

Cue Learning by Rufous Hummingbirds (*Selasphorus rufus*)

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The authors investigated the use by wild-living rufous hummingbirds (*Selasphorus rufus*) of flower color pattern and flower position for remembering rewarded flowers. Birds were presented with arrays of artificial flowers, a proportion of which was rewarded. Once the locations were learned by the birds, the array was moved 2 m, and flower color pattern and/or rewarded positions were manipulated. The birds' ability to learn which were the rewarded flowers in this 2nd array was much more strongly affected by whether the rewarded flowers occupied the same positions as in the 1st array than by their color patterns.

Most studies of learning and memory in animals are feasible only in the laboratory. However, the rufous hummingbird is proving to be a useful animal to study aspects of learning and memory used while foraging in the field (e.g., Healy & Hurly, 1995; Hurly, 1996). These birds migrate to the Canadian Rocky Mountains to breed. Once there, males ardently defend a feeding territory. They readily adopt an artificial feeder filled with sucrose solution as their prime food source and focus their attention on defending it and the surrounding area. They are little disturbed by the presence of humans, can be easily marked for identification, and learn very quickly to feed from a variety of artificial feeding devices. It is, therefore, possible to adapt laboratory tasks for use with free-living, nondeprived hummingbirds to investigate whether they use memory in foraging and, if so, what cues they use to learn and remember flowers.

The proposal that the hummingbirds do use learning and memory in their foraging comes from the observation that the male rufous hummingbird defends a territory of several hundred flowers each of which, once emptied of nectar, should be avoided, at least for the several hours it takes a flower to refill. Foraging bouts are energetically expensive as a male hovers at flowers for several seconds to feed before returning to his post to scan for females and rival males. A bird that could remember which flowers it had emptied would spend less time foraging and more time scanning. Both field and laboratory experiments have demonstrated that

these hummingbirds can learn and remember at least a small number of locations (e.g., G. S. Brown & Gass, 1993; Gass & Sutherland, 1985; Sutherland & Gass, 1995).

Despite the common folklore that hummingbirds prefer to visit red flowers, spatial location is the predominant cue used by the birds to return to flowers. We have shown this preference for spatial cues in rufous hummingbirds in two different field experiments. In one, based on an experimental design used by Brodbeck (1994), birds were presented with an array of four uniquely patterned flowers in which one flower was rewarded. After a single feeding bout (3 s–10 s) at this flower, the color pattern of the rewarded flower was switched with that of one of the other flowers. Birds returned more often to the flower in the correct position in the array than to the flower bearing the appropriate color pattern (Hurly & Healy, 1996; see also Miller & Miller, 1971). In a second experiment, birds were required to remember one rewarded flower in an array of five. When the array was compact (spacing was less than 40 cm), hummingbirds seemed to remember the rewarded flower according to its relative position in the array (Healy & Hurly, 1998). This preference for local landmarks has been well documented in other species, vertebrates and invertebrates (for review, see Cheng & Spetch, 1998). When flowers were spaced further apart, however, birds seemed to remember the spatial locations of flowers seemingly in relation to more global cues (Healy & Hurly, 1998, Experiment 1). Similar results were found in more complex arrays with 8 of 16 flowers rewarded (Healy & Hurly, 1998). In both the simple and complex arrays, birds switched their cue preference in flower choice based on a spatial scale: They used the positions of flowers relative to other flowers in the array with spacing less than 40 cm and used the absolute (based on global cues) locations of flowers when flowers were spaced further apart. Sometimes this led to birds hovering in the air at about the site of a previously rewarded flower with the actual flower 80 cm distant. This apparent priming of the formerly appropriate local memory by the surrounding landscape has also been described for rodents by Etienne, Teroni, Hurni, and Portenier (1990) and Mackintosh (1973; also see Rotenburg & Muller, 1997).

In laboratory experiments, animals often demonstrate preferences for certain sets of cues, typically intra- versus extramaze cues. Such preferences are frequently specific to each experiment

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(see Biegler & Morris, 1996). In our hummingbird experiments, the birds received minimal training and were tested within a few hours of first exposure to the experiment. We suggest that the observations of switches in cue preference are not based on specific experimental designs but rather on the kinds of cue preference changes the birds may use in real foraging situations.

In this article, we investigate how free-living hummingbirds use two cue types while foraging: positions flowers occupy in an array and the color patterns of those flowers. Hummingbirds in experimental tests generally prefer positional cues and seem to ignore color cues (e.g., Lyster, Riess, & Ross, 1950; Miller & Miller, 1971; Miller, Tamm, Sutherland, & Gass, 1985). However, in the experiments described above, we found that providing each flower in the array with a unique color pattern facilitated learning which of the flowers were rewarded. When arrays were moved to an overlapping location, birds then used spatial cues to make choices and appeared to ignore the flower color patterns (see also G. S. Brown & Gass, 1993). We did not, however, investigate whether this change in cue use was due to birds having forgotten the color patterns or whether they simply preferred to use the spatial cues. There is evidence that birds do learn and remember flower colors, but usually under conditions in which the flower color signals differential rewards (e.g., Collias & Collias, 1968; Hurly & Healy, 1996; Meléndez-Ackerman, Campbell, & Waser, 1997; Miller et al., 1985).

In the following experiments, we investigated whether the birds did remember a flower's color pattern. We presented the birds with arrays of flowers in which they were required to learn which of the flowers were rewarded. Once a bird reached our criterion level, the array was moved so that there were 2 m between array locations. Flower color pattern and position were manipulated, and the bird

was required to reach criterion for a second time. We predicted that we would find evidence that the hummingbirds could remember flower color patterns but that the position of the flower would take precedence in flower choice, if birds were made to choose between cue types.

Experiment 1A

In this first experiment, we investigated whether the birds preferred to use or remember position cues rather than color cues by presenting the birds with an array of 10 flowers, only 1 of which contained a reward of sucrose solution. This test also allowed us to determine whether the previously observed effect that color pattern appeared to aid the learning of a spatial location also enhanced the memory for that location. The birds were required to learn which was the rewarded flower, and then the array was moved and the bird was required to learn for a second time which was the rewarded flower. There were three array types, each designed to test different aspects of possible cue use (see Table 1). Once the array was moved (2 m) the bird could no longer use the global cues it may have used to locate the rewarded flower in the first phase of the trial. If the bird used additional cues learned in the first phase, such as flower color pattern or flower position in the array, then we would expect it to learn which was the rewarded flower in the second phase with fewer errors than in the first phase. In the same-unique array, flowers were uniquely colored in Phase 1, and both color and position cues were maintained from Phase 1 to Phase 2. This array allowed us to determine whether the positional and/or color information a bird gained in Phase 1 was remembered in Phase 2. We presented birds with two further arrays: different-unique arrays in which the flowers also bore unique color patterns

Table 1

Cues Provided in Each Array Type in Phase 1, Changes Made in Phase 2, and Information Available to the Birds for Learning Which Was the Rewarded Flower in Phase 2 Following the Array Shift

Array type	Phase 1	Phase 2	Information from Phase 1
Same unique	Unique color patterns	As in Phase 1	Color pattern Position in array
Different unique	Unique color patterns	Novel unique patterns	Position in array
Same single	All flowers the same	As in Phase 1	Position in array
Change position	All flowers the same	Different reward flowers	Misleading position
Rotate	Unique color patterns	Array rotated 90°	Color pattern Position in array
3 same unique (Experiments 2 & 3)	Unique color patterns	As in Phase 1	Color pattern Position in array
3 different unique (Experiments 2 & 3)	Unique color patterns	Novel unique patterns	Position in array
3 same single	All flowers the same	As in Phase 1	Position in array
3 rearrange	Unique color patterns	Flower positions scrambled	Color pattern Misleading position
3 change shape	Unique color patterns	Array shape changes to triangle	Color pattern
3 change position	Unique color patterns	Different reward flowers	Misleading colors Misleading position
Neighbors	Unique color patterns Flowers contiguous		
Not neighbors	Unique color patterns Flowers not contiguous		
3 change shape (Experiment 5)	Unique color patterns	Change in array shape	Color pattern
3 change color and shape	Unique color patterns	Change in array shape Novel unique patterns	Nothing useful

in Phase 1. Between Phases 1 and 2, the position of the rewarded flower remained the same but the color patterns were changed. These arrays allowed us to determine whether the facilitatory effect of color pattern was exerted only when learning which was the rewarded flower, as color information learned in Phase 1 was not relevant for determining which was the rewarded flower in Phase 2. In same-single arrays, all the flowers had the same color pattern, and in Phase 2 the position of the reward flower was maintained. Therefore, color pattern could facilitate neither the learning nor the remembering of the rewarded flower. Thus, if color pattern plays a role in remembering which was the rewarded flower, then birds should learn more slowly and remember less well which is the rewarded flower in Phase 2. In Experiment 1, we made the following predictions:

1. If flower color pattern facilitates the learning of the rewarded flower, then Phase 1 performance (number of errors made before learning which were the rewarded flowers) should be similar for the same-unique and different-unique arrays and worse for the same-single array.

2. If either color pattern or flower position are remembered and contribute to the learning in Phase 2, then birds should make fewer errors when learning which flowers hold reward in Phase 2 than in Phase 1 on all arrays. However, if memory for the two cues contributes in an additive fashion to learning in Phase 2, then the difference between the phases in errors made before learning should be greater on same-unique arrays than either different-unique or same-single arrays.

