Israel Journal of Plant Sciences *Vol. 57* *2009* *pp. xx–xx*
DOI: 10.1560/IJPS.57.3.xx

Learning of colored targets with vertical and horizontal components by bumblebees *(Bombus terrestris* L.)

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(Received xxx; accepted in revised form 25 January 2009)

ABSTRACT

Colorful tufts of bracts, which attract insect pollinators, terminate the vertical inflorescences of several plant species. These flag-like bracts contrast in color with the leaves below them, and are oriented perpendicular to the flowers on the inflorescence. We studied how color contrast and perpendicular orientation affect the feeding choices of bumblebees in laboratory experiments. We trained bees to feeders with perpendicular two-color displays, and subsequently recorded their choices among feeders that displayed only one of these cues. The bees preferred perpendicular displays that resembled the training model in the color of the horizontal component. We then evaluated the effects of the horizontal vs. vertical display component on foraging choices. After training bees to two-color, perpendicular displays, we allowed them to choose between displays with either the same horizontal or the same vertical component as the training model. Foragers mostly oriented to the horizontal displays to which they had been trained. We conclude that (a) bumblebees learn perpendicular, two-color displays; (b) horizontal display components influence foraging choices more than vertical components; (c) vertical visual cues might guide the approach to a feeder, serving as landlmarks. We discuss possible implications of our findings for the role of extra-floral bracts in pollination.

Keywords: bee, learning, color contrast, perpendicular orientation, extra-floral display

INTRODUCTION

Extra-floral display structures exist in many insect-pollinated plant species. These displays include secondary structures associated with flowers, such as colorful leaves, sepals, or sterile flowers, which are adjacent to but spatially segregated from flowers on the plant. Such structures, collectively called bracts, often have been proposed to enhance the visual display advertised to potential pollinators (Faegri and Van der Pijl, 1979; Barth, 1985; Gottsberger and Hartmann, 1988; Raven et al., 1999). Some extra-floral displays are specialized in that they form colorful flag-like structures at the top of vertical inflorescences. In the Mediterranean flora, for example, flag-like bracts develop in three species of *Leopoldia*, in *Laminum moschatum* Mill., in *Salvia viridis* L., and in *Lavandula stoechas* L. These displays were shown to enhance visitation of flowers by pollinators in a few cases (Herrera, 1997; Keasar et al., 2006).

Why are pollinators attracted to flag-like bracts? Previous workers have suggested the bracts' large size is of importance. Large displays may function as "detective cues", i.e., make inflorescences more conspicuous for pollinators at a distance. They may also provide "selective cues", i.e., signal abundant floral food rewards

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to foraging insects (Cohen and Shmida, 1993). It was further suggested that one large bract, visible from afar, can advertise many flowers on an inflorescence, and therefore provides a very efficient signal (Faegri and van-der Pijl, 1979; Gottsberger and Hartmann, 1988). However, flag-like bracts share other features in addition to their large size. Although composed of leaves, they are colorful, and contrast in color with the foliage and flower petals. They are also located perpendicularly to the plane of the flowers: the bracts form a vertical display, while the flowers are commonly seen as a horizontal surface when viewed from above. This raises the question whether the color contrast and vertical orientation of flag-like extra-floral bracts also represent visual cues used by pollinators to find floral rewards.

It is well known that pollinators learn a variety of visual cues to locate food sources. Color seems to be the most important visual dimension for flower recognition in bees, a major group of pollinators (von Frisch, 1967; Menzel and Backhaus, 1991; Menzel and Shmida, 1993; Lehrer and Bischof, 1995; Giurfa et al., 1996; Orth and Waddington, 1997). Bees also learn the shape, symmetry, and patterns of the visual display, and these features affect flower recognition and foraging choices (Menzel and Lieke, 1983; Giger and Srinivasan, 1996; Lunau et al., 1996; Lehrer, 1999; Hempel de Ibarra et al., 2001, 2002; Ne'eman and Kevan, 2001; Hempel de Ibarra and Giurfa, 2003; Rodríguez et al., 2004; Stach et al., 2004). Evidence for the attractive role of color contrast arises from the finding that bees prefer displays that contrast strongly with their background over displays with low background contrast (Lunau et al., 1996). In addition, large, high-contrast displays are detected more rapidly than displays that are small and/or low-contrast (Spaethe et al., 2001). In the present study we address the question whether bees can learn complex spatial targets with colored components arranged in the vertical and horizontal plane. We also ask about the relative importance of the perpendicular orientation vs. the color cues of the target components in mediating learning. These questions extend previous research on color and pattern learning by insects, which focused on visual targets arranged in a single (horizontal or vertical) plane. We addressed the following specific questions:

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1. Can bees learn to associate displays with perpendicularly oriented, color-contrasting components with the presence of a food reward?
2. Which of the display cues affects the bees' foraging choices more strongly?
3. How are the horizontal and the vertical components of the display evaluated and used for target recognition?

