

Location and Color Learning in Bumblebees in a Two-Phase Conditioning Experiment

Muriel Ney-Nifle,¹ Tamar Keasar,^{2,4} and Avi Shmida^{2,3}

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Bees use spatial and visual cues that characterize flowers to make dietary choices. If two such cues always appear together nonambiguously, they provide identical information. In such cases, do bees base dietary choices on one cue and ignore the other, or do they consider both cues? We allowed bumblebees to forage on two patches of artificial flowers that differed in location, color, and reward presence in a two-phase experiment. We switched either the display color, the location, or both the color and the location associated with the rewarding patch between phases. We tested for the effects of the switch on the bees' choices. Immediately following a switch in the location or both the location and the color of the rewarding patch, the bees' performance decreased, as they continued to visit the patch that was previously rewarding. This decrease did not occur when only the color of the rewarding patch was changed or in no-change controls. We suggest that the bees' foraging choices were guided mostly by a location cue when both the location and the color conveyed the same information.

KEY WORDS: Bees; color; foraging; learning; location.

¹Laboratoire de Physique, Ecole Normale Supérieure, 69364 Lyon Cedex 7, France.

²Department of Evolution, Systematics and Ecology, The Hebrew University, Jerusalem 91904, Israel.

³Center for Rationality and Interactive Decisions, The Hebrew University, Jerusalem 91904, Israel.

⁴To whom correspondence should be addressed. Fax: 972-8-9300245. E-mail: tamark@suma.bot.huji.ac.il.

INTRODUCTION

Flower displays include a variety of chemical and visual signals that attract pollinators (Faegri and van der Pijl, 1979; Barth, 1985). Pollinating insects perceive and learn cues such as floral odor, color, size, and shape and associate them with nectar and pollen rewards in the flowers (Proctor and Yeo, 1973; Faegri and van der Pijl, 1979; Greggers and Menzel, 1993). Bees, and possibly other pollinators, do not value the information from the various modalities equally. For example, in the case of honeybees, odor takes precedence over color, and color overshadows shape (Gould, 1993).

Honeybees also learn the location of their food sources and their position in relation to other objects (Frisch, 1967; Huber *et al.*, 1994; Chittka and Geiger, 1995; Greggers and Maulshagen, 1997). Their spatial memory has both short-term (Demas and Brown, 1995; Isnec *et al.*, 1997; Chittka, 1998) and long-term (Chittka, 1998) components. To forage successfully, bees probably integrate information on the location of their food sources with information about their odor and visual properties. Hierarchical integration of location cues with display cues was found in carpenter bees that foraged on vertical inflorescences of artificial flowers (Orth and Waddington, 1997). The carpenter bees used both the location and the color of the artificial flowers to make foraging choices. However, they used spatial information only in the absence of color information. This suggests that color cues dominated location cues in this system.

Two lines of evidence suggest that the learning of flower locations in bees may involve different mechanisms than the learning of flower display cues. First, honeybees that are trained to choose a feeder according to location cues, rather than display cues, continue to do so in a novel test situation. Such transfer does not occur in bees that are trained to choose feeders according to one display cue (such as color) and to ignore another display cue, such as odor (Klosterhalfen *et al.*, 1978). Second, spatial learning includes motor components, such as making the correct turns while following a flight route (Thomson, 1995; Chittka, 1998), while learning of displays does not. For humans, and other mammals and birds, motor memory is more resistant to being forgotten than are sensory memories (Stamps, 1995). These arguments suggest that spatial cues may be learned and retained differently than display cues.

In the present experiment, we studied how bumblebees use a display cue (color) versus a location cue when the two cues were perfectly correlated, so that each of them was sufficient to indicate the presence of food reward. Our working hypothesis was that bees process color and location cues hierarchically, *i.e.*, one of the cues is more important for the recognition of food sources than the other (as in odor/color cue combinations). The alternative

hypothesis was that location and color cues receive equal weight by foraging bees, possibly because they are processed and learned in different ways.

