and the rest were 5.5 cm in length. On each of 20 training trials (1 trial per visit), the subject was offered a choice of two targets positioned 10 cm apart, as in the diagram, which shows a pair of targets differing both in color and length. The correct target contained a 100- μ l drop of 50% sucrose solution, and the incorrect target contained a drop of tap water (unacceptable to the animals and distinguishable from the sucrose only by taste); the drops were situated at the ends of the targets nearer to the outside. The target on which the subject landed first was recorded, and if that target was the incorrect one, the subject was permitted at once to correct its choice. After landing on the correct target, the animal would feed to repletion and leave for the hive, returning to the training situation a few minutes later for the next trial. The targets used on each trial were drawn from a pool of targets, washed at the end of the trial, and then replaced in the pool, a procedure that served to randomize extraneous stimuli.

Each subject in each of four groups was trained with targets of both colors and both lengths, but the targets were paired differently for the different groups. The pairings are shown in the right panel of Figure 1. For two groups of subjects (C1 and L1), the members of each pair differed only in one dimension, the relevant dimension, which was color for Group C1 and length for Group L1; the irrelevant dimension had the same value for both members of any given pair. For two other groups (C2 and L2), again with color relevant for one (C2) and length relevant

Figure 1. Left panel: diagram (approximately to scale) of the training situation. The width of the enclosure is 56 cm. Right panel: pairings of the targets used in the training of the four groups. For Group C1 (color relevant), the two members of each pair differed from each other only in color; for Group L1 (length relevant), the difference was only in length; for Groups C2 (color relevant) and L2 (length relevant), the members of each pair differed both in color and in length. Position was irrelevant for all groups, each target appearing equally often in each position.

for the other (L2), the targets of each pair differed in two dimensions, the irrelevant as well as the relevant dimension. Each pair of targets was presented equally often in each of two lateral arrangements, and each of the four pairings shown for each group was used on 5 of the 20 trials in balanced, quasi-random order. For half the animals in Groups C1 and C2, blue was reinforced, and white was reinforced for the rest; for half the animals in Groups L1 and L2, the longer target was reinforced, and the shorter target was reinforced for the rest.

On the visit following the 20th training trial, there was, for each subject, a 10-min extinction test with a single pair of targets, both targets now containing a drop of tap water. Using hand-held switches, the experimenter recorded all contacts of the animal with each of the targets, and printing counters were programmed to register stored frequencies of contact at 30-sec intervals. Half the subjects in Groups C1 and C2 were tested with pairings of the targets that had been used in the C1 training—targets differing only in the relevant color dimension; 2 subjects of each group had each of the four pairings (see Figure 1). The rest were tested with pairings of the targets that had been used in the C2 training—targets differing in both dimensions; 2 subjects of each group had each of the four pairings. In the same way, half the L1 subjects and half the L2 subjects were tested with pairings that had been used in the L1 training—targets differing only in length—and the rest with pairings that had been used in the L2 training—targets differing in both dimensions. The purpose of the test was to assess learning about color and length under the two training conditions with factorial control for the similarity of training and testing conditions.

RESULTS

In Figure 2, acquisition in the four groups is plotted in terms of mean errors in five successive blocks of four training trials. The curves show that more errors were made by the length-relevant groups (L1 and L2) than were made by the color-relevant groups (C1 and C2). The curves show also that more errors were made by the groups trained with pairs of targets differing in both dimensions (C2 and L2) than were made by the groups trained with pairs differing only in the relevant dimension (C1 and L1). A 2×2 analysis of variance (ANOVA) yielded a significant dimension (color vs. length) effect [$F(1,60) = 22.05, p < .0001$] and a significant effect of training con-

Figure 2. The course of acquisition in the four groups plotted in terms of mean errors per block of four training trials.

dition (mode of pairing) [$F(1,60) = 7.58, p = .0078$], with no significant training condition $\times$ dimension interaction ($F < 1$). It also yielded a significant block effect [$F(4, 240) = 7.38, p < .0001$], with no significant training condition $\times$ block or dimension $\times$ block interaction ($F < 1$). Although there was some preference for blue over white in the color groups, the difference was not statistically significant [$F(1,30) = 2.73, p = .11$], and neither of the lengths was preferred to the other ($F < 1$).

In the left panel of Figure 3, the test performance of all animals trained with pairs of targets differing only in the relevant dimension (Groups C1 and L1 combined) is compared with the performance of all animals trained with pairs of targets differing in both dimensions (Groups C2 and L2 combined). Plotted in terms of the mean cumulative number of responses to the previously positive (S+) and negative (S-) alternatives over successive 30-sec intervals of the 10-min testing period, these curves show a clear preference for S+ over S-, but no effect of the way in which the targets were paired in training. An overall ANOVA based on (uncumulated) frequencies of response in four 2.5-min blocks yielded a significant stimulus (S+ vs. S-) effect [$F(1,56) = 120.05, p < .0001$], as well as a significant block effect [$F(3,168) = 153.05, p < .0001$], and a significant stimulus $\times$ block interaction [$F(3,168) = 56.60, p < .0001$], with negligible interactions of stimulus $\times$ training condition and of stimulus $\times$ training condition $\times$ block ($F < 1$). The results were the same for both dimensions (color and length). The interactions of stimulus $\times$ dimension, stimulus $\times$ dimension $\times$ block, stimulus $\times$ dimension $\times$ by training condition, and stimulus $\times$ dimension $\times$ training condition $\times$ block were all insignificant ($F < 1$).