METHODS

General

The experimental system and laboratory are described in detail in Keasar (2000). Experiments were carried out in a 3 × 4 m flight room. Temperatures ranged from 25 to 30 ºC, and relative humidity from 20 to 54%. The room was illuminated during 08:00–20:00 by six pairs of D-65 fluorescent lights of 100-Hz frequency. Experiments were conducted during November 1999–October 2000.

Colonies of naive *Bombus terrestris* (L.) were obtained from Kibbutz Yad Mordechai, Israel. The queens of the colonies were treated by the suppliers to forego hibernation, so that the colonies were active year-round. Pollen was supplied ad libitem, directly to the colony. The bees were allowed to fly freely inside the room, and to feed ad libitem on 30% w/v sucrose solution between experiments. During the experiments, only one bee, marked by a number tag, was allowed to forage at a time. Computer-controlled feeders, placed on a 1.40 × 2.40 m green table, were used for the experiments. All feeders had a removable colored plastic landing surface that could be replaced during the experiment. A 30% sucrose solution was used in the feeders as nectar substitute. The feeders dispensed either 1 microliter sucrose solution per visit, or no sucrose solution at all, according to experimental design. Feeders that were programmed to dispense sucrose solution were refilled immediately after the bee left them. Non-dispensing feeders contained sucrose solution that was not accessible to the bees, so that they could not be discriminated by their odor. Head insertions of bees into the feeders were automatically recorded. Horizontal and/or vertical rigid plastic visual displays were attached to the feeders. These displays were blue, yellow, or purple in color. Reflectance spectra for the displays are provided (Fig. 1). Bees from four colonies were used, and each bee participated in one experiment only. The feeders and experimental table were wiped with a water-moistened paper towel between experiments, and between experimental phases, to eliminate odor marks. Feeders were randomly arranged on the table.

Pre-Training

Each bee was pre-trained prior to participating in an experiment. During the first stage of the pre-training, the bees were conditioned to fly to the experimental table to feed. Sucrose solution was first placed in a Petri-dish feeder just outside the bee colony. After a bee learned to obtain sucrose solution from this feeder, it was gradually removed away from the colony until it was placed on the experimental table. The bees required

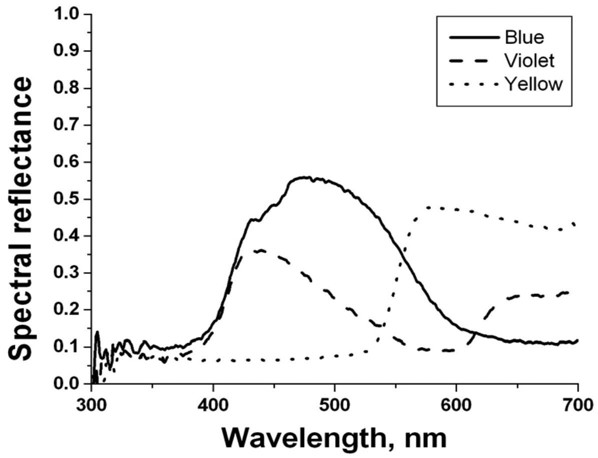

Fig. 1. Reflectance spectra for the color displays attached to feeders in the experiments.

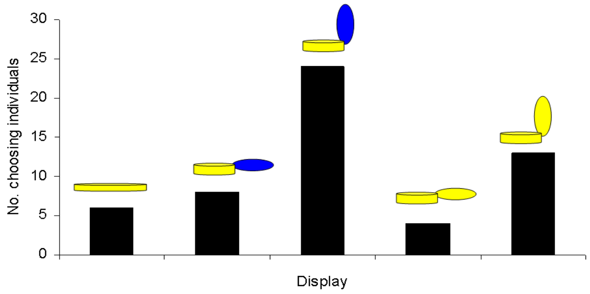

Fig. 2. The distribution of first choices of 55 naive individuals in the preliminary experiment. Each bee was presented with the five displays shown in the figure.