We tested our hypotheses through a two-phase conditioning experiment. In the first phase of the experiment, bumblebees learned to associate food rewards with a location and color signal. In the second phase, we switched the color, the location, or both the color and the location associated with the reward. We observed the bees' food choices in these treatments and compared them to those in a treatment where nothing changed between the two phases. Under our working hypothesis, we expected the bees to focus on only one cue (e.g., location) during the first phase of the experiment. Thus, we expected most incorrect second-phase foraging choices in treatments that involved a change in the dominant cue (for example, changing the location associated with the reward, with or without a color change). Under the alternative hypothesis, we expected fewer correct choices after switching both reward-associated cues than after switching only one of them.

METHODS

General

Experiments were carried out in a 3 × 4-m flight room. The temperature ranged from 26 to 30°C, and the relative humidity from 40 to 70%. The room was illuminated from 0630 to 1830 with fluorescent light tubes. Observations were conducted between February and June 1996, between 0800 and 1630. The furniture and equipment in the room (e.g., bee colony, experimental table, computer) could be used as landmarks by the bees.

Colonies of naive *Bombus terrestris* (L.) were obtained from Kibbutz Yad Mordechai, Israel. A total of 84 bees from four colonies was used for the experiment. All individuals in the colonies were marked within 3 days of emergence. Pollen was supplied without restriction, directly to the colony. The bees were allowed to fly freely in the room between observation sessions. They were allowed to feed on nectar *ad libitum* for 2–3 h after each observation session. Then the feeder was removed and the bees were starved until the next observation session, on the following morning.

Artificial Flowers

Forty computer-controlled artificial flowers were used for the experiment. The flowers were tube-shaped and 10 cm tall. They were arranged in two patches, 130 cm apart, on top of a 1.40 × 2.40-m hardwood table, about

2 m from the colony. Each patch consisted of a 5×4 array of artificial flowers. The distance between array rows was 10 cm, and the distance between columns was 20 cm. Each flower was placed above a $10 \times 10 \times 8$ -cm box that contained its electronic parts. A removable round plastic landing surface of 3.7-cm diameter was placed on top of each flower. These landing surfaces were colored human-blue in one of the patches and human-yellow in the other patch. Spectral properties of the flower colors are provided by Keasar *et al.* (1997).

The design of the electronic flowers is described in detail by Keasar (1997). Briefly, each flower consisted of a cylindrical container that held a 30% sucrose solution, and a 1- μ l miniature cup that was refilled when programmed to dip into the sucrose-solution container. Only foragers that landed on the top part of the flowers and probed them correctly were able to access this cup and feed. Each artificial flower was equipped with a photodetector that was activated when the foraging bee inserted its head into the flower. The photodetector signals were automatically recorded in a computer file. They allowed us to track flower visitation sequences for each forager. Flowers in one of the patches refilled after each foraging visit by a bee, while the sucrose solution in the flowers of the second patch was never accessible.

Experimental Design

We observed workers that foraged singly on the two patches of artificial flowers. These workers had collected sucrose solution from a petri dish feeder prior to the experiment but had not been exposed before to artificial or real flowers. The first bee that approached the artificial flowers within each experimental session was selected for observation. Other bees that approached the floral arrays were caught and caged until the end of the session.

We used a two-phase design. At the beginning of the first phase the flowers in the unrewarding patch were covered, invisible and inaccessible to the bee, so that it was forced to make its first visit to a reward-containing flowers. The unrewarding flowers were uncovered during the bee's first visit. The bee was allowed to choose between the 20 rewarding flowers and the 20 unrewarding flowers for the rest of the experiment. In the first phase, we allowed a bee 50 visits in the artificial flowers. Then we caged the bee for 15 min outside of the colony. During this break, we introduced a one-time change in the foraging environment. In the second phase, we allowed the bee 200 additional foraging visits in the changed environment. We used three types of changes (Fig. 1).