3. If birds learn and remember both position and color pattern, then changing color patterns for Phase 2 of different-unique arrays might result in birds making more errors during Phase 2 than Phase 1 before reaching criterion performance. However, when provided with only position cues as in same-single arrays, there is no disruption by color cues between Phases 1 and 2. Performance in Phase 2 should then be better on same-single arrays than on different-unique arrays.

Method

Subjects. The experiment was conducted along the length of a valley (1400-m elevation) in the Eastern Rocky Mountains, 20 km southwest of Beaver Mines, Alberta (49° 29' N; 114° 25' W), Canada. Eleven experimentally naive, male rufous hummingbirds (*Selasphorus rufus*) were used as subjects in Experiment 1. All individual birds were identifiable by the application of a small amount of colored ink onto the breast feathers. Trials were run between 0800 and 1930 Mountain Standard Time from May through July 1997.

Initial training. Artificial feeders containing 14% sucrose solution were placed in potential territories during mid-May, and by late May most feeders were defended by males. A bird could then be ink marked and, after removal of the feeder, trained to feed from small artificial flowers. The feeder was returned following training and between experimental trials. The flowers consisted of a cardboard disk (5.8-cm diameter), the center of which was pierced by a syringe tip forming a well, capable of holding 120 μl of sucrose solution. The colored cardboard discs were painted with a pattern, using one contrasting color. All flowers were a combination of two colors (e.g., brown, white, pale blue, dark blue, pale green, dark green, pink, red, orange, yellow, purple, or lilac). The patterns were a range of geometric designs (e.g., white parallel lines on a blue background, pink dots on a pale green background). The flowers were mounted on 60-cm wooden stakes (height above the ground). The bird learned to feed from a single flower, which contained 20% sucrose and which was moved a short

distance (approximately 1 m) after each visit. When the bird had fed three times (< 1 hr), the experiment began.

Experimental protocol. Ten flowers were laid out in arrays as depicted in Figure 1 with 30 cm between flowers, center to center. One flower contained 120 μl of 20% sucrose solution. There were two different kinds of arrays: (a) same-unique and different-unique arrays, with all 10 flowers having unique color patterns; (b) same-single arrays, with all 10 flowers having the same color pattern (see Table 1).

In Phase 1 of a trial, the male hummingbird was required to visit the array and sample from the flowers until it had learned which flower contained sucrose. The rewarded flower was randomly assigned such that 9 of the flowers were chosen as reward sites without replacement. The 10th flower, the 4th flower at the end of the middle row, was never used as a rewarded flower but was provided as a potential orientation cue for the bird to use. Following this first visit to the array, the flower the bird had drained of sucrose was refilled with sucrose solution, and the remaining 9 flowers were filled with water. The birds prefer to avoid water-filled flowers (Hurly & Healy, 1996). Although it is possible that the bird watched the filling of

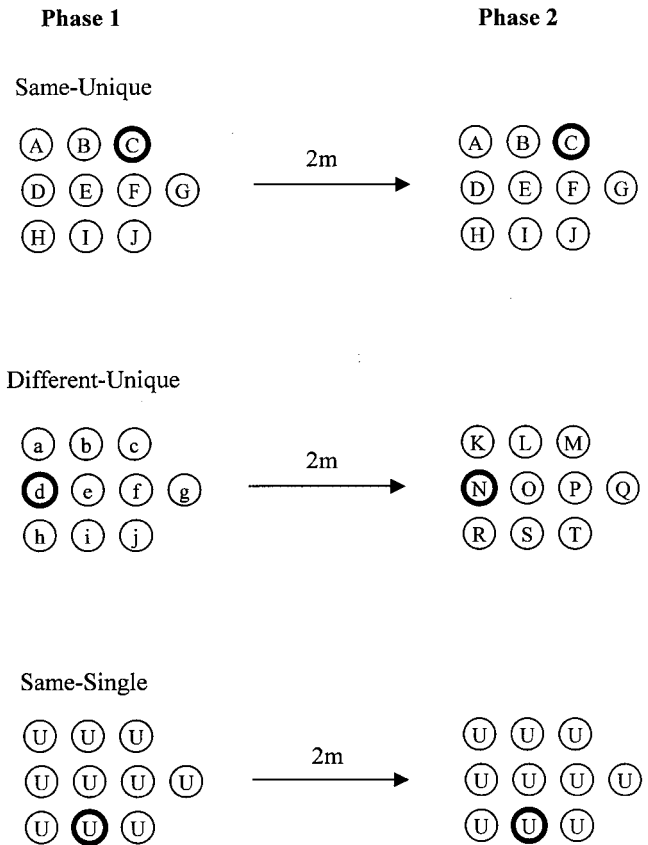


Figure 1. A schematic of the experimental design as used in Experiment 1 (and from which the other experiments follow). Each circle denotes a flower, with the boldface black circles representing the flower rewarded with sucrose solution. In Phase 1 of same-unique and different-unique arrays each of the flowers bore a unique color pattern (indicated by the different letters), but in Phase 2 the flowers in the different-unique array bore novel, unique patterns. The relative position of the rewarded flower remained the same across the phases, although the entire array was moved 2 m in one of the four major compass directions. In the same-single arrays, all of the flowers bore the same color pattern both within and between phases. The letters and symbols show systematically that the flowers bore unique color patterns; they do not designate any particular color or pattern.

the flowers, the syringes used to dispense the sucrose and the water were almost identical with the differences unlikely to be visible to a bird perching more than 15 m away. The reward flower was always refilled once the bird had left the array. The hummingbird was considered to have learned the location of the rewarded flower when it had made three consecutive visits to the array, during which it visited the rewarded flower and no more than one other flower. On many occasions, the bird visited only the rewarded flower on three consecutive visits to the array. Immediately following the last of these three criterion visits, the array was moved 2 m in one of the four main compass directions in preparation for Phase 2. This 2-m shift was such that there were at least 2 m between the front edge of the array in Phase 1 and the hind end of the array in Phase 2 and not simply that each flower was moved 2 m. This direction was counterbalanced both within and across birds as was the order of presentation of array types.

In the same-unique and same-single trials, all the flowers in Phase 2 remained the same as in Phase 1, as did the position of the rewarded flower within the array. In different-unique trials, all of the flowers in Phase 2 were replaced with new unique flowers while the position within the array of the rewarded flower remained the same. The rewarded flower was refilled with sucrose, and all others contained water. Phase 2 of a trial began when the bird returned to the array. For each visit to the array, we recorded the flowers visited and refilled the emptied flowers before the bird returned. Phase 2 of the trial ended when the bird reached the same performance criterion as required in Phase 1. A trial then consisted of two phases, and within each phase there were multiple visits made to the array. During a single visit to the array the bird might check the contents (by probing with his tongue) of a number of flowers. This behavior was always distinctive—a bird would pause above a flower and his bill would enter. This action constituted a probe. Birds very rarely probed the same flower twice within a visit to the array, and such revisits were not included in the data analysis. Flowers were unique to each trial. Each bird completed two trials of each kind of array, a total of six trials per bird. Intervisit and interphase intervals are presented in Table 2.

Results

Two measures of performance were used to compare hummingbirds' ability to learn the location of the rewarded flower in the different arrays: (a) the total number of incorrect flowers probed

before reaching criterion in each phase; and (b) the number of errors made before locating the rewarded flower on the first visit, following the shift of array location. Repeated measures analyses of variance (ANOVAs) were used to make these comparisons. In addition, we tested the three specific a priori predictions about how birds would perform on the different arrays and between the phases.

Number of errors. There was no difference among the array types, $F(2, 20) = 1.47, p > .10$; a significant difference between the phases, $F(1, 10) = 5.62, p < .05$; and the interaction between the two main effects was not significant, $F(2, 20) = 0.77, p > .10$ (see Figure 2a). Birds made fewer errors (probes to incorrect flowers) in Phase 2 ($M \pm SE = 8.88 \pm 0.66$) than in Phase 1 (11.55 ± 0.80), but there were no differences among the array types (see Figure 2a).

Visit 1, Phase 2. If the birds were performing at chance levels, then they should have taken an average of 5.5 probes to find the rewarded location on this first visit in Phase 2. We used a Monte Carlo simulation to determine chance performance. We included the correct choice and made the assumption that birds sampled from the 10 flowers without replacement. On same-unique and different-unique arrays, birds performed better than at chance, but on the same-single array their performance was no better than chance: one-tailed, one-sample t test, same-unique, $t(10) = -2.90, p < .01$; different-unique, $t(10) = -3.18, p < .01$; same-single, $t(10) = -1.39, p < .10$ (see Figure 2b). There was no difference among the array types in the number of flowers taken to find which contained the reward in the first visit birds made to the shifted array, $F(2, 20) = 0.49, p = .62$.