2–4 days for this part of the pre-training. During the next stage, the bee was trained to the morphology of the experimental feeder. The Petri-dish feeder was replaced with one computer-controlled feeder, marked by a black circular horizontal landing surface of 3.7 cm diameter. The feeder was programmed to refill with 1 microliter 30% sucrose solution, immediately after the bee withdrew her head at the end of probing and feeding. The bees usually returned to the feeder after a short flight in the room, and were rewarded again. Pre-training on the computer-controlled feeder lasted until more than 5000 probes to the feeder were recorded per bee within 12 h. This stage typically required 1–3 days.

Preliminary experiment—testing preferences of naive bees

Prior to the main experiments we explored the innate reaction of bees to feeders of complex orientation and/or color contrast. We exposed each of 55 naive bees, originating from a single colony, to 20 sucrose-rewarding feeders with five combinations of orientation/color displays (shown in Fig. 2). Each display type was attached to four feeders at randomly determined locations. We recorded the display of the first feeder probed by each bee.

Experiment 1

The aim of this experiment was to test whether bumblebees can learn to associate perpendicular color-contrasting displays with the presence of a food reward. If yes, we wished to assess the relative importance of perpendicularity vs. color contrast in the learning process. We used a two-step experimental design. In the training phase of the experiment, we exposed each of 17 inexperienced bees, originating from two colonies, to feeders of two types: twenty feeders carried a perpendicular display with color contrast (blue round horizontal and yellow elliptical vertical displays, Fig. 3), and dispensed 1 μl sucrose solution whenever probed. Twenty other feeders carried a blue horizontal round display with no vertical component and no color contrast, and contained no food reward. The round displays were of 5.2 cm diameter. The vertical displays were ellipses with diameters of 4 cm and 2 cm. We used one of four random spatial arrangements of the feeders for each bee. Each bee was allowed to visit the feeders 200 times, and was then caged individually for 45 min while the test phase of the experiment was prepared.

In the test, the bee was exposed to non-rewarding feeders with the following five displays: 1. Horizontal yellow; 2. Horizontal purple; 3. Horizontal purple + vertical purple; 4. Horizontal yellow + vertical yellow; 5. Horizontal, half purple and half yellow (Fig. 4). We did not use blue displays in the test, because they were associated with both rewarding and non-rewarding feeders in the training phase, hence we did not have

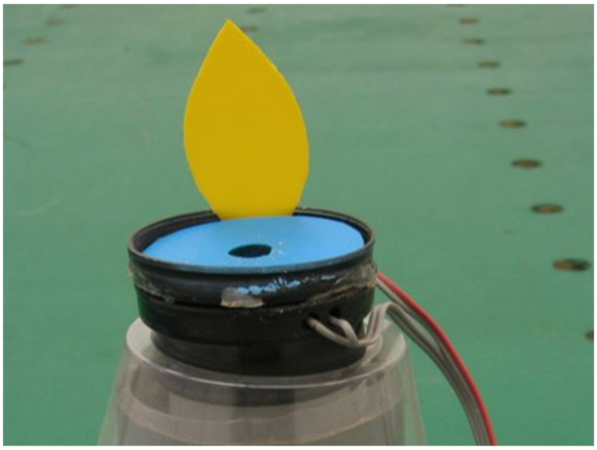

Fig. 3. Example of a color-contrasting, perpendicular display, as used in the training phase of Experiments 1 and 2.

Fig. 4. Design of Experiment 1. In the training phase (top), we allowed each of 17 naive bees 200 foraging visits to feeders of two displays that were either rewarding (+) or non-rewarding (–). In the test phase, we exposed each bee to feeders of five displays and recorded their first choice. Feeders are drawn schematically from a side view.

a clear expectation regarding their effect on forager choices. Each display was attached to eight feeders. Feeder locations for each bee followed one of seven random arrangements. We recorded the bees' choices on their first visit in this phase.

