FACTORS AFFECTING SPATIAL ASSOCIATION LEARNING BY HUMMINGBIRDS

by

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ABSTRACT

Numerous studies of learning in the laboratory have led to the general conclusion that animals associate cues and locations of response that are contiguous much more rapidly than ones that are spatially separated. Despite the fact that numerous animals readily use both contiguous and discontiguous cues to guide choices of good foraging locations in nature, there is no adequate explanation for the common observation of slow learning with discontiguous cues in standard laboratory learning tasks. Consequently, little is known about the process of spatial association learning.

This thesis examined spatial association learning by rufous hummingbirds (*Selasphorus rufus*) in a series of six experiments. The first two experiments served to demonstrate that hummingbirds learn associations between red light cues and spatially separated feeders at virtually the same rate as they learn associations between cues contiguous with feeders. The spatial separation (2.5 cm) was small in those experiments but similar to separations between floral cues and locations of nectar in natural hummingbird-visited flowers. Later experiments, however, showed that hummingbirds can learn with considerably greater separations between cues and feeders (at least 12 cm). Rapid learning by the hummingbirds was likely due to the experimental situation, which imitated certain characteristics of their natural foraging environment, and to the experimental procedures, which allowed them much of their natural foraging behavior. These results

with hummingbirds suggest that other animals should show improved learning with discontiguous cues if tested with learning problems analogous to those they encounter in their natural environments.

The major goal of the rest of the thesis was to develop a theoretical framework for studying spatial association learning. The Gestalt principles of perceptual grouping were adopted as a candidate framework and experiments 3 and 4 tested hypotheses predicting specific responses to particular spatial arrangements of cues and response locations. The assumption underlying these hypotheses was that any factor which produced visual grouping of cues and their corresponding response locations should result in faster learning of the relationship between them.

Experiment 3, based on the principle of spatial proximity, showed that birds performed well on three treatments in which strong visual grouping was predicted due to the proximity of cues and their feeders relative to the proximity of other cues and other feeders. They performed significantly less well on the treatment which predicted disruption of visual associations between cues and feeders due to relative proximity of other cues and other feeders.

Experiment 4, based on the principles of connectedness and closure, showed that birds performed well on two treatments in which strong visual grouping within cue-feeder pairs was predicted due to the placement of visible features between each cue and its feeder. Complete lines linked cues with their feeders in one treatment and partial connections linked

them on another, much as 'nectar guides' link the external surface cues of natural flowers with the nectar rewards that flowers contain . As predicted, birds learned faster on both of these arrays compared to one with no features between cues and feeders. Principles of Gestalt theory suggested the hypotheses and successfully predicted the results for each experiment whereas associative learning theory did not. Consequently, Gestalt theory should be considered as a useful framework for the study of spatial association learning.

The final two experiments (5 and 6) each provided evidence that hummingbirds learned geometric spatial relationships as they foraged from the cue-feeder arrays. Other non-spatial learning mechanisms could have explained their success in the experiments of this study, but successful learning of a diagonal cue-feeder relationship and good performance following removal of visible connections between cues and feeders were consistent with the possibility that they learned spatial relationships.

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CHAPTER 1

GENERAL INTRODUCTION

Since around the turn of the century, the experimental study of animal learning has focused mostly on determining how animals form associations between opportunities for reinforcement and the stimuli that signal them (Rescorla & Holland 1982; Mackintosh 1983). Two particular categories of relationships of stimuli to reinforcement have received the most attention. The first is the case in which stimuli are contiguous with the reinforcement they signal, and actions must be applied directly to the stimuli to obtain reinforcement. The second is the case in which stimuli signal a future opportunity for reinforcement and actions must be performed at the appropriate time to obtain (or avoid) it (Mackintosh 1983; Rescorla 1985b). Intensive study of both of these learning processes has advanced associative learning theory and resulted in the development of principles which account for the effects of particular qualitative and quantitative relations among stimuli (Mackintosh 1983).

One category of relationships between stimuli and reinforcement that has received comparatively little attention is the case in which stimuli signal a particular spatial location where performance of appropriate behaviors will result in reinforcement (Bowe 1984). One reason why this

process, called spatial association learning, has been less well studied is that separations of stimuli in space may unavoidably result in separations of stimuli in time and thus, confound learning of spatial associations (Mackintosh 1983; Bowe 1984). Consequently, no special theoretical principles may be required to understand the spatial association process.

Although only one study has rigorously examined this issue experimentally (Rescorla & Cunningham 1979), it suggests that even when special precautions are taken to control for confounding effects of temporal factors, spatial separations influence associative learning in ways that are not readily accounted for by associative learning theory. For example, studies which have examined spatial association learning consistently report that any spatial separation between cues and response locations typically inhibits learning compared to when cues and response locations are contiguous (Meyer et al. 1965; Stollnitz 1965; Cowey 1968; Bowe 1984). Even separations as small as 2 cm can inhibit learning (Schuck 1960; Polidora & Fletcher 1964; Iwai et al. 1986) and as separation distance is increased, learning rate typically declines (Stollnitz & Schrier 1962; Milner et al. 1979; Kurtz et al. 1982). Although attempts have been made to explain the general inhibitory effect of spatial separation with the principle of similarity of associative learning theory (Rescorla 1980), the results have not been convincing (Bowe 1984). In addition, the negative relationship between separation distance and rate of learning remains to be explained.

Features of stimuli, such as their size, orientation, or salience, and experimental procedures, have been considered as likely causes of the detrimental effects of spatial separation (Jarvik 1953; Blazek & Harlow 1955). However, cue characteristics alone can not adequately account for the effects of spatial separation because the same cues are readily associated with response locations when the two are contiguous (Meyer et al. 1965). In addition, experimental tests which explicitly vary features of cues confirm this conclusion (Ungerleider & Mishkin 1982; Osawa et al. 1990). Inappropriate experimental procedures are also unlikely to account for the effects of spatial separation because a variety of different paradigms have been used with a variety of animal species (Davis 1974; Bowe 1984) and in each case, separations consistently result in the same effects on learning.

One other explanation has been proposed for which there is some empirical support (Schuck 1960; Stollnitz 1965; Iwai et al. 1986; Yaginuma & Iwai 1986). According to this explanation, animals exhibit a tendency to bias their attention to response locations rather than to cues, and the likelihood with which they notice cues and attempt to relate them to response locations declines with increasing separation distance. For this explanation to be plausible, it must also explain why any bias, whether toward response locations or toward cues, should exist before an association with reinforcement has been formed. It fails to do this and a more likely interpretation of the bias that animals exhibit in spatial association studies is that they learn to do so during training procedures (Davis

1974; Rumbaugh et al. 1989). During standard training procedures, animals are exposed first to response locations which they learn to move or manipulate in some way for food rewards. Only after they have successfully mastered this part of training are they exposed to cues. By this point, however, they have already learned to associate food with the response locations and may not attempt to use cues to discriminate correct response locations during experiments.

At the present time in the study of spatial association learning, there is no complete explanation for the inhibitory effect of spatial separations and it is still unclear to what extent the negative relationship between separation distance and rate of learning accurately reflects the spatial association process. In addition, there is no active program of research based on the application of a theoretical approach which suggests promising new directions for the experimental examination of spatial association learning.

The objectives of this thesis were to (1) determine the extent to which spatial association learning is determined by distance between cues and response locations; (2) to apply a theoretical hypothesis testing approach to the issue in (1); and, to develop a program of research that should advance understanding of spatial association learning. In chapter 2, I first test the abilities of one species, rufous hummingbirds, to learn spatial associations. Hummingbirds are visually oriented foragers which use visible floral cues in their selection of profitable, nectar-producing flowers (George 1980). Thus, there is a basis for expecting

that they may be capable of learning spatial associations between color cues and feeders containing sugar solution, especially if the separations between cues and feeders are relatively small. The hummingbirds learned spatial associations rapidly in the experiments of chapter 2. Thus, in chapters 3 and 4, I tested specific hypotheses concerning how learning should be influenced by factors which promote visual grouping and association of cues and feeders independent of the absolute distance between them. These hypotheses were developed from consideration of the Gestalt principles of perceptual grouping. The success of this theoretical approach in generating testable hypotheses and in successfully predicting the results of the experiments I carried out, recommend it as a basis for a continued program of research on the process of spatial association learning.