A Priori Predictions

1. We predicted that if flower color pattern facilitated learning which was the rewarded flower, then the number of errors made to reach criterion in Phase 1 on the arrays in which the flowers were uniquely color patterned (same-unique and different-unique) would not be different. The number of errors would also be less on

Table 2
Mean (\pm SE) Intervisit Intervals for Phases 1 and 2 and Interphase Intervals for All Array Types in All Experiments

Array type	Phase 1 intervisit interval (min)	Interphase interval (min)	Phase 2 intervisit interval (min)
Same unique	9.99 \pm 0.78	8.58 \pm 0.82	9.98 \pm 0.98
Different unique	10.04 \pm 0.67	9.92 \pm 1.49	9.18 \pm 0.64
Same single	9.71 \pm 0.41	9.33 \pm 1.28	8.36 \pm 0.57
Change position	9.29 \pm 0.71	10.17 \pm 0.57	9.32 \pm 0.59
Rotate	10.85 \pm 0.71	9.50 \pm 0.79	10.48 \pm 0.78
3 same unique (Experiment 2)	6.04 \pm 0.32	7.50 \pm 0.34	5.71 \pm 0.34
3 different unique (Experiment 2)	5.80 \pm 0.38	10.16 \pm 2.79	6.04 \pm 0.39
3 same single	6.44 \pm 0.43	9.17 \pm 3.06	7.25 \pm 0.06
3 same unique (Experiment 3)	7.28 \pm 0.26	7.17 \pm 0.60	7.16 \pm 0.25
3 different unique (Experiment 3)	7.91 \pm 0.31	8.42 \pm 0.38	8.00 \pm 0.29
3 rearrange	7.32 \pm 0.28	7.83 \pm 0.47	7.11 \pm 0.25
3 change shape	7.14 \pm 0.28	7.75 \pm 0.48	7.72 \pm 0.25
3 change position	7.19 \pm 0.25	8.42 \pm 0.26	7.78 \pm 0.28
Neighbors	7.29 \pm 0.27		
Not neighbors	7.42 \pm 0.30		
3 change shape (Experiment 5)	6.48 \pm 0.23	11.81 \pm 1.85	6.59 \pm 0.20
3 change color and shape	7.33 \pm 0.24	10.33 \pm 1.51	7.40 \pm 0.29

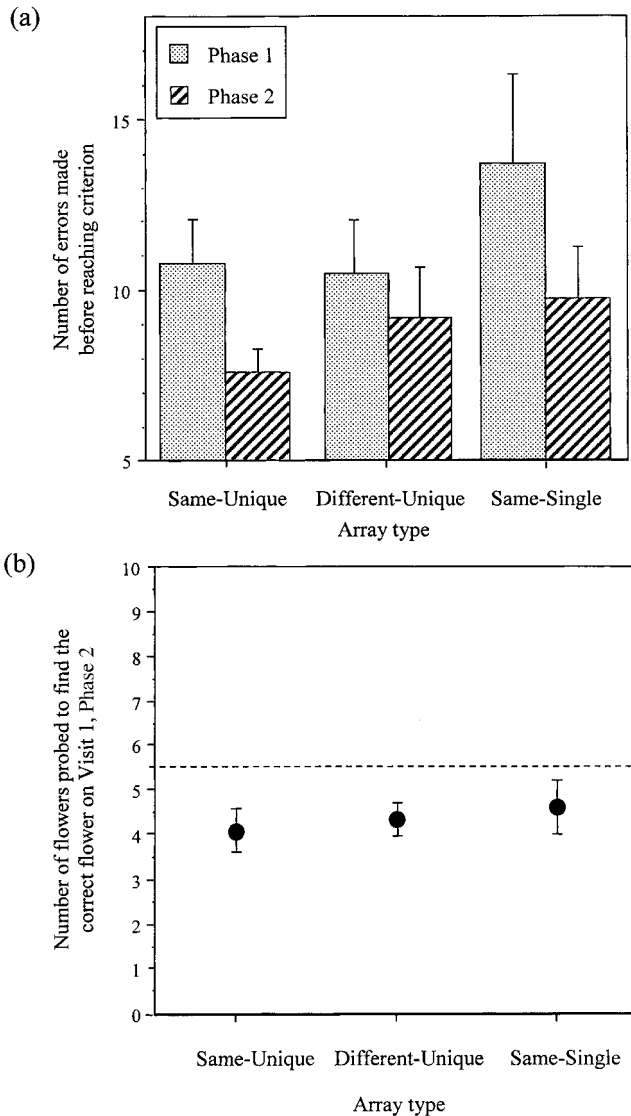


Figure 2. (a) The mean (\pm SE) number of errors made by hummingbirds in Experiment 1A when learning which flowers contained sucrose rewards following a shift and manipulation of array features. In the same-unique arrays, the flowers were uniquely patterned but were the same patterns between phases; in different-unique arrays, flowers were uniquely patterned but the patterns in Phase 2 were different from Phase 1; in same-single arrays, all of the flowers had the same color pattern. (b) The mean (\pm SE) number of flowers visited to find the correct flower in the first visit to the array of Phase 2. The dashed line denotes chance performance level (this estimate of chance includes the choice of the correct flower).

both unique arrays than on the array in which all the flowers were the same color pattern (same-single). This prediction was supported: linear contrast, $F(1, 20) = 5.19, p < .05$.

2. If either color pattern or flower position are remembered and used by the birds in Phase 2, then there should be fewer errors made before learning which flower held the reward on all the arrays. This was the case (see analysis described earlier). If, however, there was an additive effect of color and positional information, then the difference between the phases should be

greater on same-unique arrays than either of the other two arrays. As this comparison is not the one made by the overall ANOVA (that compared the three arrays separately), we tested this prediction by computing the difference in performance between the phases and then by comparing the difference among same-unique, different-unique, and same-single combined. As the difference between the phases was no better in same-unique than for the other arrays, $F(1, 10) = 0.20, p > .50$, this prediction was not supported.

3. If birds remember both color pattern and position in information in Phase 1, then there should be a disruption in performance as the birds pay attention to the new flower color patterns in Phase 2 of different-unique arrays. However, birds performed better than chance on the different-unique arrays on the first visit to the array following the shift (see analysis above). The change in color patterns on the flowers appeared not to affect learning in Phase 2 of different-unique arrays.

Discussion

In Experiment 1A, birds learned the position of a rewarded flower in an array of flowers with fewer errors when they had experience of learning the location of a rewarded flower in the same position in the same, or similar, array 2 m away. In a previous experiment (Healy & Hurly, 1998), birds learned the locations of rewarded flowers in arrays with unique color patterns, with fewer errors than when all the flowers were the same, and in Phase 1 this was also the case here. This better performance with a compound than with an elemental stimulus is also found during delayed matching-to-sample testing in songbirds (Shettleworth & Westwood, in press).

When performance relative to chance in Phase 2 was examined, it was in only the arrays in which the flowers were uniquely color patterned (same-unique and different-unique) that performance (in the first visit to the array postshift) was better than chance. The interpretation of these results is not straightforward. Better than chance performance on the same-unique arrays postshift would suggest that both the flower position and its color pattern were learned and remembered by the birds. However, the better than chance performance in Phase 2 on the different-unique arrays would suggest that birds remembered the positional information gained in Phase 1 even though the flower color patterns were different. Thus, although flower color pattern appears to play some sort of enhancing role for the learning of the flower position (same-unique and different-unique arrays learned with fewer errors than did same-single), it is not clear how well colors were remembered between phases. It is not clear whether this enhancing role is similar to that played by taste in odor conditioning or taste-mediated potentiation (e.g., see Batsell, Paschall, Gleason, & Batson, 2001; Franchina, Wright, Smith, Penn, & Soeken, 1993). However, a similar facilitation by olfactory cues on the learning of a rewarded location was found by Lavenex and Schenk (1997).

Experiment 1B

Results from Experiment 1A indicate that unique color patterns together with positional information contribute to learning, which is the rewarded flower in Phase 1. Birds seem to remember both color and position for use in Phase 2. However, when the cues were dissociated, it was not clear how well position and color

pattern were each remembered, although it appeared as if information about the flower's position might have been remembered better than color pattern cues. To examine further how well positional information is remembered, we devised two new array types for Experiment 1B. In change-position arrays, all the flowers were the same single color (i.e., without pattern), but in Phase 2 the position of the rewarded flower within the array was changed. If the birds remember the position of the rewarded flower in Phase 1 for use in Phase 2, then they may take longer to learn which is the rewarded flower than they did in Phase 1. In rotate arrays, the flowers all bore unique color patterns, but when the array was shifted for Phase 2, it was also rotated 90°. This rotation should diminish the utility of the position cues, unless the birds track the rotation perfectly. Acquisition with fewer errors in Phase 2 than in Phase 1 would indicate use of color pattern and/or positional cues. If birds made more errors before learning which was the rewarded flower, then this would indicate that birds attempted to transfer position cues to the rotated array without compensating for the rotation. Thus, in Experiment 1B we manipulated the arrays between the phases to try to manipulate the utility of memory for spatial cues in Phase 2.

In Experiment 1B, we made two predictions:

1. If the hummingbird uses the information it gained in regard to the rewarded flower's position from Phase 1 in change-position arrays when learning which was the rewarded flower in Phase 2, then it should make more errors on these arrays in Phase 2 than it did in Phase 1.
2. If the information from the flower's color pattern and/or its position of the flower with the array overrides any information concerning the array orientation, then performance following the array rotation should be better in Phase 2 than in Phase 1 on the rotate arrays.