- Changing the location of the rewarding flowers to the location that was previously nonrewarding (treatment L).

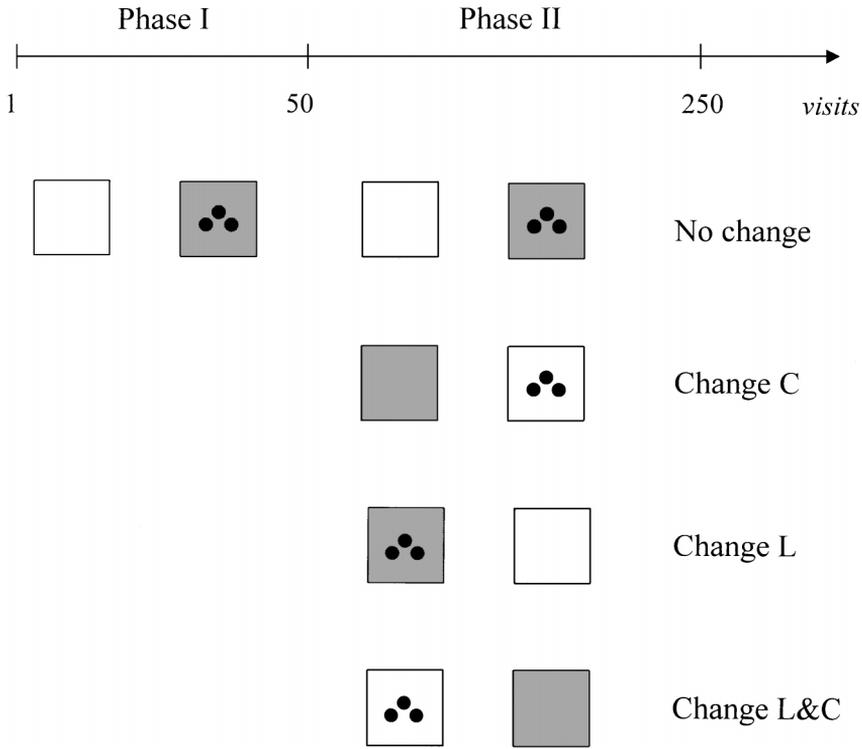


Fig. 1. The experimental design. Each square represents a patch of 20 color-marked flowers. Flowers of only one of the two patches have accessible nectar (three black dots). At the end of phase I, we changed nothing (NC), the color associated with the food (C), the location of the food (L), or both the color and the location (L&C).

- Changing the color of the rewarding flowers to the color that was previously associated with nonrewarding flowers, and vice versa for nonrewarding flowers (treatment C).
- Changing both the color and the location that were associated with rewarding flowers (treatment L&C). This is equivalent to moving the reward to the patch that was previously unrewarding.

There was also an additional treatment in which no changes occurred during the break.

- Changing nothing (treatment NC).

For each of these four treatments, the choice patterns of 16 bees were observed. One-half of the bees in each treatment were rewarded by yellow

flowers during the first phase of the experiment, while the remaining bees obtained reward in the blue flowers. This was done to control for possible prior color preferences. Similarly, the reward was located in the left-hand patch for one-half of the bees, and in the right-hand patch for the other half, to minimize the effect of possible preferences for location. Thus, the four possible combinations of reward with color and location were represented in each treatment. Individuals from the four bee colonies were allocated to treatments in the following way: treatment L—15 bees from colony 1 and 1 from colony 4; treatment C—14 bees from colony 1, 1 from colony 3, and 1 from colony 4; treatment L&C—7 bees from colony 2, 8 from colony 3, and 1 from colony 4; and treatment NC—9 bees from colony 1, 6 from colony 2, and 1 from colony 4.

Data Analysis

The data analysis aimed to detect effects of the change on foraging decisions. The number of unrewarding flowers visited by the bees during phase I of the experiment varied significantly among treatments (see Table I). Since foraging conditions were identical for all experimental treatments in the first phase, this suggests that our sample of bees was not homogeneous. Therefore, we standardized the choice behavior between individuals. We compared different treatments in two ways.