CHAPTER 2

A DEMONSTRATION OF SPATIAL ASSOCIATION LEARNING BY HUMMINGBIRDS

INTRODUCTION

Animals necessarily learn many associations between features of their environments, the particular reinforcements these afford, and behaviors that are required to obtain, or possibly prevent, the reinforcements. For example, many foragers learn that striking coloration patterns frequently signal unpalatable or noxious prey; foliage-gleaning birds learn that irregularly shaped leaves indicate the presence of cryptic insect prey; and, nectarivores learn that particular colors or odors of flowers signal likely nectar sources. In these examples, the cues and objects to which animals respond for reinforcement are contiguous, but this is not always the case. Cues also can be spatially separated from locations at which appropriate behaviors are reinforced and the spatial relationship between the cues and response locations must be learned if the cues are to be useful. This process is called spatial association learning.

There are many examples of the use of spatially separate cues in nature. Numerous aerial and terrestrial predators use the conspicuous flight pattern of vultures circling over dying prey to locate the prey

themselves (Houston 1983; Rabenold 1983). Bees use a correlation between the colors of spots on banner petals and the nectar secretion rates of flowers, both of which change with age, to select flowers with greater average nectar rewards (Gori 1983, 1989). Coastal ospreys observe the fish catches of other individuals and use this information to select among many potential, and sometimes remote (< 5 km), fishing locations (Greene 1987). In each of these examples, the specific utility of using discrete spatial cues is clear: animals increase their foraging efficiency by using them in deciding where to go and what to do.

The ability to learn spatial associations has been studied in a number of species including rats (Milner et al. 1979), pigeons (Richardson & Evans 1975; Rescorla & Cunningham 1979), chimpanzees (Gellermann 1933; Jenkins 1943), monkeys (e.g. Meyer et al. 1965; Abordo & Lee 1977; Iwai et al. 1986), and human children (Murphy & Miller 1959; Jeffrey & Cohen 1964). Various laboratory testing procedures have been used in these studies but they consistently obtain the same result: any separation between cues and response locations impairs learning, even one as little as a few centimeters (Schuck 1960; Polidora & Fletcher 1964; Iwai et al. 1986; Yaginuma & Iwai 1986). With increasing separation, learning generally becomes progressively slower and may not occur at all (Stollnitz & Schrier 1962; Milner et al. 1979). Special training procedures and prolonged testing over hundreds of trials on the same choice problem may facilitate learning (Stollnitz & Schrier 1962; Schrier et al. 1963), but even so, learning is slow compared to when cues are part of the objects

that animals respond to for reinforcement (see reviews by Meyer et al. 1965; Stollnitz 1965; Cowey 1968; Mackintosh 1983; Bowe 1984). Thus, the process of spatial association learning has been resistant to study in the laboratory.

Why animals learn poorly in laboratory tasks is puzzling for several reasons. First, animals apparently learn both separate and contiguous cues in nature. Second, laboratory tasks have used only small cue-response separations relative to those in some natural problems. And third, natural cue-response separation problems may be more complex than controlled laboratory problems since relative locations of cues and response sites are unlikely to be identical in different encounters of the same problem.

Spatial separation between cues and response locations consistently impairs learning, yet its effects are poorly understood. Consequently, factors other than spatial separation have been sought to explain why animals learn slowly in the laboratory. Obvious factors, such as cue size and orientation, do not account for the effects of spatial separation on learning (Meyer et al. 1965; Cowey 1968; Iwai et al. 1986) and neither do other more subtle ones, such as the potentially confounding effects of temporal separations between perception of cues and outcome of responses (Rescorla & Cunningham 1979). The systematic testing of contiguous and separate relations among cues, response locations, and reinforcement locations has only better established that learning is best when all three lo-

cations are contiguous and worst when cues and response sites are separated; learning depends least on the location of reinforcement (Murphy & Miller 1958; Miller & Murphy 1964; Polidora & Thompson 1965).

Despite considerable evidence that learning is impaired when cues are separated from response locations, two concerns that question the general validity of this observation remain to be addressed. First, primates have been the predominant subjects in spatial association studies; other species must be tested before the general conclusion can be made that cue-response separations retard learning (Bowe 1984). Second, considerable individual variation in learning and performance is frequently noted within and between studies and this suggests that effects of cue-response separation could be an artifact of inappropriate or suboptimal testing procedures (Davis 1974; Rumbaugh et al. 1989).

In this study, I examined the ability of visually oriented foragers, hummingbirds, to learn an association between noncontiguous cues (small red lights) and response locations (feeders) in two experiments. In experiment 1, I used a simple free-feeding protocol to compare how well hummingbirds learn the fixed location of the one profitable feeder in an array of six visually identical feeders with and without a spatially separated cue. In experiment 2, I used a standard trial-based protocol, in which the location of the cued feeder was unpredictable from one trial to the next, to compare how well birds learn contiguous and discontiguous light cues. The discontiguous cue was 2.5 cm from feeders in both experi-

ments -- a spatial separation which is relatively small but which significantly impairs learning in macaque monkeys (Yaginuma & Iwai 1986), rats (Milner et al. 1979), and pigeons (Rescorla & Cunningham 1979; Richardson & Evans 1975).

EXPERIMENT 1

In the absence of cues, hummingbirds can learn the spatial location of a single profitable feeder anywhere in a horizontal array of six feeders within six hours (Miller et al. 1985). In the present experiment I asked 1) whether such learning is facilitated with a constant visible cue near the profitable feeder, much as petal markings identify certain natural sources of nectar (Gori 1989), and 2) to the extent that a constant cue is used, whether it facilitates learning of a particular (absolute) feeder location versus a relative location defined by the cue.

This experiment consisted of two parts. In the first part, I compared how well hummingbirds learned the location of a profitable feeder without a cue (Control treatment) and with a constant but spatially separate cue (Cue treatment) to assess the relative value of spatial association learning and spatial location learning. Both of these learning processes are possible in the Cue treatment, however, and better performance with a cue would not distinguish between the two possibilities that 1) birds learned only the spatial relationship between the cue and profitable

feeder, or 2) that birds learned particular feeder locations better in the presence of a cue. Thus in the second part of this experiment, I used a sudden switch in the location of the cue and profitable feeder midway through the experiment to distinguish between these two possibilities. If high performance before the switch results from spatial association learning, birds should transfer the association immediately to the new location and should continue with no change in performance. If high performance results from spatial location learning, however, birds should continue to visit the formerly profitable location in spite of the switch in location of the cue and should suffer decreased performance until they learn the new location.

Methods

Subjects

The subjects in both experiments were adult rufous hummingbirds, Selasphorus rufus, captured near Port Mellon, British Columbia in May, 1988. They were housed individually in wood-framed plastic mesh cages (60 x 65 x 91 cm) in a large holding room on a controlled natural photoperiod. They were fed commercial hummingbird nectar (Nektar Plus, Nekton USA, Inc.) on weekdays and 20% (mass/mass) sucrose solution supplemented with vitamins and minerals on weekends. Live Drosophila were available at all times in their home cages but not in experimental rooms. Birds were never deprived of food but were kept on a closed economy (Collier & Rovee-

Collier 1981) during the long experimental sessions in which they could feed only by visiting profitable feeders. Given the high metabolic requirements of hummingbirds, I assumed they would be well motivated to make correct choices. The five male and seven female hummingbirds used in experiment 1 had completed a short-term memory experiment using contiguous cues approximately one month earlier.

Experimental Environment

Both experiments were conducted in two rectangular rooms (1.3 x 2.5 x 2.5 m high) each lit by two overhead 40 W incandescent bulbs. A portion of one end wall in each room contained a horizontal array of six feeders at 11 cm spacing on a thin metal panel painted flat green. Feeders were marked by round 19 mm diameter fluorescent orange Avery labels with central 3 mm holes, and a 4 mm diameter red LED protruded slightly through the panel 2.5 cm above each feeder. Hummingbirds fed while hovering by probing their bills through the holes to reservoirs on the other side (disposable syringe needle fittings; see Tamm 1987, Fig. 2). When birds arrived at profitable feeders, a miniature solenoid valve (General Valve Corporation, Series 3) immediately dispensed 2 μl of 20% sucrose solution (mass/mass) into the reservoir. Hummingbirds were free to fly and visit feeders at will. Between brief foraging bouts to feeder arrays and short non-foraging flights around the room, they spent most of their time on a central perch (1.5 m high and 1.8 m from the center of the feeder array) which placed them at eye level with the feeders. A computer controlled

the LEDs, dispensed the food, and recorded the time and duration of all visits to feeders and perches by monitoring photocells (see Gass 1985, Tooze & Gass 1985, and Tamm 1987 for other applications).