Method

Subjects. The subjects in this experiment were the same 11 male rufous hummingbirds used in Experiment 1A. Experiment 1B followed immediately after completion of Experiment 1A, and therefore no initial training was used.

Experimental protocol. Ten flowers were laid out in change-position and rotate arrays in a manner similar to those shown in Figure 1 with one flower containing 120 μ l 20% sucrose solution and 30 cm between flowers, center to center. All 10 flowers in the change-position arrays bore the same color, whereas the 10 flowers in the rotate arrays bore unique color patterns (see Table 1). As in Experiment 1A, in Phase 1 of a trial the bird was required to visit the array and sample from the flowers until it had learned which flower contained sucrose. As in Experiment 1A, the arrays were presented in different locations inside the birds' territory. No exact location was ever re-used. Criterion level was the same as in Experiment 1A. Immediately following the last of these three criterion visits, the array was moved 2 m in one of the four main compass directions for Phase 2. This direction was counterbalanced within birds as was the order of presentation of array types (i.e., order of trials for 5 birds was change-position, rotate, rotate, change-position and for the remaining 6 birds, it was rotate, change-position, change-position, rotate). In trials with change-position arrays, the position within the array of the rewarded flower was changed between phases. This rewarded flower was filled with sucrose, and the original flower was filled with water as were the remaining eight flowers. In trials with rotate arrays, the array was rotated 90° clockwise or counterclockwise (each direction once for each bird). The position of the rewarded flower and the flower color patterns remained as in Phase 1. The number and position of flowers probed were recorded until the bird reached the crite-

rium used in Phase 1. The trial ended at this point. Each bird completed two trials of each kind of array, a total of four trials per bird. The flowers used were unique to each trial and were not those used in Experiment 1A. Intervisit and interphase intervals are presented in Table 2.

Results

Performance was assessed in the same way as in Experiment 1A. There was no difference in the number of errors made before reaching criterion between the array types, $F(1, 10) = 2.89, p > .10$; no difference between the phases, $F(1, 10) = 0.17, p > .50$; and the interaction between the two main effects was not significant, $F(1, 10) = 0.05, p > .50$. Criterion was reached with fewer errors in rotate arrays (8.25 ± 0.29) than in change-position arrays (10.77 ± 0.58), but there was no difference between the phases for either array type in the number of errors made before reaching criterion (see Figure 3a).

There was a significant difference between the array types in the number of errors made in the first visit of Phase 2 before the bird located the rewarded flower: paired t test, $t(10) = 2.25, p < .05$ (see Figure 3b). Performance was better than chance on the first visit of Phase 2 on rotate arrays: one-sample t test, $t(10) = -1.95, p < .05$, but not on change-position arrays (see Figure 3b).

A Priori Predictions

1. Errors made before reaching criterion in Phase 2 on change-position arrays were no greater than those made in Phase 1 (see analysis described earlier). Performance was also no different from chance in the first visit to the array postshift. Learning which was the rewarded flower in Phase 1 seems to have neither helped nor hindered the birds in learning which was the rewarded flower in Phase 2. Birds appear to have treated the array in Phase 2 as a new array, just as they treated same-single arrays in Experiment 1A.

2. Performance on rotate arrays following the array shift was no better in Phase 2 than in Phase 1: repeated measures ANOVA, $F(1, 10) = 0.07, p > .50$. However, birds' performance on the first visit to the array in Phase 2 was better than expected by chance. It appears that information gained in Phase 1 was of some use in Phase 2. Rotation of the array appeared to only partially disrupt performance.

Discussion

In Experiment 1A, birds appeared to have remembered information about both the color pattern and position of the rewarded flower learned in Phase 1 to learn which flower contained the reward, with fewer errors in Phase 1. In Experiment 1B, we made positional information useless, and possibly misleading, by changing the position of the rewarded flower in Phase 2 of the change-position array. This manipulation did not appear to impede learning in Phase 2. Thus, memory for the position of the flower in the array in Phase 1 appears quite easily overridden. Although birds performed better than at chance on the first visit to rotate array postshift, they did not learn which was the rewarded flower with fewer errors in Phase 2 than they did in Phase 1. It is not possible to determine whether the accuracy of the first visit was based on memory for the flower's position in the array or for its color pattern. It is also not clear why there is a discrepancy between the two measures of performance. The Phase 2 performance in both

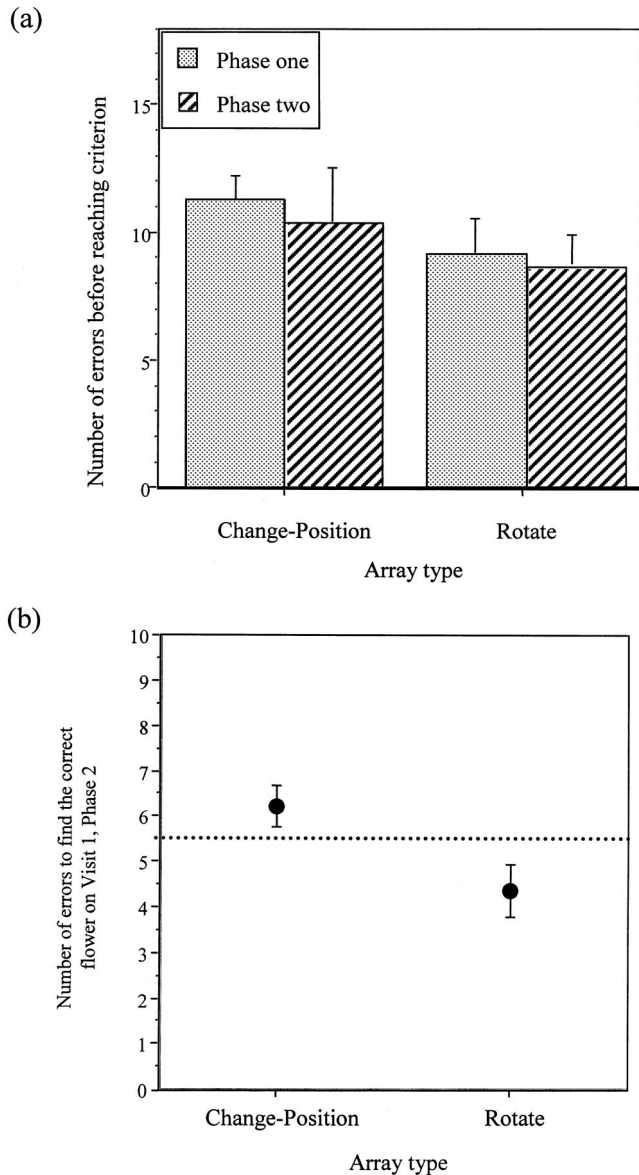


Figure 3. (a) The mean (\pm SE) number of errors made by hummingbirds in Experiment 1B when learning which flowers contained sucrose rewards following a shift and manipulation of array features in change-position arrays. All of the flowers had the same pattern in both phases, but the location of the rewarded flower changed between the phases. In rotate arrays, flowers were uniquely patterned and were unchanged between the phases, but the array was rotated 90° after Phase 1. (b) The mean (\pm SE) number of errors made before finding the correct flower in the first visit of Phase 2. The dashed line denotes chance performance level (this estimate of chance includes the choice of the correct flower).

arrays would suggest that even if birds do remember information regarding the rewarded flower from Phase 1, they very quickly ignore it.

Experiment 2

In Experiment 1, we investigated whether information concerning a single rewarded flower (position and/or color pattern) was

learned in one array and then remembered for use in a second array set in a new location. The hummingbirds appeared to use at least some of this information while searching for the rewarded flower in the second array, as they learned the new flower with fewer errors than they made on the first array. Although this enhanced learning seemed to depend most on position cues, color pattern information also seemed to be learned and remembered.

Some of the flowers rufous hummingbirds feed on are single and others are clumped together on the same inflorescence or bush. It is possible, then, that birds may learn about multiple rewarded flowers and transfer this information to a new patch of flowers/bush/array. In Experiment 2, we wanted to determine whether the results we found in Experiment 1A were specific to the learning of a single rewarded flower or whether birds would respond differently with multiple flowers. If, for example, multiple rewarded flowers are learned with respect to their spatial relationship to each other, then position information may become even more important than when used to remember the location of a single flower. If this was the case, then it was not clear whether the minor facilitatory role we found for color on memory for the rewarded flower in Experiments 1A and 1B would be observed here. We presented hummingbirds with arrays similar to those from Experiments 1 but with three flowers rewarded rather than one. Arrays 3-same-unique and 3-different-unique contained 10 uniquely color patterned flowers, and 3-same-single contained 10 flowers of all the same color pattern. Once the birds had learned which flowers contained reward, the arrays were moved the same distance and manipulated just as were the arrays in Experiment 1A (also see Table 1).

On the basis of the outcomes of the manipulations in Experiment 1A, in this experiment we made the following two predictions:

1. If flower color pattern facilitates the learning of the rewarded flower, then the number of errors made before reaching criterion in Phase 1 on 3-same-unique and 3-different-unique arrays would be fewer than those made on 3-same-single arrays.
2. If variation in flower color in some way facilitates the memory as well as the learning of the positions of the rewarded flowers, then the difference in errors between the phases should be greater on 3-same-unique arrays than on 3-different-unique arrays.