Experiment 2

The aim of this experiment was to test whether bees orient to the horizontal or to the vertical component of a perpendicular display, using a two-choice design. Here, too, we conducted a two-step experiment. In the first training phase of the experiment, we exposed each of twelve experimentally naive foragers to feeders of two types: twenty feeders carried both a blue horizontal and a yellow vertical display, and dispensed 1 μl sucrose solution whenever probed. Twenty other feeders carried a yellow horizontal display with no vertical component and no color contrast, and contained no food reward. The experimental design is depicted in Fig. 5. We used one of four random spatial arrangements of the feeders for each individual. Each bee was allowed to visit the feeders 200 times, and was then caged individually for 15 min while the second phase of the experiment was prepared. In the second training phase, each bee was allowed 200 additional visits to 20 rewarding feeders with a perpendicular display but no color contrast (yellow horizontal and yellow vertical displays), and to 20 non-rewarding feeders with a blue horizontal display with no vertical component or color contrast (Fig. 5). We recorded the forager's sequence of visits in both phases. We randomly rearranged the feeders on the experimental table between experimental phases, to prevent the possibility of location learning. To control for possible color biases, we replicated the experiment with twelve additional foragers that were exposed to the reciprocal color combinations. The shapes and sizes of the horizontal and vertical display components were as in Experiment 1. Bees originated from two colonies in this experiment.

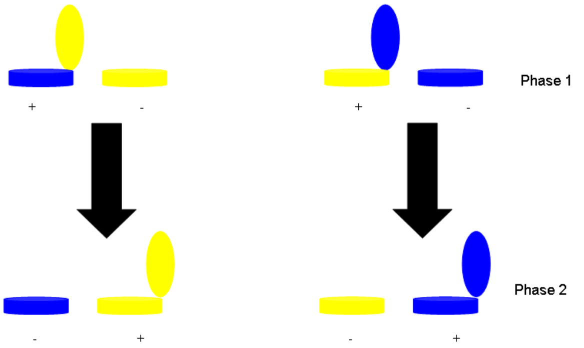

Fig. 5. Design of Experiment 2. In the training phase (top), we allowed each of 24 naive bees 200 foraging visits to feeders of two displays that were either rewarding (+) or non-rewarding (–). Rewarding feeders carried color-contrasting, perpendicular displays, while non-rewarding feeders had horizontal one-color displays. One half of the bees were trained to blue horizontal displays (left figure), and the remaining bees were trained to horizontal yellow displays (right figure). In the test phase, the bees made 200 additional visits to feeders that carried either the same horizontal or vertical display components as rewarding feeders in the training phase. Feeders are drawn schematically from a side view.

RESULTS

Preliminary experiment: Choices by naive bees

Most of the bees chose, in their first visit, a feeder with an ellipse attached vertically (67.3%, chi-square test, $p = 0.01$, Fig. 2). They preferred one of the feeders with a blue vertical ellipse (24 bees out of 55) to those with a yellow vertical ellipse (13 bees out of 55, chi-square test, $p < 0.001$). Fewer bees selected feeders with horizontally attached ellipses (blue or yellow) or the enlarged horizontal disc feeder. The blue ellipses that were presented horizontally or vertically were not strongly attractive to the bees per se, since such feeders were not preferred over the others (chi-square test, $p = 0.22$). However, the blue vertical display was almost twice as attractive as the yellow vertical display, and the blue horizontal display was almost twice as attractive as the yellow horizontal display. We concluded that naive bees were paying attention to the vertical ellipse attached to a feeder, an important condition for studying the learning of such stimuli. Additionally, the bees may have preferred blue displays over yellow ones.

Experiment 1—Learning and relative weight of the color contrast and perpendicular orientation

Seventeen naive bees were exposed to forty feeders, half of which were rewarding and equipped with a vertical ellipse while the other half were not. Since we wished to record a learning curve, but noticed previously that bees were particularly attentive to a feeder with blue vertical ellipse, we swapped the colors in the current rewarding feeders. Thus, the horizontal disc was blue and the vertical ellipse was yellow, whereas the unrewarding feeders displayed only a horizontal blue disc.

Thirteen of sixteen bees directed their first visit to a two-colored feeder with a vertical component. Manual recording of the first visit of one of the bees differed from the computer record, therefore the first-visit record for this bee was discarded. As in the preliminary test, feeders with a two-color, perpendicular display were significantly preferred (one-tailed sign test, $p = 0.01$). At the end of the training phase, all bees directed most of their visits to the rewarding two-colored feeders, indicating that they discriminated firmly between feeders that had vertical display components and those did not.