Training

Birds spent the day before the experiment in training cages fitted with single wall feeders identical in appearance to experimental feeders but which supplied food ad libitum. Two hours before the end of the day, I moved the birds to the experimental rooms where food was available from a standard commercial hummingbird feeder hanging in front of a middle array feeder (the other five feeders were covered). I removed the standard feeder the next morning and set the single exposed array feeder to provide 2 μl on each visit. Birds usually visited this training feeder with little hesitation. I uncovered the other five feeders after several visits; birds could and did visit these, but the initial training feeder remained the only profitable one. After several more visits to the profitable feeder, approximately 1 h after training began, the experiment started at about 0900 hours with a change in location of the profitable feeder. The only difference in treatments was that in Cue, the LED above the profitable feeder was lit continuously whereas no cue was lit in Control.

Testing

Each hummingbird received both treatments in random order separated by four days in their home cages. Each treatment day consisted of the initial training as described above followed by two successive 5 h periods between which the computer suddenly reassigned the position of the profitable feeder. Nothing signalled the change in Control except that the previously profitable feeder no longer delivered food. In Cue, the LED above the new profitable feeder was lit and the LED above the previously profitable feeder was turned off. Data were recorded for the entire 10 h, then birds were returned to their home cages. A different pair of profitable feeders was used for the two treatments (feeders 2 and 5 in Control, and feeders 3 and 6 in Cue). To control for position biases (Tamm & Gass 1985), I presented half of the birds in each treatment with the pair of feeders in one order (e.g. 3 then 6) and the other half with the feeders in the opposite order (6 then 3).

Data analysis

In nature, rufous hummingbirds typically alternate between brief bouts of foraging, during which they visit a sequence of flowers in rapid succession, and longer periods of perching (approximately 5 - 10 min in duration; Wolf & Hainsworth 1977; Gass & Sutherland 1985) and they behaved similarly in this experiment. The measures I used to assess learning in this experiment are based on the feeders visited during successive foraging bouts. A foraging bout was defined as the period between the begin-

ning of a flight from the perch on which at least one feeder was probed, and either arrival back at the perch or absence from the array for greater than 20 s. The first feeder visited during a bout is termed the first choice. If it was profitable, it was a correct first choice. Any unprofitable visits were incorrect choices (i.e. errors). If the profitable feeder is visited at least once during a feeding bout, it is a successful bout.

Analyses of the first 5 h of each treatment and the entire Cue treatment were based on 12 birds. Two birds performed poorly in the second 5 h of Control and were retired to their home cages after 2 h so as not to endanger their health; analyses for that period were based on 10 birds. All performance measures based on proportions were arcsine transformed before statistical analysis. Measures based on frequencies, in which variance was proportional to the mean, were square root transformed.

Results and Discussion

Effects of profitable feeder position

In the experiment by Miller et al. (1985), speed of learning feeders depended on their position within the linear array; birds learned feeders at the end of the array more quickly than central feeders. In the Control treatment, feeders 2 and 5 should have been equivalent in difficulty because they were both one position removed from the ends of the arrays.

Birds should, therefore, have performed similarly in both 5-h periods independent of whether they experienced feeder 2 or 5 first. Mean percentage correct choices were indeed equivalent in the first 30 min (two-tailed paired t test: $t = .253$, $df = 9$, $p = .806$) and in the last 30 min ($t = .427$, $df = 9$, $p = .679$) of each period. In Cue, feeders 3 (a central feeder) and 6 (an end feeder) should have differed in difficulty, but percentage correct choices were nonetheless the same in the first 30 min ($t = .821$, $df = 11$, $p = .429$) and the last 30 min ($t = .326$, $df = 11$, $p = .750$) of both 5-h periods. I concluded that any differential responses to feeder position were small relative to the responses to each treatment and therefore proceeded with the analysis.

Effects of treatment order

To determine whether treatment order influenced learning within treatments, I tested whether the group starting on Control performed similarly to the group starting on Cue, both before and after the switch in location of the profitable feeder (eight separate two-tailed t tests). Mean percentage correct first choices of the two groups differed neither in the first 30 min nor the last 30 minutes of the 5 h period before the switch (Cue: first 30 min, $t = .508$, $p = .623$; last 30 min, $t = .898$, $p = .390$; Control: first 30 min, $t = .834$, $p = .424$; last 30 min, $t = 1.713$, $p = .118$; for all tests, $df = 10$). Neither did they differ in the first nor the last 30 min of the 5 h period after the switch (Cue: first 30 min, $t = 1.987$, $df = 10$, $p = .623$; last 30 min, $t = .692$, $df = 10$, $p = .504$;

Control: first 30 min, $t = .094$, $df = 8$, $p = .928$; last 30 min, $t = 1.547$, $df = 8$, $p = .160$). Consequently, I concluded that treatment order had no effect on individual performance. For further analysis, I combined results for the 10 birds who completed Control, and the 12 birds who completed Cue in each 5 h period.

Behavior during the first five hours

Hummingbirds learned to visit the profitable feeder almost exclusively both with and without the cue but, they learned more rapidly with it (Fig. 1a). They made few if any errors after 1.5 h in Cue; eight birds visited unprofitable feeders eight or fewer times out of 7622 total visits in the last 3.5 h. Most foraging bouts in Cue were successful; eight birds found the profitable feeder on every bout after the first hour. More importantly, nearly all first choices were correct after the first hour in Cue. In Control, birds started near chance but improved throughout the 5 h. Even so, their mean performance by the last half hour was no different than performance of the birds in Cue in the first half hour (61.1 vs. 58.0%, respectively; two-tailed paired t test: $t = .626$, $df = 11$, $p = .546$) and it was still far below their performance in Cue in the last half hour (61.1 vs 93.4%, respectively; $t = 4.963$, $df = 11$, $p < .001$). Birds made many more incorrect choices in Control (Fig. 1b), but after 1.5 h, they found the profitable feeder nearly as often in feeding bouts as birds did in Cue (Fig. 1a).