Method

Subjects. The 7 male rufous hummingbirds used as subjects in Experiment 2 had all been subjects in Experiments 1A and 1B, therefore we did not carry out any initial training. There were 14.2 ± 3.3 days between experiments.

Experimental protocol. Ten flowers were laid out in the arrays as described in Experiment 1, with three flowers containing $30 \mu\text{l}$ 20% sucrose solution and 30 cm between flowers, center to center. There were two different kinds of arrays: (a) 3-same-unique and 3-different-unique arrays, with all 10 flowers having unique color patterns; (b) 3-same-single arrays, with all 10 flowers having the same color pattern (color patterns were unique to each trial). The rewarded flowers were assigned such that they were contiguous nearest neighbors. As in the previous experiments, the 10th flower, the 4th flower at the end of the middle row, was never used as a rewarded flower. Also as previously noted, in Phase 1 of a trial the male hummingbird was required to visit the array and sample from the flowers until it had learned which contained sucrose. Following the first visit to the array, we refilled the flowers the bird had drained of sucrose with $30 \mu\text{l}$ sucrose solution, and we filled the remaining 7 flowers with water. The hummingbirds were considered to have learned the locations of

the rewarded flowers when they had made three consecutive visits on which the percentage of correct flowers visited was 75% or better. As in Experiments 1A and 1B, immediately following the last of these three criterion visits, the array was moved 2 m in one of the four main compass directions (determined as described previously). In trials with the 3-different-unique array, all of the flowers were replaced with new unique flowers, but the positions within the array of the rewarded flowers remained the same. The rewarded flowers were refilled with sucrose, and water remained in the other 7 flowers. Phase 2 of a trial began when the bird returned to the array. The number and position of flowers visited were recorded until the birds reached the criterion used in Phase 1. The trial ended at this point. Each bird completed three trials of each kind of array, with a total of nine trials per bird. Flowers were unique to each trial but had been used in Experiment 1A.

Results

Performance in this experiment was assessed by comparing the total number of errors birds made before reaching criterion in each phase, using repeated measures ANOVAs. We also addressed our a priori predictions.

There was a significant difference among the array types in the number of errors made before criterion was reached, $F(2, 12) = 8.64, p < .01$; a significant difference between the phases, $F(1, 6) = 32.0, p < .01$; but the interaction between the two main effects was not significant, $F(2, 12) = 0.15, p = .86$ (see Figure 4).

Linear contrasts were used to investigate the differences among the array types. In Phase 1, there were no significant differences in the pairwise comparisons, but the hummingbirds tended to make fewer errors in 3-same-unique and 3-different-unique arrays than in 3-same-single arrays: 3-same-unique versus 3-different-unique, $F(1, 6) = 0.07, p = .82$; 3-same-unique versus 3-same-single, $F(1,$

$6) = 4.99, p = .07$; 3-different-unique versus 3-same-single, $F(1, 6) = 5.67, p = .06$. In Phase 2, there was a significant difference in the number of errors between 3-same-unique and 3-same-single arrays and a close to significant difference between the 3-different-unique and 3-same-single arrays in the number of errors made: 3-same-unique versus 3-same-single, $F(1, 6) = 8.69, p = .03$; 3-same-unique versus 3-different-unique, $F(1, 6) = 2.64, p = .16$; 3-different-unique versus 3-same-single, $F(1, 6) = 5.87, p = .05$.

A Priori Predictions

1. The prediction that the number of errors made to reach criterion in Phase 1 on 3-same-unique and 3-different-unique arrays would be fewer than those made on 3-same-single arrays was supported: linear contrast, $F(1, 12) = 11.32, p < .01$. This result supports the results from Experiments 1A and 1B that flower color pattern is used to learn which are the rewarded flowers.

2. If variation in flower color in some way facilitates the memory as well as the learning of the positions of the rewarded flowers, then the difference in errors between the phases should be greater on the 3-same-unique arrays than on the 3-different-unique arrays. This prediction was not supported: repeated measures ANOVA, $F(1, 6) = 0.35, p > .50$.

Discussion

The results from Experiment 2 are consistent with those found in Experiments 1A and 1B: Both cues are learned and remembered for use in Phase 2 and seemingly have an additive effect on performance. However, the memory for color patterns appears to be insubstantial as there was no difference between the two arrays that had flowers of varying color patterns. We had speculated that presenting the birds with three rewarded flowers in an array rather than one might alter the relative preference the birds had for the two cue types, but this did not appear to be the case. It also seemed to be the case that birds learned about three rewarded flowers with much the same ease as learning about one (compare the data in Figures 2 and 4).

Experiment 3

In Experiment 2, it was clear that both flower color pattern and flower position within the array were salient cues that were used to learn the locations of rewarded flowers. However, information about color pattern appeared to be used when learning which was the rewarded flower, but evidence for the color pattern being remembered was slim. It is not clear whether hummingbirds did not remember the color pattern information or whether they merely preferred to rely on positional information. From the results of other experiments, the apparent precedence of spatial information over color information is not that surprising (e.g., Experiment 1, Hurly & Healy, 1996). However, in light of data showing that these birds can learn color-reward associations (e.g., Experiment 2, Hurly & Healy, 1996) we wanted to make a greater effort to determine under what circumstances color information can be shown to be remembered. To do this we presented birds with a series of arrays similar in kind to those in Experiment 2 but in which the color information learned in Phase 1 varied in value among the arrays in Phase 2 (see Figure 5).

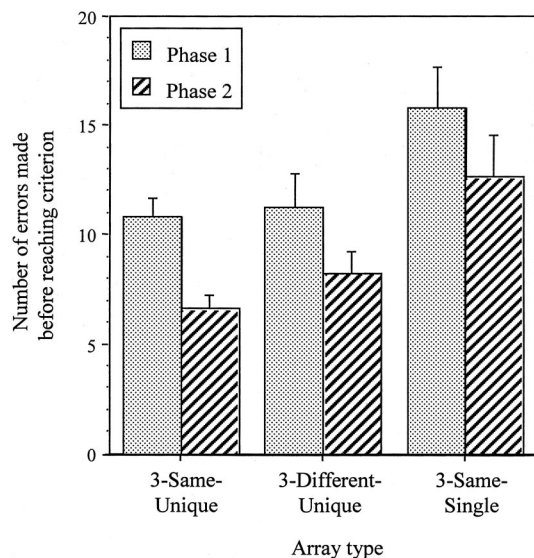


Figure 4. The mean (\pm SE) number of errors made before reaching criterion in each of the two phases in Experiment 2. In 3-same-unique arrays, all of the flowers were uniquely patterned and retained the same pattern and position in Phase 2 as in Phase 1. In the 3-different-unique arrays, the flowers were uniquely patterned in both phases, but the patterns differed between the phases. In 3-same-single arrays, all of the flowers bore the same pattern both within and between phases.

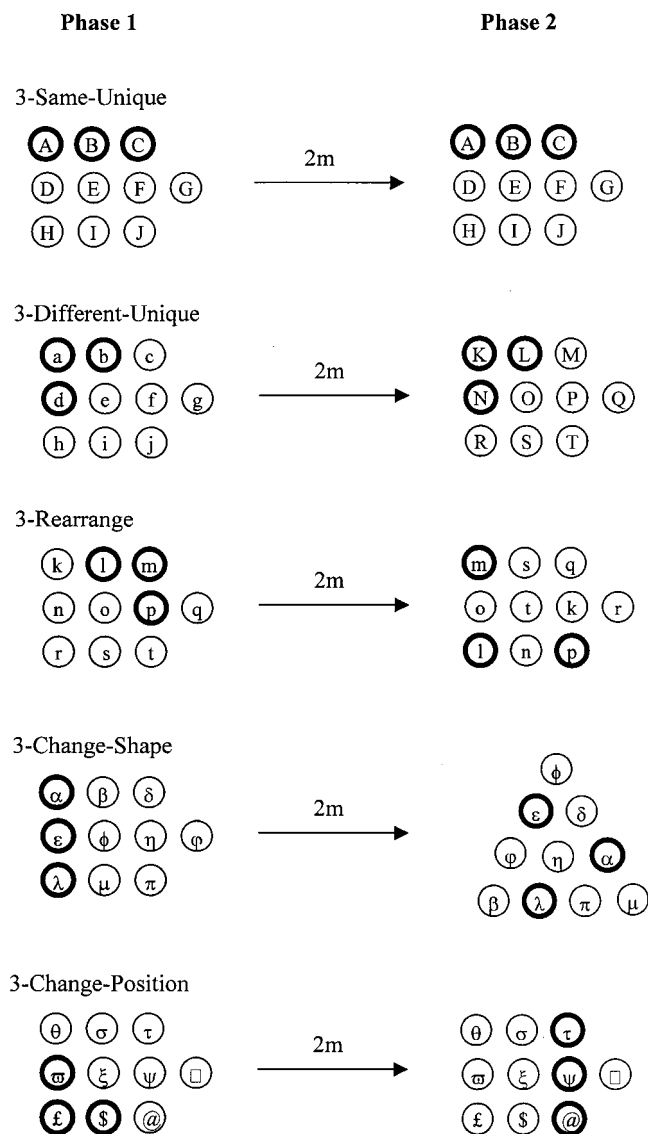


Figure 5. A schematic of the experimental design used in Experiment 3 (and from which the other subsequent experiments follow). Each circle represents a flower, with the boldface black circles representing flowers rewarded with sucrose solution. Flowers had unique color patterns in all arrays. Each array was moved 2 m between Phases 1 and 2 and may have been manipulated in other ways as well. In the 3-same-unique arrays, the positions and color patterns of all flowers were maintained. In the 3-different-unique arrays, position remained the same, but all flowers were given new unique color patterns. In the 3-rearrange arrays, all color patterns were maintained, but flower position was scrambled. In the 3-change-shape arrays, all color patterns were maintained, but flower position was scrambled as the shape of the array was changed. In the 3-change-position arrays, the positions and color patterns were maintained, but different flowers were rewarded. The letters and symbols show systematically that the flowers bore unique color patterns; they do not designate any particular color or pattern.