1. We counted the number of visits to unrewarding flowers during the last 10 visits in phase I and the first 10 visits in phase II and calculated the difference between them for each bee separately. We averaged the differences over all bees in a treatment.

2. We counted the number of visits to unrewarding flowers between the first and the T th visit ($1 \leq T \leq 250$). This quantity is denoted $n(T)$. We then averaged the ratio $n(T)/n(250)$ over all the bees in an experimental treatment and plotted this ratio as a function of T . This plot describes the temporal distribution of visits to unrewarding flowers. Normalizing by the total number

Table I. Percentage of Visits to Unrewarding Flowers in Phase I and Phase II for the Four Treatments^a

Phase	Treatment			
	NC	C	L	L&C
I	2.25 ± 1.28	4.25 ± 1.26	8.0 ± 3.3	14.5 ± 3.1
II	2.3 ± 0.6	4.0 ± 1.2	9.2 ± 1.5	13.9 ± 2.5

^aBetween phases either no change (NC) or a switch in color (C), location (L), or both location and color (L&C) associated with reward was performed. Mean and standard error are calculated for the sample of 16 bees for each treatment.

of visits, $n(250)$, allows a comparison between experimental treatments. As a cumulative curve, it increases monotonically from the lower corner to the upper corner of the graph. If bees visit the unrewarding patch at regular time intervals, then this plot oscillates around the diagonal. When bees start to visit more often the unrewarding patch, then this plot takes a curvature with a concave-up shape. This way, the plot can be seen as a graphical means to detect deviations from periodicity in visits to unrewarding flowers.

Finally, we calculated the mean distance between this curve and the diagonal. This is the difference between T and $n(T)/n(250)$ averaged over all values of T . A negative (positive) distance means that the curve lies below (above) the diagonal on average.

RESULTS

Foraging Choices in Phase I

The first visit was devoted to a rewarding flower, as planned, in 82 of the 84 individuals. The two remaining bees landed on a rewarding flower without probing it, and made their first probing visit to an unrewarding flower, after the unrewarding patch was uncovered. The bees typically visited several flowers in succession within each patch. These “runs” of visits were typically longer in the rewarding patch than in the unrewarding patch. Although experimental conditions were identical for all treatments in the first phase, the numbers of visits to the unrewarding patch differed significantly from one treatment to the other (Table I; Kruskal–Wallis test, $df = 3$, $H = 16.153$, $P < 0.01$). We tested for possible effects of source colony, bee age, colony age, and observation date on the variation in the number of phase I visits to unrewarding flowers. Only the effect of the source colony was statistically significant ($df = 3$, $H = 16.131$, $P < 0.01$), probably because many individuals within each treatment originated from the same colony.

Foraging Choices Following the Transition to Phase II

We tested whether the introduction of a 15-min break at the transition from phase I to phase II caused a change in the bees’ foraging choices. For this purpose, we counted the number of visits to unrewarding flowers during the last 10 visits in phase I and the first 10 visits in phase II in treatment NC. Visits to unrewarding flowers after the break were less frequent than before the break by 0.69 ± 0.59 visit (mean \pm SE), suggesting that the break did not elicit visits to the unrewarding patch. This was confirmed by a plot of the temporal distribution of visits to the unrewarding patch throughout both phases, which showed no irregularities at the break (Fig. 2).