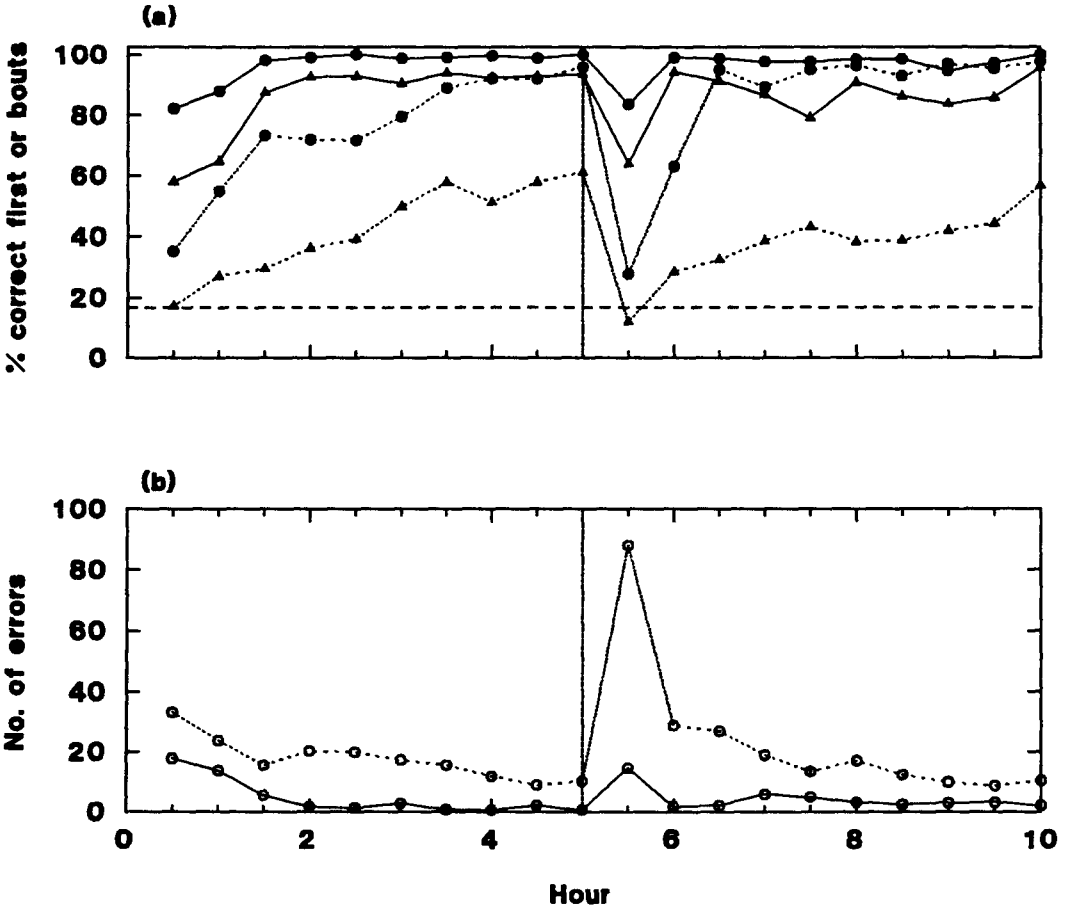


Figure 1. Performance in experiment 1. The vertical dashed line at 5 h indicates the time that the position of the profitable feeder was switched. (a) Mean percentage correct first choices (triangles) and mean percent successful feeding bouts (circles). The horizontal dashed line indicates chance performance for percentage correct choices (16.7%). (b) Number of errors in 30 min intervals. For both panels, solid lines indicate Cue and dashed lines indicate Control. Sample size is N = 12 birds for all of Cue and before the switch for Control and N = 10 after the switch for Control.

Birds clearly learned even without cues, performing nearly identically to those in a similar experiment in the same laboratory (Miller et al. 1985). Performance was so much better in Cue, however, that there is no question that light cues aided foraging in some way. Improved performance by my measures of learning also meant improved performance energetically. Net energy intake was higher in Cue because Control birds made more errors and spent approximately three fold more time probing and moving between unprofitable feeders (one-tailed paired t test: $t = 4.844$, $df = 11$, $p < .001$).

Immediate responses to the switch

After the unsignalled switch in profitability of feeders, all 12 Control birds probed either the 'old', previously correct feeder (seven birds) or one next to it (five birds) on their first visit at the feeder array. The five birds who missed the previously correct feeder on their first choice probed it next. That is, all 12 birds behaved as they had before the switch. This result and the fact that Control birds who had no visual cues improved in percentage of correct first choices before and after the switch is strong evidence that they used spatial memory, corroborating the conclusion reached by Miller et al. (1985).

Birds also used spatial memory when correct feeders were cued; eight of the 12 birds probed the old correct feeder first after the switch, and a ninth visited a feeder beside it. On their very next move, four of

these nine birds skipped over the two intervening feeders to the newly profitable feeder, thus demonstrating they had also learned the spatial association. This suggestion is strengthened by the fact that hummingbirds rarely pass over two feeders in my experiments with linear arrays (only 5.8% of all 3919 moves between feeders recorded in this experiment) and in the field, moves tend to be to nearest flowers as well (Gass & Montgomerie 1981; Pyke 1978). The other five of the nine birds who chose the old correct feeder first after the switch visited more incorrect feeders before locating the new profitable feeder, but each individual discovered it in many fewer moves in Cue (mean for five birds = 4.8) than they did in Control (mean = 17.2). This suggests that they too had learned the spatial association but relied on it less strongly than the other Cue birds had.

More compelling evidence for spatial association learning is that the remaining three of 12 birds went directly from their perches to the new correct feeder on their first bout after the switch. Only spatial association learning can completely account for this result. These birds learned the spatial location of the old correct feeder too, however, since in the first half hour after the switch 60% of errors by two of them (three of five errors in each case) and 47% of errors by the third (seven of 15 errors) were to the old correct feeder.

If the above interpretations are correct, then it follows that all 12 birds learned both spatial locations of profitable feeders and spatial

associations between cues and profitable feeders in the Cue treatment. Some individuals relied more on the learned spatial association but most relied more on the learned spatial location. Although most birds incorrectly visited the old profitable feeder first, their behavior was not inappropriate: they returned to the location from which they had obtained food over many foraging bouts but then quickly switched to using the spatial association to locate the new profitable feeder.

Behavior during the second five hours

As in the first 5 h, birds learned the correct feeder both with and without cues in the second 5 h, but learned more rapidly with them (Fig. 1a). Birds who had relied more on spatial location learning (all birds in Control and nine of 12 birds in Cue) suffered initially low performance; the three birds in Cue who had relied more on spatial association learning did well from the start.

In Cue, most birds found the newly correct feeder in one or two moves following the switch and the average (± SD) for all birds was 2.3 ± 3.1 moves. All birds in Control took much longer to find the newly correct feeder (mean ± SD = 16.8 ± 13.3 moves) and the difference between the two treatments was highly significant (two-tailed paired t test: $t = 5.253$, $df = 11$, $p < .001$). Perhaps the most telling evidence that birds had greater difficulty locating the profitable feeder without cues after the switch in Control was that two of them visited the profitable feeder

so few times that I returned them to their home cages at hour seven so as not to risk their health.

Visits to unprofitable feeders increased considerably in both treatments in the 30 min following the switch although many more were made in Control than in Cue (Fig. 1b). Most of these errors were to previously profitable feeders (Cue: mean = 57.7%; Control: mean = 47.7%) but by the end of the first hour following the switch, birds visited previously profitable feeders no more than expected by chance (Cue: mean = 21.5%; Control: mean = 19.5%; chance = 20%). Learning in both treatments progressed similarly to what it had in the first 5 h.

EXPERIMENT 2

Experiment 1 demonstrated that hummingbirds can learn spatial associations with small separations between cues and feeders when the profitable feeder and its cue remain in the same spatial position over many foraging bouts. The constant position of cues and feeders, however, allowed them to use both spatial location learning and spatial association learning to reach high performance.

In experiment 2, I used the same feeder arrays but tested hummingbirds with a standard trial-based procedure in which the cue and its corresponding feeder vary unpredictably in location from trial to trial. Under these conditions, spatial location learning is still possible within each trial but only spatial association learning will result in choice of

the correct feeder each trial. I evaluated learning by comparing performance on one treatment in which cues were separate from feeders with performance on a second treatment in which cues and feeders were contiguous.

Methods

Subjects

Four male and four female adult rufous hummingbirds were subjects in this experiment (see experiment 1 for a description of capture and care). None had been used in any experiments since their capture three months earlier.

Experimental environment

Testing rooms were as described in experiment 1. In one room (designated the Separate treatment), the feeder array and cues were identical to those used in experiment 1: six feeders were spaced at 11 cm intervals, each with a red LED 2.5 cm above it. In the second room (designated the Contiguous treatment), each feeder was surrounded by a translucent white Plexiglass disc (32 mm diameter) which could be uniformly illuminated from behind by four red LEDs. The profitable feeder was cued by lighting the LED or the disk during trials. All feeders were marked with 19 mm round purple Avery labels. Experimental procedure and data collection were as described for the first experiment.

Training

The initial training was similar to that in experiment 1. On the morning of the day before testing, hummingbirds were placed in training cages similar to their home cages with an ad libitum feeder identical in appearance to those in the testing rooms. That afternoon, they were moved to the experimental rooms where a standard commercial feeder marked with a purple Avery label around the access hole was hung in front of a middle array feeder (the other five were covered) until the following morning.

We removed the standard feeder from the room at the beginning of the next day and set the array feeder behind it to deliver 3 μl of 20% (mass/mass) sucrose solution on each visit. After several feedings, the LED or Plexiglass disk associated with the feeder was lit and training continued. After several more feedings, all other feeders were uncovered and the cue and profitability were assigned to a new feeder. This transfer procedure was repeated until birds had fed several times from each feeder. The training period lasted 2 - 2.5 h and testing began between 1030 - 1100 hours.

Testing

Each bird was tested in both Contiguous and Separate treatments in one day, half of each sex in each order. After initial training, birds completed 40 feeding trials in the first treatment. The profitable feeder and its cue were reassigned randomly among feeders each trial but the same

random sequence was used for all testing periods. If one bird finished before the other, I hung a standard feeder in its testing room, and when both had finished I exchanged them, trained them again as above, and immediately began 40 trials of testing under the new treatment. After the second treatment I returned birds to their home cages. The 40 trials for each treatment required about 2 h; training and testing for both treatments lasted between 8 and 10 h. One bird who experienced Contiguous first and two who experienced Separate first were reluctant to visit feeders under the second treatment. I promptly terminated their testing, hung a standard feeder in front of the (covered) array, and then trained and tested them without difficulty the following morning.