We presented birds with 5 kinds of arrays, all of which had 10 uniquely color-patterned flowers, 3 of which were rewarded in Phase 1. Once the birds had learned which flowers held the reward,

we shifted the array and they were faced with a Phase 2 of five different types:

1. 3-same-unique. This array was the same as that described in Experiment 2, and it acted as a control array, as both position and color information was the same in both phases. The number of errors made before learning which flowers contained reward in Phase 2 could be reliably expected to be significantly lower than in Phase 1.

2. 3-different-unique. This array was also an array type as used in Experiment 2 and was included here to make within-experiment comparisons of performance with the other four array types. In this array, position remains constant while color patterns change.

3. 3-rearrange. In this array, the rewarded flowers had the same color patterns as in Phase 1 but were now in different positions in the array. In this array, color patterns remain constant while positions change.

4. 3-change-shape. In Phase 2, the shape of the array was changed to that of a triangle, but all of the colors of the flowers remained the same as in Phase 1. Flowers did not have the same neighbors as in Phase 1. In this array, then, it was not possible to use information learned about flower position in Phase 1 when learning which were the rewarded flowers in Phase 2.

5. 3-change-positions. The color patterns of the flowers in this array remained the same between the phases, but the positions of the three rewarded flowers were changed. As in Experiment 1B, neither kind of information is useful in Phase 2 in this array.

On the basis of the results from Experiments 1 and 2, we made the following four a priori predictions:

1. If flower color pattern facilitates both the learning and memory for the positions of rewarded flowers, then the reduction in errors between the phases would be greater on same-unique than on 3-different-unique arrays.

2. If birds preferentially use or remember flower position better than color pattern, then the reduction in errors between the phases would be greater on 3-different-unique arrays than on 3-rearrange arrays.

3. If information about color pattern learned in Phase 1 is not remembered for use in Phase 2, then there should be no reductions in the number of errors in Phase 2 relative to the number made in Phase 1 of 3-change-shape arrays.

4. Birds quickly learn to ignore both color and position information learned previously. If birds are presented with the same array in Phase 2 as they were in Phase 1 but in which three different flowers contained the reward (3-change-position), then performance in Phase 2 will be no worse than in Phase 1.

Method

Subjects. Eight experimentally naive, male rufous hummingbirds were used as subjects in Experiment 3. All individuals were marked as described in Experiment 1. Trials were run between 0800 and 1930 Mountain Standard Time from May through July 1998.

Initial training. Initial training was carried out in the same manner as was described in Experiment 1A.

Experimental protocol. Ten flowers were laid out in arrays as described above and in Figure 5 (also see Table 1). The arrays were of the same shape as described in Experiments 1A and 1B with 3 neighboring flowers containing 30 μ l 20% sucrose solution and 30 cm between flowers, center to center. The remaining 7 flowers held water. In Phase 1 of all five types of trial the 10 flowers had unique color patterns. The experimental

protocol was the same as that for Experiment 2 with the same criterion level to be achieved. It was in Phase 2 (after a 2-m shift of the array) that the five trial types were distinguished: (a) with the 3-same-unique array, the same flowers in the same array positions were rewarded; (b) with the 3-different-unique array, the positions of the rewarded flowers remained the same, but all color patterns were replaced with unique previously unseen color patterns; (c) with the 3-rearrange array, the array had the same flowers as in Phase 1, but their positions in the array were scrambled so that each occupied a new position. The rewarded flowers had the same color patterns as in Phase 1 but were now in different positions and were not next to each other; (d) with the 3-change-shape array, the array had the same flowers as in Phase 1, but the shape of the array was an equilateral triangle (flowers all 30 cm apart) in which the positions of the flowers were mixed so that they were not next to previous neighbors. The color patterns of the rewarded flowers were the same as in Phase 1; (e) with the 3-change-positions array, the array had the same flowers as in Phase 1, but three different flowers were rewarded. The flowers were unique to each trial.

Birds were given 2 trials of each array type, a total of 10 trials per bird. The order of trial types was pseudorandomized with birds, with the restriction that a bird received all 5 trial types before having the first of the second set of trials.

Results

As in the previous experiments, performance was assessed by measuring the number of errors made before reaching criterion on each of the array types. We compared the number of errors for each array type, using repeated-measures ANOVAs. There was no difference among the array types in the number of errors made, $F(4, 28) = 0.27, p > .50$; a significant difference between phases, $F(1, 7) = 14.27, p < .01$; and a significant interaction between array type and phase, $F(4, 28) = 3.37, p < .05$ (see Figure 6).

Repeated-measures ANOVAs were used to investigate further the difference between the phases for each array type. Birds made significantly fewer errors in Phase 2 for 3-same-unique and 3-different-unique arrays: 3-same-unique, $F(1, 7) = 8.85, p < .05$; 3-different-unique, $F(1, 7) = 7.32, p < .05$; but not for the other three arrays, 3-rearrange, 3-change-positions, and 3-change-shape, $0.15 < F < 2.39, 0.17 < p < .71$ (see Figure 6). This difference among the arrays seems to have produced the interaction term in the analysis above.

A Priori Predictions

1. If flower color pattern facilitates learning as well as memory for the positions of rewarded flowers, then the reduction in errors between the phases would be greater on 3-same-unique than on 3-different-unique arrays. This prediction was not supported: paired t test, $t(7) = 0.72, p = .50$.

2. If birds preferentially use or remember flower position better than color pattern, then the reduction in errors between the phases would be greater on 3-different-unique arrays than on 3-rearrange arrays. This prediction was supported: paired t test, $t(7) = 2.48, p < .05$.

3. If information about color pattern learned in Phase 1 is not remembered for use in Phase 2, then there should be no reductions in the number of errors in Phase 2 relative to the number made in Phase 1 of 3-change-shape arrays. This prediction was supported: linear contrast, $F(1, 28) = 1.32, p > .20$.

4. If birds quickly learn to ignore both color and position information learned previously, then when presented with the same

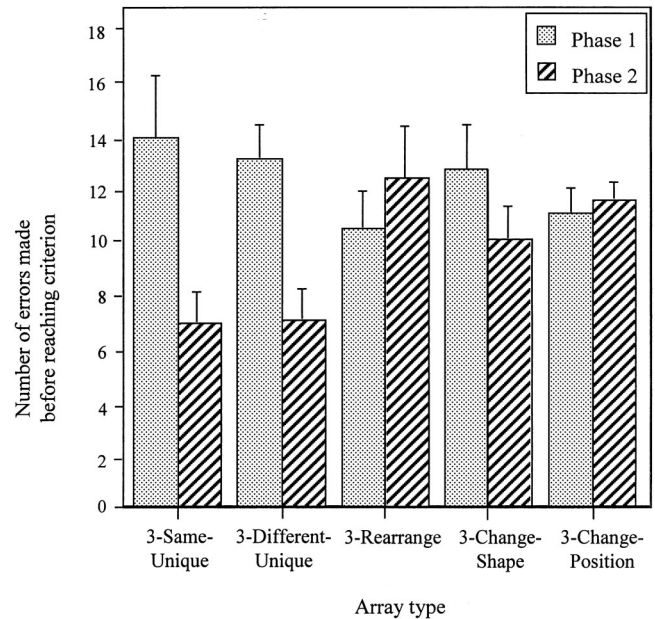


Figure 6. The mean (\pm SE) number of errors made before reaching criterion in Phases 1 and 2 of Experiment 3. In Phase 1, all flowers had unique color patterns. In Phase 2, flower color patterns and positions were manipulated in the following ways: In 3-same-unique arrays, the positions and color patterns of all flowers were maintained. In 3-different-unique arrays, position remained the same, but all flowers were given new unique color patterns. In 3-rearrange arrays, all color patterns were maintained, but flower position was scrambled. In 3-change-shape arrays, all color patterns were maintained, but flower position was scrambled as the shape of the array was changed. In 3-change-position arrays, the positions and color patterns were maintained, but different flowers were rewarded.

array in Phase 2 as in Phase 1 but in which three different flowers contain the reward (3-change-positions), their performance on Phase 2 should be no worse than on Phase 1. This prediction was supported: linear contrast, $F(1, 28) = 0.23, p > .60$. If anything, the trend was to an increase in errors, which may have been caused by birds that attempted to rely on position cues, which were irrelevant or misleading.