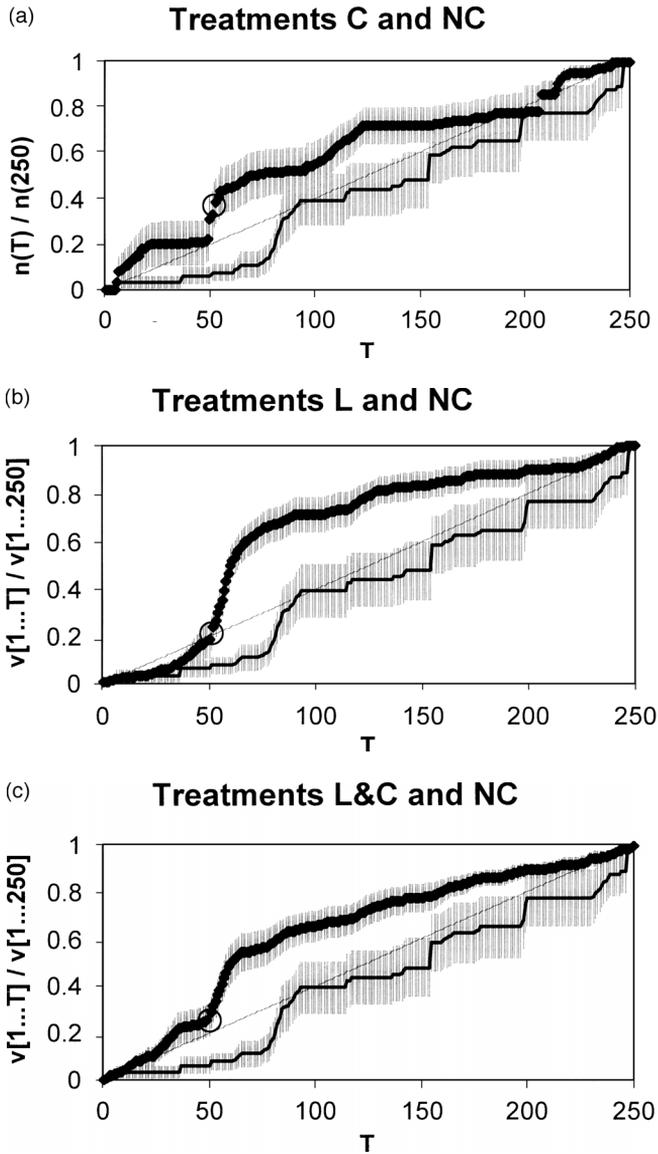


Fig. 2. Frequency of visits to empty flowers during phase I and phase II of treatments C (a), L (b), and L&C (c). The transition between phases is indicated by the open circle. Treatment NC is plotted (lower curves) for comparison. For each visit T , the mean and standard error were calculated from the pool of N bees that made at least one visit to the empty patch, where N depended on the treatment: C, $N = 14$; NC, $N = 11$; L, $N = 16$; and LC, $N = 15$. The thin diagonal line is a reference line that corresponds to a perfectly constant rate of visits to empty flowers.

Our main goal was to study the effect of the change in conditions between phases on the bees' foraging choices, while taking into account the unplanned phase I differences in choice behavior between treatments. The total frequency of visits to unrewarding flowers was similar in both phases, for all experimental treatments. This led us to analyze the temporal distribution of the visits to unrewarding flowers within each treatment. In particular, we tested whether visits to unrewarding flowers were more common immediately after the switch to phase II than immediately preceding it. Visits to the unrewarding patch were more frequent in the first 10 visits in phase II than in the last 10 visits in phase I in all noncontrol treatments. Their number increased by 0.63 ± 0.68 (mean \pm SE) in treatment C, by 3.31 ± 1.20 in treatment L, and by 3.13 ± 1.45 in treatment L&C. This increase is statistically significant for treatments L and L&C (paired *t* tests, *df* = 15, $P < 0.05$).

Next we characterized graphically the temporal distribution of visits to the unrewarding patch throughout both phases of the experiment (Fig. 2). Here, too, we found that unrewarding flowers were visited at a higher frequency after the transition to phase II in treatments L and L&C. This sharp increase did not occur in treatments NC and C. This is confirmed by the results on the distance of this curve to the diagonal. The mean distance from the curve to the diagonal was -20 ± 22 and 24 ± 20 for treatments NC and C and 37 ± 12 and 33 ± 12 for treatments L and L&C. These distances are significantly different from zero for treatments L and L&C only (tests for a sample statistic against an expected value, $P < 0.01$). Finally, the amplitude of the increase in visits to unrewarding flowers immediately after the break was compared for treatments L and L&C in a plot of phase II only (Fig. 3).