In the subsequent unrewarded test, bees were presented with five novel displays distributed randomly among 40 test feeders. The blue training color was replaced by a purple or by the training yellow color. The resulting displays on the test feeders were composed of a yellow disc and a yellow vertical ellipse, a purple disc with a purple vertical ellipse, a yellow disc only, a purple disc only, and a two-colored yellow–purple disc (Fig. 4).

Thirteen individuals probed feeders with purple horizontal and vertical components on their first choice in the test (Fig. 6). We defined this choice as a “success” in a Bernouli experiment. The probability of obtaining 13 out of 17 successful outcomes, if the success probability is 0.2 (i.e., if the bees choose randomly among the five displays), is <0.0001 (binomial test), indicating a strong preference for this display. Four bees probed a feeder with a horizontal purple disc only. To test for a possible influence of the spatial location of the rewarding feeders during the training phase, we compared the position of the rewarding feeders with that chosen by the bees in the test. Nine bees visited locations that had not been rewarding during the training phase. Only six individuals visited a location that had been previously rewarding. Two individuals were excluded from this analysis because of ambiguous recording of the coordinates of the first visit. We conclude that it is very unlikely the bees memorized the positions of rewarding feeders, and that this influenced their choices in the test.

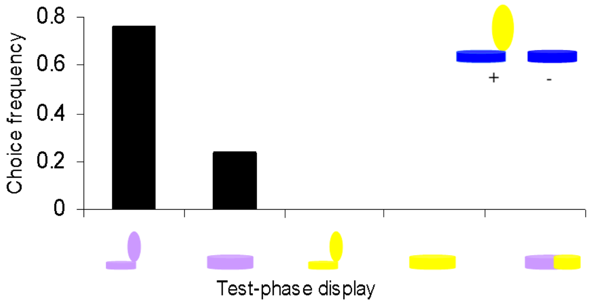

Fig. 6. The frequency of choices of the five displays offered in the test phase of Experiment 1. First choices of 17 bees, which had completed the training phase, were recorded. The rewarded (+) and unrewarded (–) training displays are shown at the top right.

Experiment 2—The roles of the horizontal and vertical display components

An important finding, in both the preliminary experiment and Experiment 1, was that bees were highly attracted to feeders that carried a combination of horizontal and vertical display components. In the second experiment we therefore asked which display feature, the horizontal or the vertical, more strongly affected the bees landing choices.

A new group of bees learned to discriminate a two-colored feeder with a horizontal blue disc and a yellow vertical ellipse from non-rewarding feeders with a horizontal yellow disc. After a first training phase identical to Experiment 1, the vertical yellow ellipses were attached to feeders with a yellow horizontal disc, which became rewarding in the second training phase. The remaining feeders with only a horizontal blue disc became unrewarding in this phase. Thus, we expected bees to gradually relearn the color features of the rewarding feeders, if they used the horizontal component of the display as a foraging cue during the first training phase. We expected them to switch immediately to the new rewarding feeders, if they used the vertical component of the display as their main foraging cue.

A second group of bees was trained to feeders with the reversed color arrangement, i.e., a horizontal yellow disc and a blue vertical ellipse versus non-rewarding feeders with a horizontal blue disc. In the second training phase the rewarding feeders displayed blue horizontal and vertical components against non-rewarding feeders with a horizontal yellow disc. The results were very similar for both groups of bees, and were therefore pooled for analysis. In the first training phase, 91.6% of the bees (n = 24) directed their first visit to one of the feeders with a horizontal and vertical two-color display, which also dispensed sucrose reward. Consequently, it

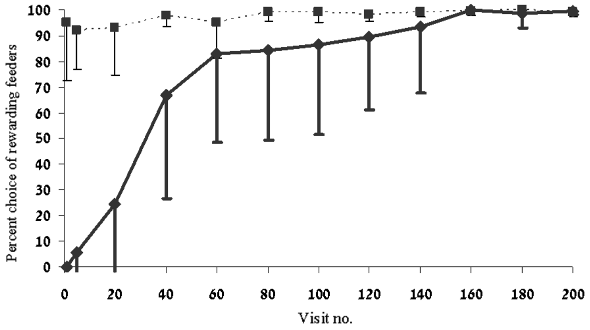

Fig. 7. Mean visit frequency to rewarding feeders in the first (dashed line) and second (solid line) phase of Experiment 2. Data are based on visit records of 24 bees in the first phase, and 17 individuals in the second phase. Error bars are 1 SEM.