Discussion

In Experiment 3, we attempted to determine under which conditions birds can be shown to have remembered individual flower color pattern. We could find no convincing evidence that birds did remember color patterns when they encountered the arrays post-shift. As performance on 3-different-unique arrays shows (and as we found in Experiments 1 and 2), if the position of the rewarded flowers remained constant, the birds showed a similar decline in error making from Phase 1 to 2 as they did on 3-same-unique arrays (see Figure 6). The results from the other three arrays also concur with this outcome: If flower positions are altered in Phase 2, then birds appear to perform as if they are encountering an entirely new array. Again the evidence seems to be that color plays a facilitatory role in learning a position but is either not well remembered or easily ignored.

Experiment 4

One possible reason for the birds to prefer to use the position rather than the color pattern of rewarded flowers in an array might be because neighboring rewarded flowers could be remembered as a simple flight pattern or the bird may “chunk” the three flowers together (Dallal & Meck, 1990). The individual color patterns of the three flowers, on the other hand, may require more attention to detail. As the birds fly into the arrays very quickly and spend only 3 s–10 s on each visit to an array it would seem a little easier to encode the relative positions of flowers rather than their individual visual features. If the birds do find it easier to encode flowers by their relative positions, then we would predict that the pattern formed by three nearest neighbor flowers (i.e., when rewarded flowers are arranged contiguously) is simpler and, thus, easier to learn than when the rewarded flowers are distributed more patchily within the array. In this experiment, we used arrays similar to those in the previous experiments. In arrays designated “neighbors” the three rewarded flowers were nearest neighbors, whereas in the other arrays (“not-neighbors”) they were scattered around the array so that no rewarded flower was next to another rewarded flower. We predicted that birds would learn which were the rewarded flowers in neighbor arrays with fewer errors than in not-neighbor arrays.

Method

Subjects. The 5 male rufous hummingbirds used as subjects in this experiment had all been subjects in Experiment 3, therefore we did not carry out any initial training. Subjects were chosen by their availability for the experiment, not based on performance in Experiment 3.

Experimental protocol. Ten flowers were laid out in neighbor and not-neighbor arrays with 3 flowers containing 30 μ l 20% sucrose solution, the remaining 7 containing water and with 30 cm between flowers, center to center. In both types of trial, the 10 flowers had unique color patterns but in neighbor arrays the reward flowers occupied contiguous positions, although they were not necessarily all in the same row or column of the array (i.e., flowers could be arranged such that the rewarded flowers formed a 90° angle). In not-neighbor arrays, the rewarded flowers were separated from each other by at least one water-containing flower. Birds had to reach the same criterion level for flower visits as in Experiments 2 and 3 in both phases. Each bird was given three trials of each array type, given in alternate sequence, a total of six trials each. The first trial for three of the birds was a neighbor trial, and the other two birds received a not-neighbor trial first. The flowers used were unique to each trial, and birds had not seen them before.

Results

As in the previous experiments, we assessed performance in Experiment 4 by counting the number of incorrect flowers probed before reaching criterion and compared between the array types by using repeated-measures ANOVAs. Birds made fewer errors on neighbor than not-neighbor arrays before reaching criterion, $F(1, 4) = 9.47, p < .05$ (neighbor arrays = $11.48 M \pm 2.35 SE$; not-neighbor arrays = $15.76 M \pm 2.22 SE$).

Discussion

In Experiment 4, hummingbirds were presented with flower arrays in which the three rewarded flowers were either contiguous

neighbors or not. We predicted that the birds would learn with fewer errors the positions of flowers when the flowers were contiguous. This was indeed the case. We propose that this is because the flight pattern connecting these neighboring flowers was simpler than that connecting more dispersed flowers. Although it might be the case that we are reinforcing a natural tendency to visit adjacent flowers, it may also be that the birds are able to “chunk” the neighboring flowers more easily, and therefore, remembering three flowers together is easier than recalling three spatially disparate flowers (Dallal & Meck, 1990).

Experiment 5

The results from the first three experiments all suggest that once hummingbirds have learned the positions of the rewarded flowers in the array this is largely the only information they use when presented with a new but similar array. Does this mean the birds either do not remember or do not use the flower color pattern information at all? The results from the 3-change-shape arrays seen in Figure 6 in Experiment 3 might suggest that the birds can remember and use color pattern to some slight but insignificant degree (the number of errors tended to be fewer in the second phase). Perhaps the birds became so used to the shape of the arrays used in these previous experiments (the square with the 10th flower at the end of the middle row) that they learned across the experiment to give more weighting to the positional information. After all, hummingbirds can learn information about flower color (e.g., George, 1980; Hurly & Healy, 1996; Meléndez-Ackerman et al., 1997; Stiles, 1976). In this final experiment, we attempted to determine more definitively whether they do use information about flower color pattern when presented with new arrays. To do this, we removed the possible confounding effects of array shape from the previous experiment by presenting the birds first with arrays of different shape in Phase 1 and then changing the shape in Phase 2. One of the array shapes was the same as described for the previous experiments, and in the other, the flowers were arranged in an equilateral triangle with four flowers along each side. In one array (3-change-shape), the flowers' patterns are used for both Phase 1 and Phase 2. This array was one of those used in Experiment 3. In the other array (3-change-color-and-shape), new unique flowers were presented in Phase 2. We predicted that if birds had no opportunity to utilize position cues between the phases, then we would see a reduction in errors made in learning in Phase 2 of 3-change-shape arrays but no reduction on 3-change-color-and-shape. In an effort to reduce the utility of position cues in Phase 1, rewarded flowers were not near neighbors.

Method

Subjects. Ten male rufous hummingbirds were used as subjects in Experiment 5. Four birds, which were used in Experiment 3, were tested in 1998, and 6 experimentally naive birds were tested in 1999. All individuals were marked as described in Experiment 1A. Trials were run between 0800 and 1930 Mountain Standard Time from June through July 1998 and May through June 1999.

Initial training. Naive hummingbirds were trained as described in Experiment 1A.

Experimental protocol. Birds were presented with an array of 10 unique flowers, 3 of which were rewarded with sucrose as in the previous experiments. The remaining 7 flowers held water. The array was either the

shape used in the previous experiments or an equilateral triangle (see Table 1, Figure 5). In either array, the rewarded flowers were not near neighbors. Once the bird had reached the criterion level described in Experiment 2, the array was moved to a location 2 m distant. In Phase 2, the flowers in 3-change-shape arrays were the same flowers as those used in Phase 1, whereas in 3-change-color-and-shape arrays the flowers were new and uniquely color patterned. For both arrays in Phase 2, the array shape was changed either to a triangle or to the rectangular array, such that it differed from the array shape used in Phase 1. There was no relationship between reward positions in Phase 1 and Phase 2. Birds were given three trials of each array type, six trials in total. The flowers used were unique to each trial but had been used in Experiment 3 (therefore seen previously by 4 of the 10 birds).

Results

Before examining performance on the two differing array types, we determined that there was no effect of array shape on performance (errors before reaching criterion) in Phase 1, $F(1, 9) = 3.35$, $p > .10$. We examined performance as in the previous experiments by measuring the number of errors birds made before reaching criterion. We used repeated measures ANOVAs to compare between the array types. There was no significant difference between the array types, $F(1, 9) = 0.93$, $p > .10$; a significant difference between the phases, $F(1, 9) = 17.56$, $p < .01$; and the interaction between the two main effects was not quite significant, $F(1, 9) = 4.60$, $p = .06$ (see Figure 7). This suggested that birds did perform better in Phase 2, given Phase 1 on the 3-change-shape arrays than on the 3-change-color-and-shape arrays. We compared the performance in Phase 2 between the two array types, and birds did perform significantly better on 3-change-shape arrays than 3-change-color-and-shape arrays, $F(1, 9) = 10.45$, $p = .01$. We also carried out linear contrasts to test whether there was a signif-

icant change between the phases for each array type, and the difference was significant only for the 3-change-shape arrays, $F(1, 9) = 22.65$, $p < .01$, not for the 3-change-color-and-shape arrays, $F(1, 9) = 2.98$, $p > .10$.

Discussion

In this experiment, the hummingbirds could not use position information from Phase 1 when learning which flowers were rewarded in Phase 2; rewarded flower color pattern was preserved in 3-change-shape arrays, but not in 3-change-color-and-shape arrays. From the birds' performance on the two array types, it appears that the birds can use flower color cues to improve learning in the second array, but only when all possibility of using spatial information is removed.

General Discussion

We investigated how hummingbirds use color pattern and flower position information while learning to distinguish between rewarded and unrewarded flowers in an array of 10 flowers. Hummingbirds learned the rewarded flowers in a new nearby array with fewer errors when the rewarded flowers occupied the same positions as in the first array. We found very little evidence to show that the birds used information about the flowers' color patterns learned from the first array when learning which flowers were rewarded in the second array. Furthermore, if the spatial information was available, the color patterns on the flowers could be changed without affecting the birds' performance. Information about flower position seemed to have its greatest effect when rewarded flowers were contiguous within the array: Birds made more errors before learning which flowers were rewarded when those flowers were dispersed around the array. It was not very clear whether color pattern was remembered from one phase to another, but it did facilitate learning the rewarded flowers within an array. Birds made fewer errors before reaching criterion performance when each flower had a unique color than when they were identical. The final experiment, in which we tried to remove any value to the spatial information, provided some evidence for the memory of color pattern cues from one array to another. We conclude that rufous hummingbirds have a very strong preference for using information about the positions of rewarded flowers in arrays over their individual color patterns. Variation in color pattern appears to facilitate initial learning but then spatial information takes precedence. This striking preference for spatial information over color cues has been demonstrated in comparisons of cue use between food storing and nonstoring birds: Food stors prefer spatial cues whereas nonstors have no preference (e.g., Brodbeck, 1994; Clayton & Krebs, 1994). This preference has been considered to be associated with both the extra demand for spatial memory required for retrieval of many caches and the enlargement of the hippocampus seen in food stors. Nothing is known about the relative size of the hippocampus in these hummingbirds, but we have proposed that these birds may be faced with the problem of remembering which flowers they have visited and when, through the course of the day, a not dissimilar problem to that faced by food stors having to remember sites in which they have stored food.