Feeding trials began 2 min after preceding trials ended or as soon thereafter as birds perched. Simultaneously, a soft buzzer sounded for 0.5 s, the cue to the profitable feeder was lit, and the profitable feeder was set to provide 3 μl on each visit. Birds usually perched facing the array, and quickly learned to turn their heads toward it when the buzzer sounded. They could visit any sequence of feeders, and obtain food from the correct feeder up to eight times (i.e. <24 μl). I terminated feeding trials if 1) birds visited no feeders within 15 s, 2) they probed the profitable feeder eight times within 15 s, or 3) they visited any feeders then perched within 15 s of the start of the trial. The light cue was turned off when trials ended and the previously profitable feeder delivered no more food. In early trials, birds usually sat for most of the 15 s time limit before flying from the perch to probe feeders but they 'sat

out' few trials. If birds visited no feeders during trials, the same profitable feeder was used on the next trial. Within 10 trials, most flew toward the array well within 1 s after the start of feeding trials. It took them .8 - 1.2 s to cross the room to the array and they completed feeding bouts well within 15 s. When birds had obtained the food limit and the cue light went out, they usually flew promptly back to the perch. The feeders remained exposed between trials and although they were uncued and delivered no food, birds often probed them (particularly during the early trials of the first treatment). By the second treatment, birds usually perched between trials but often flew close to and hovered in front of the array, and then returned to the perch without probing any feeders.

Data analysis

I mainly evaluated learning in this experiment by the strictest criterion: correct first choices in feeding trials. Mean scores for successive blocks of 10 trials were virtually identical within treatments, regardless of treatment order. Differences between treatment orders were insignificant in Separate (one-way repeated measures ANOVA: $F_{1,6} = 0.47$, $p = .520$) and all birds achieved perfect scores in Contiguous after trial 10, so I lumped results for individuals within treatments for all comparisons.

Results and Discussion

All birds quickly learned to visit cued feeders in both treatments (Fig. 2). As expected, they averaged significantly more correct first choices in 40 trials in the Contiguous treatment (mean ± SD = 38.5 ± 1.1 correct choices) than in the Separate treatment (mean ± SD = 31.8 ± 5.0 correct choices; two-tailed paired t test: $t = 3.95$, $df = 7$, $p = .006$). In Contiguous, no bird made more than three wrong first choices in 40 trials and none made any after the first 10 trials. Two birds made no wrong first choices on any trials. In Separate, however, half of the birds made 10 or more wrong first choices in 40 trials although two birds made only two. Performance differed significantly between the two treatments in each of the first three blocks of 10 trials (two-tailed paired t tests; all $t > 2.29$, $df = 7$, $p < .05$). By the last 10 trials, however, the birds in Separate averaged nearly 100% correct choices and their performance was no longer distinguishable from Contiguous (two-tailed paired t test: $t = 1.53$, $df = 7$, $p = .171$).

Experiment 2 corroborates the results of experiment 1 and demonstrates unequivocally that hummingbirds can use either contiguous or separate cues to guide their foraging under standard randomized trial-based procedures. Birds achieved perfect average performance after 10 trials with Contiguous cues, and did nearly this well after 30 trials when cues and feeders were separated by 2.5 cm.

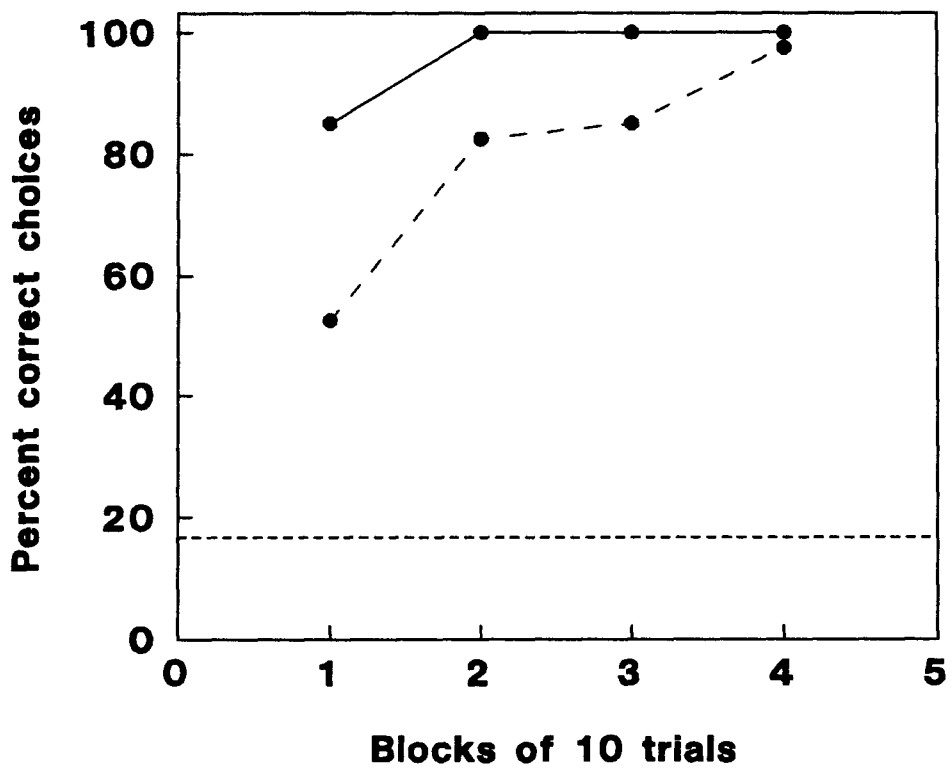


Figure 2. Mean percentage correct choices in experiment 2. Solid lines indicate the Contiguous treatment and dashed lines indicate the Separate treatment. Sample size is N = 8 for both treatments. The horizontal dashed line indicates the performance level expected by chance (16.7%).

Although experiment 2 showed that hummingbirds can learn spatial associations and that cues separated by 2.5 cm are only slightly less useful than contiguous cues, the latter interpretation involves assumptions that must be considered. On one hand, the Contiguous cues that I used were much larger than the Separate cues (eight times the diameter and 63 times the lighted area). On the other hand, the small LEDs were much brighter than the disks. Depending on whether the area or the brightness of the cues was more salient to hummingbirds under the conditions I used, the results of this experiment may over- or underestimate the difference in value of the two kinds of cues and the effect of separation.

GENERAL DISCUSSION

The experiments of this study showed that rufous hummingbirds quickly learn spatial associations with small cue-response separations (2.5 cm). Experiment 1 provided strong evidence that hummingbirds can simultaneously learn spatial associations and spatial locations when the profitable feeder and cue remain in the same position over a series of unrestricted foraging bouts. It also supported the conclusions of other studies that hummingbirds use spatial memory to locate profitable locations when visible cues are not available (Gass & Sutherland 1985; Miller et al. 1985). Experiment 2 showed that hummingbirds learn spatial associations under standard trial-based procedures in which spatial location learning cannot be an important component of performance.

Perhaps the most striking result is that the hummingbirds learned so fast and performed so well after such little training. Even in my second, trial-based experiment, the eight naive birds received all training in one hour immediately before testing, all of them performed well above chance level (16.7%) within 20 trials of testing, and only two made any errors (one each) after 30 trials. Other animals have performed well at similar separations (e.g. one of the rhesus monkeys in Schrier et al. 1963), but they typically require several days of pretraining to accustom them to the test apparatus, followed by hundreds of trials of testing (e.g. Iwai et al. 1986; Yaginuma & Iwai 1986) to reach performance levels similar to the hummingbirds. Learning and performance in other animals has also been facilitated with special procedures such as extensive training under gradually increasing cue-response separations (Stollnitz & Schrier 1962; Schrier et al. 1963). In contrast, the hummingbirds were trained and tested on one separation only.

Why Did Hummingbirds Perform So Well?

The dramatic difference between the results of this study and those of previous studies demands an explanation. I cannot provide this at present because this study was not designed to test different possibilities. Three kinds of explanations, however, are likely: 1) hummingbirds are uniquely capable, among the animals that have been tested, of associating spatially separated cues and response/reinforcement locations; 2) hummingbirds are similar to other animals in this respect, and some feature(s) of

my experimental procedure accounts for their better performance; or, 3) some combination of 1) and 2).