is no wonder that almost all subsequent visits were also directed to these feeders (Fig. 7), i.e., the bees learned them immediately. Seven bees stopped their foraging activity before the start of the second training phase. Therefore, only 17 individuals completed the training in the second phase of the experiment. At the onset of the second phase, all bees (n = 17) visited a feeder that had the same horizontal display as the rewarding feeders in the first phase and became non-rewarding in this phase. Since spatial positions of feeders were changed between the first and second phases, this clearly indicates that bees learned the color information contained in the feeder displays, but had a strong orientation towards the color of the horizontal disc when making their first decision to probe a feeder. Three individuals persisted in visiting non-rewarding displays only during the second training phase. The remaining bees gradually shifted to visiting mostly rewarding feeders, suggesting gradual relearning (Fig. 7).

DISCUSSION

Our experiments provide information on the spontaneous and learned responses of bumblebees to visual displays that combine horizontal and vertical components with color contrast. Experiment 1 was designed to test whether vertical orientation and color contrast contribute equally to the bees' choices, or whether they are processed hierarchically. In this experiment, bees were first trained to perpendicular, color-contrasting displays. Naive bees showed a spontaneous preference for these displays. This preference could reflect an innate response bias, improved detectability of the displays, or a novelty effect to a rich stimulus by bees that were reared and pre-trained in a stimulus-poor environment. It is not clear whether the increased display area, the three-dimensional stimulus, or the color contrast caused this preference. Our preliminary test with 55 bees suggests a strong influence of the perpendicular orientation (and possibly also of the blue color) on spontaneous choice behavior, rather than an effect of the enlarged area. Additional choice experiments, with each of these stimuli presented separately, are needed to address this question.

In the test phase of Experiment 1, we presented the bees with feeders that had either color contrast or vertical orientation, or neither of them. We expected the bees to choose the color-contrasting display in the test phase if they learned to associate color contrast with reward during training. Similarly, we expected them to visit the two uniform-colored perpendicular displays in the test phase, if they formed an association between perpendicular orientation and sucrose reward during training. None of the bees chose a color-contrasting feeder, suggesting that their choices were not primarily guided by the color-contrast signal. However, the possibility that the bees learned to orient to perpendicular displays was not clearly supported either: most foragers chose the purple perpendicular displays, but none of them chose the yellow perpendicular display.

Two interpretations could explain the bees' landing pattern. First, the foragers may have been attracted to any display with a large purple area, regardless of their experiences in the training phase. This interpretation is compatible with the fact that a few individuals chose purple horizontal displays in the test phase, and with evidence for innate preference for blue color components in bumblebees (preliminary experiment of this study; Keasar et al., 1997; Gumbert, 2000; Chittka et al., 2004). Alternatively, bees that had been trained to blue horizontal displays may have oriented to displays of a similar color (horizontal purple) in the test phase. The color distance between purple and blue in the perceptual color space of bumble bees is about 3.3 units (RNL model of bee color vision, for details see Hempel de Ibarra et al., 2001) as compared to 11.7 units between purple and yellow. This interpretation is consistent with previous evidence that color dominates shape in the hierarchy of cues that affects foraging decisions of bees (Gould, 1993). It is also compatible with the tendency of bees to generalize learned color-reward associations, i.e., to visit displays that are similar in color to those that had rewarded them in the past (Gumbert, 2000; Dyer and Chittka, 2004a). The ability of bees to discriminate between pairs of similar colors diminishes if they are not exposed to both colors concurrently (Dyer and Chittka, 2004b; Giurfa, 2004; Dyer and Neumeier, 2005). This was the case in Experiment 1, since foragers were first trained to blue displays, and only later exposed

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to the purple feeders. This design may have increased the bees' tendency to visit purple feeders on the basis of their color similarity to the training feeders. This interpretation implies that the horizontal component of the perpendicular display in the training phase (blue) may have affected the bees' later foraging choices more than the vertical component (yellow). Thus, bees in Experiment 1 may have learned to orient to a blue/purple horizontal surface with any kind of vertical attachment. Possibly, the vertical disc guided the approach of the bees, but the horizontal disc guided their landing decisions. This possibility is explored in Experiment 2, and supported by its results.