Patterns of Visits to the Unrewarding Patch, Comparing Phase I and Phase II

Did the increased number of visits to unrewarding flowers at the start of phase II result from a higher tendency to fly into the unrewarding patch, a lower tendency to leave it, or both? The frequency of shifts from the rewarding to the unrewarding patch did not differ significantly from phase I to phase II in treatments L, C, and L&C (Table II). Next we analyzed runs of visits in the unrewarding patch. The first run in phase I and the last one in phase II had a similar length in these treatments. On the other hand, the last run in phase II was significantly longer than the first one in this phase in treatments L and C and, to a lower extent, in treatment L&C (Table III; see footnote *a* for statistics).

Phase II

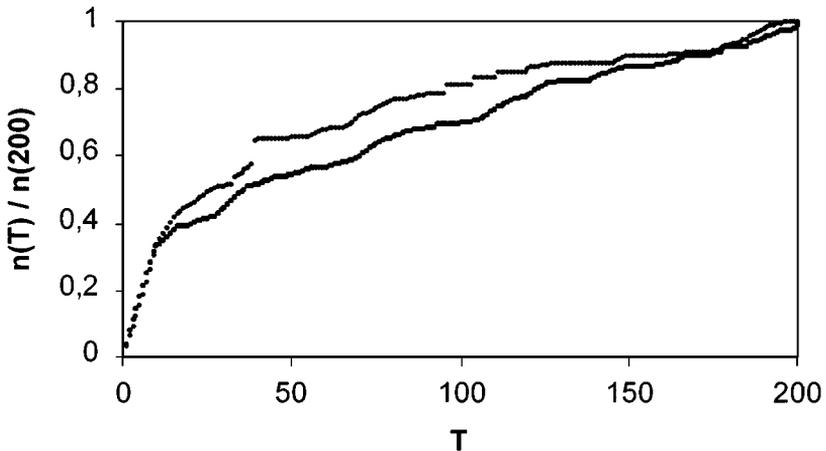


Fig. 3. Frequency of visits to empty flowers during phase II of treatments L (lower curve) and L&C (upper curve).

DISCUSSION

Foraging Choices in Phase I

All bees in the experiment experienced an identical foraging situation in phase I. In spite of this, there were significant differences between treatments in the frequency of visits to unrewarding flowers in phase I. These

Table II. Number of Arrivals in the Unrewarding Patch in Phase I and Phase II for Three Treatments^a

Phase	Treatment		
	C	L	L&C
I	3.24 ± 0.56	3.76 ± 0.55	5.5 ± 1.1
II	2.0 ± 0.6	2.25 ± 0.6	3.7 ± 0.7

^aSince the two phases differ in length (50 visits in phase I and 200 in phase II), we give the number of arrivals per 200 visits by multiplying the phase I data by 4. The no-change treatment is not included since so few visits to the unrewarding patch were recorded. The difference between phase I and phase II is not statistically significant for any of the treatments (one-tailed *t* tests, *df* = 15, *P* = 0.07, *P* = 0.34, and *P* = 0.16 for treatments C, L, and L&C, respectively).