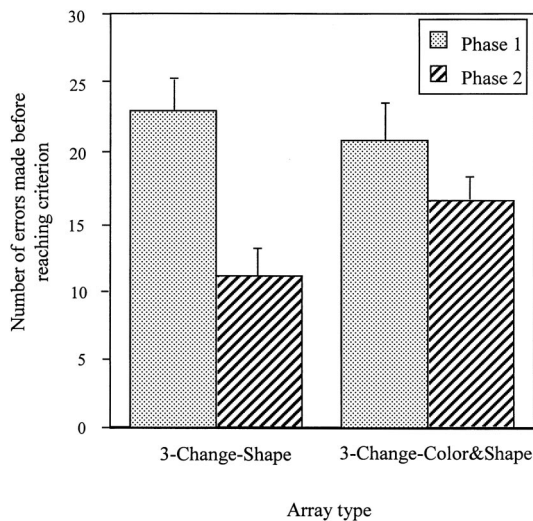


Figure 7. The mean (\pm SE) number of errors made before reaching criterion in Phases 1 and 2 of Experiment 5. Arrays were changed between the rectangular and triangular shapes to eliminate the possibility of relative position cues indicating the rewarded flowers. In the 3-change-shape arrays, all flowers had unique color pattern cues and only these cues indicated the rewarded flowers in Phase 2. In 3-change-color-and-shape arrays, all flowers had new unique color patterns, such that there was no useful information regarding the reward flowers available in Phase 2.

Investigating the cognitive mechanisms underpinning navigation often involves determining which cues the animals are using (see reviews in Healy, 1998). There is, for example, a wealth of data concerning the use of intramaze versus extramaze cues with the conclusion sometimes being fundamental (e.g., use of reliable cues, Biegler & Morris, 1996), but more often the conclusion is specific to the testing environment (see Cook, 1993). In the experiments described here, we wanted to determine the relative contribution of position cues and color pattern cues to hummingbirds learning which flowers in an array were rewarded. There were two reasons for this. First, the literature contains conflicting evidence on the use of spatial pattern cues by hummingbirds. Sutherland and Gass (1995) showed that rufous hummingbirds were able to learn positions of rewarded feeders in arrays of 64 feeders separated by 11 cm. Learning occurred more quickly when the feeders were arranged in simple patterns than when the patterns were complex. The ability to learn such small-scale patterns of reward might be useful in nature if pattern in rewarded flowers within or between inflorescences were repeated locally within a plant species as it seems to be in some of the flowers pollinated by the Hymenoptera: On most vertical inflorescences, lower flowers open before upper flowers and, thus, should contain more nectar (Pyke, 1978). This spatial patterning has resulted in predictable movement rules used by bees when foraging on these flowers: They begin at the bottom of such inflorescences and move upward. Such patterning of flowers has not been reported for species used extensively by hummingbirds, such as scarlet gilia (*Ipomopsis aggregata*), and hummingbirds do not appear to use movement rules in foraging as seen in the Hymenoptera (Hainsworth, Mercier, & Wolf, 1983; Pyke, 1978). At this stage, then, demonstrating that the rufous hummingbirds pay attention to, remember, and use information about rewarded flower positions when presented with a similar context, has no obvious ecological corollary, just as demonstrations of cue use in the laboratory may also bear little or no relation to the importance or use of such cues by animals in the field.

The second reason for studying the cues used by foraging hummingbirds concerns confusion over the role of color in choosing flowers to probe for nectar. When color pattern signals differential reward, it may play a major role in the selection of novel flowers. The use of color pattern in this fashion may have led to the misconception that hummingbirds inherently prefer the color red, when they may have actually learned a general rule about the profitability of red flowers because many hummingbird-pollinated flowers seem to have converged on the color red. Goldsmith and Goldsmith (1979) suggested that red is the color least likely to attract Hymenopteran pollinators, and thus reduced interspecific competition might increase the value of red flowers to hummingbirds (but see Chittka & Waser, 1997). Our experiments here show that hummingbirds can use flower color patterns alone in learning about the value of flowers within an array, but they also show that position cues take precedence over color pattern cues. It makes intuitive sense that color would be useful to both birds and plants during detection of and learning about new flowers. However, once the characteristics of particular flower species have been learned (e.g., typical nectar content and concentration), the way the bird would discriminate between individual flowers of the same species is through their spatial location–position. The striking preference for using position information rather than flower color

pattern when learning about the flowers in the second array seems very likely to be due, at least in part, to the relative salience of the cues provided. Our flowers are largely two dimensional in their visual aspects, and although we assume it highly likely that the birds can see and differentiate between the flowers from a distance as they always flew into the arrays from above, real flowers are three-dimensional and their color is likely to be discriminable from greater distances than the flowers we used. Our flowers were also patterned, rather than of single colors, but then most natural flowers are of more than one color. However, we still feel that the order of cue preference that we have shown here is likely to be reflective of a real cue preference for several reasons. First, location or position cues are more reliable than are color cues. Flowers are likely to change their visual characteristics over time through aging and damage, but they do not move. Second, flower color patterns were salient. The birds could obviously distinguish amongst the flowers on the basis of their visual features, and they used this information to learn and to remember which flowers contained rewards (results from Experiments 1A and 2; Healy & Hurly, 1998). Third, experiments by others who used rewarded feeders differing in visual features in three dimensions have also found a preference for spatial over color cues (e.g., Miller et al., 1985). Finally, in all cases prior to the experiments, our birds were trained with flowers of a single color that were moved small distances between each visit. The relevant information between visits was, therefore, the color and not the location of the flower. Training, thus, might be expected to have enhanced preference for using color pattern cues in the experiment, and if this was the case, then, we might have underestimated the role of spatial information.

It is difficult to determine whether the preference the birds showed for the spatial arrangement of flowers over their individual identities is different from cue preferences in other animals. For example, Greene and Cook (1997) tested rats with configurations of landmarks that changed in visual identity, geometry, or both. They also switched positions of the landmarks. All of these manipulations had an immediate effect on the choice efficiency of the rats. On the other hand, Benhamou and Poucet (1998) found that when rats had to pinpoint a location by using three landmarks, they preferred to use geometric information rather than the featural information provided by the landmarks, each of which could be discriminated by the rats. After 5 days of training, the rats did not use featural information to distinguish between geometrically equivalent locations. It seems that the hummingbirds in our study took much less training than the rats to do something apparently similar. Although Behamou and Poucet explicitly discussed their results only in the context of mammalian exploration, pigeons and domestic chicks have also been shown to be capable of using geometric cues to locate goals (e.g., Spetch, Cheng, & Mondloch, 1992; Vallortigara, Zanforlin, & Pasti, 1990), therefore preference for geometric cues over visual features would appear to be context related rather than taxonomic. Furthermore, a study by Kelly, Spetch, and Heth (1998) revealed that the relative control in spatial decision making by featural and geometric information in pigeons depended on initial learning experience.

The use of local views to guide spatial behavior has been discussed in the context of terrestrial mammals and flying Hymenoptera, the latter in particular, using stereotyped routes (Collett & Zeil, 1998). It is not clear how hummingbirds in flight use local views to guide revisits to rewarded flowers. However, humming-

birds do seem to learn a simple but abstract pattern of rewarded flowers, which might easily be accomplished by using a snapshot method of orienting. Alternatively, the birds could have learned a set of motor responses, as suggested by Olthof, Sutton, Slumskie, D'Addetta, and Roberts (1999) as a possible explanation for the results of M. F. Brown and Terrinoni (1996), who found that their rats seemed to learn and subsequently use pattern information for guiding pole choice (rewards were provided on the tops of poles). Brown and Terrinoni's own suggestion was that the rats had learned the geometric pattern formed by the locations of food rewards. Although the differences in the number of errors made by the hummingbirds before learning the two patterns in Experiment 4 appear to support a motor response explanation (birds learned reward positions with fewer errors when the rewards were immediate neighbors), the birds used the information learned in the first array of each experiment when learning reward locations in the second array. Olthof et al. (1999) used a similar experimental design to determine the conditions under which rats would show transfer of an abstract cognitive map. It therefore seems possible that hummingbirds might be capable of forming such a map-like representation. Three-dimensional flight observations would be required to determine whether the hummingbirds when learning and revisiting rewarded locations use a snapshot method like the Hymenoptera, a learned set of motor responses, or some other more complex representation (e.g., a topological representation).

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