Experiment 2 was constructed as a binary choice design to reduce the variability generated by multiple choices in Experiment 1. An additional improvement of Experiment 2 over Experiment 1 lies in its reciprocal design: in the training phase of Experiment 2, one half of the bees foraged on color-contrasting, perpendicular display feeders with a blue horizontal component, while the remaining bees experienced similar feeders but with a yellow horizontal component. This design allowed us to assess whether the bees associated the reward with a particular color (e.g., blue) or a particular orientation (e.g., horizontal) during training.

In the first phase of this experiment, as at the onset of Experiment 1, almost all experimentally naive bees were attracted to two-colored feeders with a vertical display component. In the second phase, on the other hand, all bees chose a uniformly colored horizontal display that had the same color as the horizontal display of the first phase. This finding implies the following: (a) The bees learned the color of the horizontal component of the rewarding feeders during the first phase, even though the vertical component was also available as a cue. (b) This learning led them to discriminate against a color-contrasting perpendicular display that did not match the learned horizontal display at the beginning of the second phase. (c) Yellow horizontal displays were learned as effectively as blue horizontal displays.

A competing interpretation of the bees' choices at the onset of the second phase is that they had learned to avoid horizontal displays with no color contrast, since these displays did not reward them in the first phase. This interpretation suggests that negative reinforcement in the first phase strongly affected the bees' choices in the second phase. We consider this interpretation less probable because eight of the bees did not probe the non-rewarding feeders at all throughout the first phase, hence did not have an opportunity to associate their display with lack of reward. These bees nevertheless visited feeders with perpendicular displays at the start of the second phase.

The results of Experiments 1 and 2 are consistent in that they suggest a strong effect of the horizontal display component on later choices. The bees landed on the horizontal display components, and stood on them while imbibing sucrose solution. This prolonged exposure to the horizontal component may have strengthened its association with food reward for the bees. The vertical element, on the other hand, may have helped the foragers to orient towards the rewarded stimulus, and evaluate the color of the horizontal disc to make a landing decision. Vertical discs may thus have acted as landmarks, rather than as targets (Lehrer, 1993). The effect of the horizontal display was strongest in Experiment 2, where all subjects chose the color of the horizontal component that had previously rewarded them. In Experiment 1, only 13 out of 16 bees showed this choice pattern. This difference may be due to the binary design of Experiment 2, as opposed to the five-choice design of Experiment 1. Reducing the number of choices may facilitate decision-making for bees, enabling them to choose their preferred displays more accurately.

Our experiments were inspired by field studies that suggest a role for extra-floral displays, such as flag-like bracts, in pollinator attraction (Herrera, 1997; Keasar et al., 2006). We recognize the difficulty of extrapolating results obtained in a sterile laboratory setting to the behavior of animals in complex "real-life" situations. Nevertheless, a few features of bee behavior that emerged in the laboratory experiments may aid in the interpretation of field observations. First, several features of floral displays may have coevolved with the foraging preferences of their pollinators. A case in point is the high prevalence of blue-violet flowers in the European flora, which coincides with an innate preference for these colors in bees (Chittka et al., 2004). Similarly, the color-contrasting perpendicular display in flag-like bracts may have coevolved with an innate pollinator preference for such displays suggested by our results. Second, our experiments show that bees respond to the horizontal component of the display (inflorescence) more strongly than to the vertical display (flag-like bract). This behavior could be adaptive, because inflorescence development is not completely synchronized with bract development (Herrera, 1997; Keasar et al., 2006). In situations of imperfect synchrony, pollinators may enhance their foraging success by assigning greater weight to inflorescence visual cues than to the visual signal of the vertical bracts.

ACKNOWLEDGMENTS

We thank Noam Bar Shai, Noam Ra'anan, and Alon Nir for technical assistance. Yaacov Rittov and Uzi

Motro provided statistical advice. Ally Harari, Michal Segoli, Adi Sadeh, and Daphna Gottlieb commented on the manuscript. The study was supported in part by the Center for Rationality and Interactive Decision-Making, and by the Institute of Advanced Studies, at The Hebrew University.

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