If hummingbirds are unique in their ability to learn spatial associations, we should seek to understand factors in their biology that have led to its evolution. On the other hand, if procedure accounts for the difference we should expect previously less successful species to improve if tested under procedures appropriately adapted to their biology. Given my argument in the introduction that many mobile animals should benefit through improved foraging success by using spatial associations in nature, I suspect that hummingbirds are not unique. Rather, some correspondence between their biology and my experimental procedures allowed them to demonstrate an ability that is common among many species. The next sections explore this possibility.

Biological Characteristics of Hummingbirds

Hummingbirds use the most energy-expensive foraging mode among vertebrates, hovering flight, and their mass-specific metabolic rates are high even at rest (Lasiewski 1963; Bartholomew & Lighton 1986; Suarez et al. 1990). Several hours without food result in rapid weight loss (Tooze & Gass 1985) and may even jeopardize overnight survival (Gass & Lertzman 1980). The high energy demands of hummingbirds so motivates them to feed that wild birds will feed readily while held in the hand or in such unfamiliar and undoubtedly stressful contexts as laboratory experiments. Many

researchers have capitalized on this fact to study factors that regulate feeding behavior (e.g. Wolf & Hainsworth 1977; Hainsworth & Wolf 1979; Montgomerie et al. 1984; Gass 1985; Stephens & Paton 1986; Tamm 1987).

Since many animals exhibit faster learning when hungry (Mackintosh 1983; Croy & Hughes 1991), it is quite likely that the hummingbirds were well-motivated to find food in my experiments and to learn the rules for locating rewarding feeders. In addition to their high energy demands, the experimental procedures provided additional incentive to find profitable feeders. First, in experiment 1, the long (10 h) testing sessions allowed ample time for birds to incur severe energy deficits if they failed to locate the profitable feeder. Second, in experiment 2, I limited the amount of food available during each feeding trial such that the birds had to take most of the sucrose solution available to maintain their body mass and normal rates of energy intake.

Another factor of possible importance is that rufous hummingbirds live solitary rather than social lives. They are highly aggressive and territorial and no association occurs between males and females other than the act of mating itself. Females associate with their young only while caring for them until the young can feed independently (Johnsgard 1983). Consequently, rufous hummingbirds may be relatively undisturbed by the isolated testing conditions typically used in studies of spatial association learning. Other animals which have been tested typically live in or feed in groups (primates, pigeons and rats). They, like many other group-

living animals, learn food preferences (Barnett 1975; Inman et al. 1988), feeding behaviors (Galef 1976; Wechsler 1988), and foraging locations (Galef 1983; Rabenold 1987; Benkman 1988) through social interactions and often feed more readily in the presence of conspecifics or familiar group members (Hale 1956; Menzel & Juno 1985; Benkman, pers. comm.). Individuals of social species may find standard isolated, sound-proof testing chambers stressful and thus not conducive to expression of their learning abilities (Gomez-Laplaza & Morgan 1991; Washburn & Rumbaugh 1991).

Several observations support this idea. First, in a recent study (Washburn & Rumbaugh 1991) two adult rhesus monkeys more quickly mastered video tasks requiring their responses to a joystick separated from cues on a computer screen when they could see and hear each other. Learning was slower during testing periods in which they were isolated from each other. Second, marmosets tested with their familiar social group and in familiar surroundings showed strong evidence of one-trial learning of cues spatially separated (<25 cm) from test objects containing food (Menzel & Juno 1985). Spatial association learning was not the focus of that study, but it nonetheless suggests the importance of social context on learning. Third, studies of spatial association learning have occasionally reported striking position biases by some individuals (Stollnitz & Schrier 1962; Miller & Murphy 1964). Van Rooijen (1990) recently argued convincingly that position biases are expressions of stress and uncertainty. In the above studies which observed position biases, rhesus monkeys were tested

in small, isolated, restraining cages and these conditions, which were likely quite stressful for them, could explain their poor performances. Isolated testing conditions are possibly less stressful for solitary animals such as rufous hummingbirds and therefore likely to detract less from their motivation to feed and learn.

Characteristics of the Experimental Procedures

Animals commonly exhibit species-typical ways of searching for, procuring and eating food items (Zahorik & Houpt 1981; Hollis 1982; Kamil & Maudlin 1988). This fact has important consequences for the study of learning under controlled conditions. On the one hand, simple tasks may be learned with great difficulty or not at all when animals must act in ways that are incompatible with their natural or normal behavior (Breland & Breland 1961; Moore 1973). On the other hand, apparently complex tasks can be learned quite easily when they permit expression of species-typical behaviors (Kamil et al. 1982). In my experiments, the foraging behavior of the hummingbirds was analogous in several respects to their foraging behavior in nature and this may have facilitated their success.

Wild rufous hummingbirds make periodic foraging flights from one or a few habitual perches on their territories to patches of flowers from which they obtain nectar while hovering (Carpenter et al. 1983; Gass & Sutherland 1985). In my experiments, birds flew from their perches to the feeder arrays and obtained sucrose solution in bouts of visits to

profitable feeders. Wild hummingbirds feed from numerous flower species; some flowers, because they produce copious nectar or because of their morphology, require birds to probe them a number of times to obtain all of the nectar (Gass & Montgomerie 1981; Wolf & Stiles 1989). The feeders in my experiments were analogous to this type of flower and the hummingbirds quickly learned to probe them repeatedly to obtain meals. Encountering empty feeders in the arrays was also comparable to the experience of wild hummingbirds. Birds may find no nectar in flowers because they or their competitors have recently emptied them, or because nectar is not produced by some individual flowers (Brown & Kodric-Brown 1979; Feinsinger 1983).

Although I have argued that my procedures simulated the typical foraging environment of rufous hummingbirds, not all of them did. In experiment 1, birds obtained all their food from one feeder which would never be the case with any flower. Hummingbirds deplete most flowers of nectar on a single visit and the flowers will not accumulate enough nectar to be profitable for at least a time period spanning many foraging bouts (Gass & Montgomerie 1981). Hummingbird foraging behavior is apparently plastic with respect to the temporal patterning of nectar availability at individual locations, however, as hummingbirds readily adapt to nearly exclusive use of infinite-supply commercial feeders and can flexibly adjust their returns times to match replenishment rates of food sources (Gass & Sutherland 1985; Gill 1988).

Animals readily learn appropriate behavior toward cues similar to those which predict particular consequences in their natural environments and which are salient to their sensory mechanisms. Otherwise, they may learn only slowly or not at all (Garcia et al. 1974; Hollis 1982). Nectar-producing flowers are typically colorful and visually conspicuous from long distances and not surprisingly, hummingbirds use acute color vision to locate and discriminate among nectar-rich and nectar-poor food sources (Goldsmith & Goldsmith 1979; Goldsmith et al. 1981). Numerous studies have demonstrated that hummingbirds can learn to associate food with any color (Collias & Collias 1968; Goldsmith & Goldsmith 1979; Stiles 1976). Red, however, is the most common color of North American hummingbird-pollinated flowers (Grant & Grant 1968). Red contrasts strongly against green in vertebrate vision (Stiles 1976; Ali & Klyne 1985) and in my experiments, the red lights that distinguished profitable from unprofitable feeders were undoubtedly highly salient cues on the green background of the feeder arrays. That red is attractive to hummingbirds is obvious in their frequently observed and often amusing investigations of nonfloral red objects (Gass 1979; Johnsgard 1983). The red lights may have been particularly easy for the hummingbirds to associate with food, even with a spatial separation between cues and feeders and in addition, they may have facilitated spatial association learning by biasing the birds' visits to feeders close to the lights.

There is some evidence to suggest that testing with salient cues should improve spatial association learning in other species. Rats, for

example, have performed poorly in spatial association tasks (Gellermann 1933; Milner et al. 1979), however, each study has required them to learn visual discriminations. Rats are primarily nocturnal (Barnett 1975) and have poor vision relative to visually-oriented animals such as diurnal birds (Ali & Klyne 1985; e.g. hummingbirds). They associate olfactory cues much more rapidly with food than visual ones (Slotnick & Katz 1974) and two studies suggest that they learn spatial associations readily when olfactory cues signal locations of response.