Table III. Run Lengths (Number of Consecutive Visits) in the Unrewarding Patch in Phase I and Phase II for Three Treatments^a

Phase	Treatment		
	C	L	L&C
I			
First run	2.75 ± 0.75 (12)	2.33 ± 0.83 (9)	5.93 ± 0.94 (14)
II			
First run	5.54 ± 1.12 (11)	12.0 ± 2.3 (16)	8.2 ± 1.42 (15)
Last run	3.0 ± 0.8 (7)	3.66 ± 0.92 (12)	5.23 ± 1.13 (13)

^aIn phase I, we averaged the length of the first run (if any) to the unrewarding patch over bees: In phase II, we considered the first and last runs the bees made in the unrewarding patch. For instance, the first run length in phase II of treatment L is an average of 16 bees: 9 made this first visit to the unrewarding patch right at the beginning of phase II, with an average run length of 18, while the run length for the remaining 7 bees was only 4.3. The number of bees is indicated in parentheses (since not all the bees visited the unrewarding patch, and some of them visited it only once in phase II). The difference between the first run in phase I and the last run in phase II is not statistically significant for any of the treatments (one-tailed *t* test, *P* = 0.41, *P* = 0.15, and *P* = 0.32 for treatments C, L and L&C, respectively). There are significant differences between the first and the last run in phase II (one-tailed *t* tests, *P* = 0.042, *P* = 0.0015, and *P* = 0.057).

differences, which can be attributed partly to differences in the bees’ source colonies, complicate the analysis of the data. The bees’ choices in phase II have to be standardized with respect to their phase I choices before different treatments can be compared. This was done through our graphical analysis, which allowed us to compare the temporal distribution of visits to unrewarding flowers between treatments.

The effect of source colony suggests that the experimental colonies differed in learning abilities, even though they were reared commercially (and thus inbred to some extent) and exposed to similar conditions outside observation sessions. Our data analysis reduces the confounding effect of source colony. Yet this effect could be overcome completely by randomly allocating bees from each colony to experimental treatments.

The Roles of Location and Color Cues in the Bees’ Choice Behavior

Choice frequency of unrewarding flowers was similar in both phases of all treatments (Table I). This suggests that none of our manipulations (switching reward color, location, or both) affected the bees’ overall tendency to visit unrewarding flowers. The next question is whether the experimental manipulations affected the distribution of visits to unrewarding flowers along the course of the experiment. Our analyses show an increase in visits to unrewarding flowers immediately after a change in reward location or in both location and color.

The presence of food rewards in phase I was indicated by a combination of location and color cues, which were perfectly correlated with each other. At the end of phase I, we changed the association between color and reward (treatment C), location and reward (treatment L), or both color and location with reward (treatment LC). In agreement with the working hypothesis, the bees visited locations that were previously rewarding at the beginning of phase II, even if not associated with the color that was previously rewarding. Contrary to the prediction of the alternative hypothesis, a change in two cues associated with the reward (treatment L&C) did not increase the rate of visits to unrewarding flowers more than a change in the location cue alone (treatment L). These findings are compatible with the hypothesis that bumblebees use location and color information hierarchically and that location predominates. Similarly, honeybees were not able to distinguish among four differentially rewarding feeders on the basis of small color marks but were able to do so when location cues were available (Greggers and Maulshagen, 1997). Hummingbirds use a similar hierarchy for evaluating location and color cues (Brown and Gass, 1993) but do not visit unrewarding flowers periodically, as in the present study. In contrast, carpenter bees used primarily color, while the location of a target flower on a vertical inflorescence was used only in the absence of color cues (Orth and Waddington, 1997). This result does not contradict ours since color and location referred to different attributes than in our experiment. There, bees were conditioned to locate flowers with a specific location and/or color *within* a “patch” (an inflorescence).

The evidence for a hierarchical organization of location and color cues in the present experiment is weakened by two factors. First, changing the color associated with the reward brought forth longer runs of visits to the unrewarding patch than before the change (Table III). This suggests that color alone does influence, to some extent, the bees’ ability to discriminate among flowers. Second, we cannot rule out the possibility that individuals that a priori tended to visit unrewarding flowers (bees in treatments L and L&C) also tended to react strongly to any change in their foraging environment. That is, the nonrandom allocation of the colonies’ workers to treatments, rather than the nature of our experimental manipulations, caused the between-treatment differences at the beginning of phase II. Therefore, the question of the hierarchy between spatial and visual cues cannot be unambiguously resolved by the present experiment.