Although performance in the extinction test was not affected by the way in which the stimuli were paired in training, it was affected to some extent by the way in which they were paired in the test. The right panel of Figure 3 compares the performance of all animals (whatever their training) that were tested with targets differing only in the relevant dimension (C1 and L1 pairings) and the performance of all animals that were tested with targets differing in both dimensions (C2 and L2 pairings). The clear preference for S+ is evident again in the curves, and here we find also an indication of better discrimination in testing with C1 and L1 pairings than in testing with C2 and L2 pairings that is confirmed by a significant stimulus $\times$ testing condition $\times$ block interaction [$F(3,168) = 2.84, p = .0396$]. The pattern was the same for the color-relevant and the length-relevant groups; the interaction of stimulus $\times$ testing condition $\times$ dimension was non-significant ($F < 1$), as was the interaction of stimulus $\times$ testing condition $\times$ dimension $\times$ block [$F(3,168) = 1.42, p = .2399$]. The interactions of stimulus $\times$ training condition $\times$ testing condition and of stimulus $\times$ training condition $\times$ testing condition $\times$ block were also nonsignificant; that is, it did not matter whether or not the test pairings had previously been encountered in training.

Figure 3. Left panel: extinction performance of Groups C1 and L1 (combined) compared with that of Groups C2 and L2 (combined) under identical testing conditions. Right panel: extinction performance of animals tested with targets differing only in the relevant training dimension (C1 and L1 pairings) compared with that of animals tested with targets differing in both dimensions (C2 and L2 pairings). S+, reinforced in training; S-, nonreinforced in training. The curves are plotted in terms of the mean cumulative number of responses to the previously positive (S+) and negative (S-) stimuli over successive 30-sec intervals of the 10-min testing period.

DISCUSSION

In acquisition, the performance of Groups C1 and L1 (trained with pairs of targets differing only on the relevant dimension) was substantially better than that of Groups C2 and L2 (trained with pairs of targets differing in both dimensions), an outcome readily understandable on the assumption that within-pairs difference in the irrelevant dimension promoted attention to the irrelevant stimuli at the expense of attention to the relevant stimuli. In extinction, with mode of pairing equated in a factorial design, there was no corresponding superiority of the C1 and L1 groups, which may suggest that what we are seeing in the acquisition data is an effect of attention on performance alone. It is possible that the extinction measure was simply not as sensitive as the choice measure used in training to differences in associative strength at the conclusion of the training, which might be argued on the ground that the colors were better discriminated than the lengths in the training but not in the test. It also is possible, however, that the better color performance in acquisition itself reflected, not a greater difference in associative strength, but a greater readiness to attend to color than to length.

What certainly must be regarded as an effect of attention on performance as distinct from learning is the somewhat better discrimination in the extinction tests with C1 and L1 pairs than in the tests with C2 and L2 pairs by animals trained with either; even so modest a pairing effect is impressive because performance in the test is not a series of discrete choices between the targets but consists in large part of alternating runs of response to each of the two targets. It is interesting in this connection to note the lack of agreement in the vertebrate literature as to whether overshadowing and blocking, which have also been attributed to competition for attention, are learning or performance effects (e.g., Miller, Barnett, & Grahame, 1995).

In any case, the acquisition results, together with the negative results obtained by Couvillon and Bitterman (1987) in analogous training with color-odor instead of color-length compounds, fit the sharp pattern established in the overshadowing and blocking experiments with honeybees: independence in intermodal but not in intramodal compounds. A reasonable explanation is that afferent interaction is more pronounced in intramodal than in intermodal compounds, which has also been suggested in the recent vertebrate literature on summation (Kehoe, Horne, Horne, & Macrae, 1994; Rescorla & Coldwell, 1995). If degree of afferent interaction rather than intramodality in itself is critical, it might be possible to find at least some intramodal compounds that show independence and some intermodal compounds that do not. It might also be instructive with given components to try to alter the degree of their interaction by changing the way in which they are presented, and so alter

the experimental outcomes. An interesting example comes from work with pigeons by Rescorla and Coldwell, who found no summation in a simultaneous compound of two visual components but did find it when the same components were presented successively rather than simultaneously, a change calculated to minimize interaction.

Such efforts should afford some valuable clues to the nature of attention in honeybees, which is now only vaguely conceived, although perhaps not much more so than in rats, pigeons, and monkeys. What continues to be impressive is how difficult it is—despite vast differences in brain structure and the remoteness of the evolutionary relationship—to find any indication that learning is fundamentally different in honeybees as compared with our favorite vertebrate subjects.

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