In one study (Galef 1983), rats identified food odors encountered on a conspecific in their home nest and later went directly to the previously learned location of that food type in a three arm maze (Experiment 3). In another study, rats used a localized odor cue positioned near ground level to select the two among eight elevated food patches (2.1 m high) that contained preferred peanuts in addition to less-preferred rodent pellets (Phases 2 - 4 in Mellgren & Brown 1988). Both of the preceding studies used nonstandard testing procedures and consequently, their results are not easily compared with other studies of spatial association learning. They do suggest, however, that the effect of spatial separations on learning may be partly an artifact of cue salience and that studies should be carried out to test this hypothesis.

I have suggested that my experimental procedures facilitated spatial association learning by the hummingbirds. It is possible however, that hummingbirds, and diurnal visually-oriented nectarivores in general,

frequently encounter natural analogues of the cue-response separation problem in the flowers they feed from. Some plant species attract pollinators by highly visible color cues on a part of the plant that is separate from the source of nectar or pollen; foragers may then learn the spatial relationship between the cue that initially attracts them and the specific location where they must respond to obtain the rewards they are seeking. Examples of this type are certain Heliconia species which attract neotropical hummingbirds to their small inconspicuous green flowers by red cincinnial bracts (Stiles 1975, 1976) and Anigosanthos manglesii (Mangles' Kangaroo Paw) of Western Australia in which red felt-like stems undoubtedly serve to attract honeyeaters and other foragers to their long tubular green flowers (Morcombe 1968). In other species, localized floral cues such as petal markings or externally-visible reproductive structures whose appearance correlates with nectar production rate are common in insect-pollinated flowers (Gori 1983) and insects apparently use them to select more rewarding flowers (Gori 1989). I do not know at present how floral structures function in nectarivore learning of nectar locations, but the above examples should provide fertile grounds for study.

A Typology of Spatial Associations

Natural examples of spatial associations may be categorized into two types. The first is characterized by an absence of any physical link between cues and response locations. Examples of this type include the circling of vultures that attract other carnivores to dying prey

(Houston 1983; Rabenold 1983), and all cases in which animals learn the locations of profitable foraging areas from other individuals while in a location, such as a colony, which is spatially separated from the foraging areas (e.g. Galef 1983; Greene 1987). I include here only examples in which the foragers use information obtained from others to locate good feeding areas independently, and not by following others to the feeding areas. In the second type, spatial cues and response locations are both part of a single physical structure. All examples of localized floral cues that correlate with the presence or absence of nectar are included in this category. Here, the relevant cues are not contiguous with where appropriate responses are reinforced but they are bounded by the physical structure of the flower. This connection may facilitate learning.

Nectar guides could represent a special case of physical connection because they provide partial or complete visible contiguity between external floral cues and concealed nectar rewards. They may facilitate, or perhaps even eliminate, the need for spatial association learning by visually directing foragers from cues to rewards. This suggestion could provide a mechanism for the observed function that nectar guides increase foraging efficiency of nectarivores by reducing handling time of flowers (Waser & Price 1983). Whether these two types of natural spatial associations differ in functional respects or require different learning mechanisms is not known at present but I am currently performing experiments designed to determine how they effect learning.

CHAPTER 3

EFFECTS OF RELATIVE SPACING AMONG STIMULI ON SPATIAL ASSOCIATION LEARNING

INTRODUCTION

Many studies have demonstrated that spatial contiguity between cues and response locations facilitates associative learning (Mackintosh 1983; Rescorla 1985a). In contrast, spatial separation between cues and response locations decreases rate of learning in a number of animals (see reviews by Meyer et al. 1965; Stollnitz 1965; Davis 1974; Bowe 1984). Under standard discrimination learning procedures, even a few centimeters of separation can significantly inhibit learning (Schuck 1960; Polidora & Fletcher 1964; Iwai et al. 1986; Yaginuma & Iwai 1986), and as separation distance is increased, learning typically becomes progressively slower (Stollnitz & Schrier 1962; Schrier et al. 1963; Milner et al. 1979; Iwai et al. 1986). The use of gradual training procedures and prolonged testing over many hundreds of trials can reduce the severity of the effects of spatial separation on learning, nevertheless, the inverse relationship between rate of learning and separation distance persists (Stollnitz & Schrier 1962; Schrier et al. 1963).

The most commonly proposed explanation for the relationship between rate of learning and distance of separation between cues and response locations is that the likelihood with which animals notice cues and attempt to relate them to their corresponding response locations declines with increasing separation distance (Schuck 1960; Stollnitz 1965; Butter et al. 1982; Yaginuma & Iwai 1986). This explanation is problematical for several reasons. First, alert, unstressed animals usually notice stimuli quickly, particularly if they are novel or in unaccustomed places (e.g. Menzel & Juno 1985; Thinus-Blanc & Ingle 1985; Menzel 1987), and the proposed explanation does not account for why they fail to do so in spatial association learning tasks. Second, the proposed explanation allows only appeals to variation between individuals and species to account for variation across studies in rate of learning at particular separations or variation in asymptotic performance at different separation distances. Both of these kinds of variation occur. Third, the proposed explanation is not based on any theoretical perspective which permits predictions of specific effects of particular spatial arrangements of cues and response locations (Bowe 1984). Greater progress in understanding of the process of spatial association should follow from the application of a theoretical perspective that has both explanatory and predictive value.

Any theoretical perspective that is applied to the study of spatial association learning must include concepts that predict how organisms should respond to spatial distributions of stimuli and to any spatial correlations that exist among those stimuli. Associative learning theory,

the most coherent and well-developed framework for the study of animal learning (Rescorla & Holland 1982; Mackintosh 1983), is unlikely to fully satisfy these requirements (Bowe 1984). Associative learning theory recognizes that spatial factors influence the formation of associations, but it does so in a general sense only through the principles of association by stimulus similarity and contiguity (Rescorla 1985b). Both of these principles predict generally that associations should be formed easily between contiguous cues and response locations (Rescorla 1980, 1985b; Mackintosh 1983), and perhaps by extension, they predict that learning should be more difficult with increasing separation. However, they do not readily generate other specific predictions concerning the effects of spatial relationships among stimuli (Rescorla 1985b).

In contrast to associative learning theory, the Gestalt principles of perceptual grouping offer a theoretical approach that does generate a rich supply of testable hypotheses concerning how particular spatial relationships among stimuli should influence learning (see Rock & Palmer 1990, for a concise account of the various principles). A basic tenant of Gestalt theory is that the ease with which relationships between stimuli are learned depends on the extent to which stimuli are perceived as more related to each other than to other surrounding stimuli (Kohler 1941; Asch 1961). Each of the Gestalt principles of perceptual grouping specifies how a particular factor should influence the perception, and thus learning, of relationships between stimuli.

Consider the Gestalt principle of spatial proximity. It predicts that adjacent stimuli should be perceived as sets or units, rather than as independent or unrelated objects, if they are closer to each other than to other neighboring stimuli (Wertheimer 1950; Pomerantz 1981). More specific predictions follow from this general one: (1) learning should be fastest when cues and response locations are contiguous; and (2) it should deteriorate with increasing separation between them. Both of these predictions are already well-supported in the literature (Stollnitz 1965; Bowe 1984), but only the first is clearly predicted by associative learning theory (Mackintosh 1983; Rescorla 1980, 1985b).