Our results are consistent with the hypothesis that one of two cues is processed more intensely by bees, if both cues are completely correlated and provide the same information. Decision-making may be harder and more time-consuming if each cue provides different information, so that both cues need to be processed. Experiments to test this hypothesis are now under way.

Color advertising by flowers and the ability of bees to perceive and learn color signals are a well-known aspect of plant–pollinator coevolution. Our results suggest that, in spite of these coevolutionary processes, bumblebees may not be guided to flowers only by their color. Rather, location may precede color. A possible reason is that flower color may not provide sufficient information on food reward to bees, since many flower species have similar color signals. Relying on location information, on the other hand, may help bees to return to the very same food patches that had been profitable in the past. Thus, location cues may be more useful than color cues for finding food under natural conditions. Our experiment, which was concerned mainly with the bees' decision-making mechanisms, did not manipulate the relative reliability of location versus color cues. Such manipulations could reveal whether foraging bees can benefit from responding to location signals more than to color signals.

Alternatively, bees may use both location and color as complementary signals, but not at the same time. At the beginning of a foraging bout, bees may fly to known *locations* where they have found rewarding flowers in the past. Then, within the location, they may be guided by color cues to identify the most rewarding species.

Our hypothesis implies that the bees first had to learn that color and location were perfectly correlated, so that they could later rely on the location cue alone to make foraging choices. This learning occurred during phase I of the experiment (first 50 visits). It would be interesting to repeat the experiment with a much shorter phase I, which may impair the learning of the color–location correlation.

Dynamics of Visits to Unrewarding Flowers

Figure 2 shows that visits to unrewarding flowers occurred regularly during phase I and during the latter part (last 150 visits) of phase II when averaged over all individuals in a treatment. The bees visited unrewarding flowers even toward the end of the 250 visits allowed in the experiment. The frequency of these visits was highly variable (in extreme cases, some bees dedicated 50% of their visits to unrewarding flowers, while others never visited them). Unrewarding flowers were temporarily visited at higher rates after a change in the location of the food source. These observations suggest that visits to unrewarding flowers can be part of a *steady-state regime*, which involves periodic visits to unrewarding flowers when foraging conditions are unchanging. Visits to unrewarding flowers may also be part of a *learning regime*, which follows a change in environmental conditions.

The steady-state regime occurs in phase I and in the last part of phase II. There, bees seem to follow a steady state similar to the one observed in phase I

(Tables II and III). In a previous experiment, where bees were allowed to choose among four types of artificial flowers, the tendency to visit unrewarding flowers periodically depended on the spatial arrangement of the flowers (Keasar, 2000). In particular, the experiment included a mixed arrangement of flowers in a single patch, so that a move from one color to the other did not imply shifting patches. This suggests that the steady-state behavior is affected by the location of the rewarding and unrewarding flowers. Steady-state visits to unrewarding flowers can be interpreted as errors in choice or as a way to sample alternative food sources (whether it is an alternative patch or an alternative flower color within the same patch) that may change in quality over time (Heinrich, 1979; Stephens, 1987; Tamm, 1987; Cohen, 1993). An innate sampling strategy has been proposed as a possible mechanism that can account for risk sensitivity and probability matching in bees (Thuijsman *et al.*, 1995).

The learning regime occurs at the beginning of phase II in treatments in which the location is changed. These visits to unrewarding flowers seem to reflect an erroneous choice of a patch that was previously rewarding. The effect of the change can be seen over more than 10 flower visits (Fig. 3 and Table III) and after a 15-min break in the experiment. These suggest that the memory involved in the learning-regime choices lasts for several minutes and may be specific to each patch. Similarly, Greggers and Menzel (1993) show evidence for the use of long-term, patch-specific memories by honeybees.

The interplay between short-term experience and the formation of long-term memory in the present experiment is the subject of current research.

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