The principle of spatial proximity predicts not only how distance between cues and response locations should influence learning, but also how relative distance among neighboring cue-response location pairs should influence learning, as well (Koffka 1935; Kohler 1947; Pomerantz 1981). Consider a linear two-dimensional array in which both vertical spacing between cues and their response locations and horizontal spacing between pairs of cues and their response locations can vary (Fig. 3). Whenever the horizontal distance between adjacent cues and adjacent response locations is greater than the vertical distance between cues and their corresponding response locations, cue-response location 'pairs' should be perceived as independent units, and vertical distance between components of pairs should dominate learning of functional spatial associations (Fig. 3, a, b & d). At any given horizontal distance, a decrease in the vertical separation between cues and their response locations should enhance visual

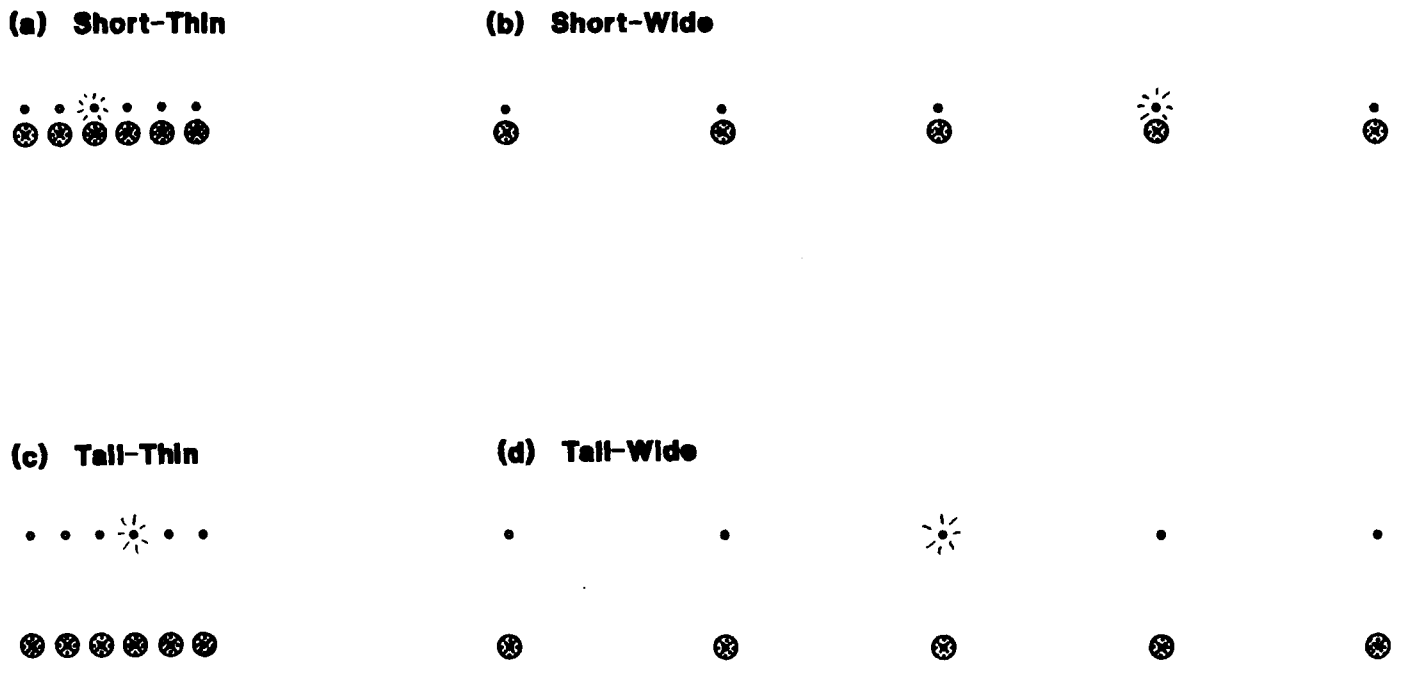


Figure 3. Four stimulus arrays which vary in horizontal and vertical spacing among stimuli. Each array represents one of the four treatments of experiment 3 and is drawn to actual scale: (a) Short-Thin; (b) Short-Wide; (c) Tall-Thin; and, (d) Tall-Wide. Cues and feeders are represented by the upper and lower rows, respectively, in each array. One cue, randomly selected, was lit during each feeding trial signalling the feeder below it as rewarding.

association within cue-response location pairs and facilitate learning. In contrast, whenever horizontal separation between pairs is less than vertical distance between components of pairs, visual association between adjacent cues and adjacent response locations should interfere with visual association of cues and their response locations (Fig. 3c). Under these conditions, learning of functional associations should be more difficult. The effect of visual interference among neighboring pairs, then, should be greatest when vertical separation is very large and horizontal separation is very small.

The principle of spatial proximity challenges the prevailing idea that spatial association learning is determined solely by distance between cues and response locations. It predicts instead that learning should be influenced by both distance between cues and their response locations and by distance among neighboring cues and among neighboring response locations. Most generally, it predicts that learning should be influenced simultaneously by the relative separations among all neighboring components in a stimulus array (Koffka 1935; Kohler 1941; Pomerantz 1981).

In this study, I tested the above predictions from the principle of association by spatial proximity. Rufous hummingbirds (Selasphorus rufus), which readily associate visual cues with food rewards of sucrose solution (Collias & Collias 1968; Goldsmith & Goldsmith 1979; George 1980), served as subjects and I tested individuals on four different arrays of cues and response locations (i.e. feeders). The cue-feeder arrays

differed in horizontal distance between adjacent cues and adjacent feeders and in vertical distance between cues and their corresponding feeders (Fig. 3). If hummingbirds group visible components of their environments by spatial proximity, then the geometric structure of the arrays of feeders and spatially separated cues to their profitability should influence the birds' ability to associate them. More specifically, both smaller separations between cues and their feeders and larger separations between cue-feeder pairs should facilitate learning. Positive support for the first part of this prediction would provide additional evidence for the suggestion from other studies of spatial association learning that learning deteriorates with increasing separation distance (Milner et al. 1979; Iwai et al. 1986). Positive support for the second part of the prediction would provide evidence for the role of a new factor in spatial association learning. It would also provide some encouragement for the potential usefulness of the Gestalt principles as a theoretical framework for studying spatial association learning.

METHOD

Subjects

Eleven female and nine male adult rufous hummingbirds were captured and tested in this study. Fifteen of the birds were captured in May, 1989 and tested after four months in captivity; the other five were captured in May, 1990 and tested after two months in captivity. All birds were

experimentally naive prior to this study. Feeding and maintenance were the same as described in Chapter 2.

Experimental design

The effects on learning of both vertical separation of cues from feeders and horizontal separation of cue-feeder pairs were examined in a single experiment in which two vertical distances of cues from feeders and two horizontal distances between adjacent cue-feeder pairs were crossed in a 2 x 2 factorial design (Fig. 3). The two vertical distances I used between cues and their feeders ('Short', 1.57 cm, and 'Tall', 10.0 cm) were slightly less than and four times greater than those used in the feeder arrays described in Chapter 2. The larger of the two horizontal distances between cue-feeder pairs ('Wide', 19.0 cm) was determined by the width of the testing rooms. The smaller cue-feeder pair separation ('Thin', 3.0 cm) was determined by the width of the photocell placed behind each feeder for recording visits by the birds. The entire array of six feeders at the narrow cue-feeder pair separation fit easily between any two adjacent cue-feeder pairs at the larger horizontal separation.

A different group of five hummingbirds was tested on each of the four treatments. The Short-Thin, Tall-Wide and Tall-Thin treatments were tested concurrently in 1989; the Short-Wide treatment was tested in 1990. The same training and testing procedures were used in both years.

Experimental environment

Three rectangular rooms (1.3 x 2.5 x 2.5 m high), each lighted by two overhead 40 W incandescent bulbs, were used for testing. A horizontal array of six feeders equally spaced on a thin metal panel painted flat green occupied a portion of one end wall in each room. Feeders were marked by round 19-mm diameter florescent orange Avery labels with central 3-mm diameter holes. Behind each feeder was an infrared photocell which detected the presence of a hummingbirds' bill. A small food reservoir (i.e. a disposable syringe needle fitting; see Tamm 1987, Figure 2) was also positioned behind each feeder and if a feeder was designated as correct (i.e. rewarding), a miniature solenoid valve released 2 μl of 20% sucrose solution (mass/mass) into the reservoir immediately upon insertion of a birds' bill into the feeder. If a bird visited a feeder designated as incorrect, no sucrose droplet was released into the feeders' reservoir. A small red light (4 mm diameter LED) protruded slightly through the metal panel above each feeder; a lighted one signalled that the feeder directly below it was profitable. A computer controlled the LEDs, dispensed the food, and recorded the time and duration of all visits to feeders and perches.

Hummingbirds were free to fly and visit feeders at all times even though they could obtain food only during feeding trials and only from correct feeders. Between brief foraging bouts and short non-foraging flights around the room, they spent most of their time on a perch (1.5 m

high and 1.8 m from the center of the feeder array) which placed them at eye level with the feeders.

Training

On the morning of the day before testing, hummingbirds were placed in training cages identical to their home cages except that food was available only from an array feeder similar in appearance to those in the testing rooms. Birds quickly learned to feed from these feeders and they were moved to the experimental rooms in the afternoon. Until experimental training began the following morning, a standard commercial feeder was hung in front of a central array feeder and marked with a florescent orange Avery label around the access hole. The other array feeders were covered.

At 0800 h the next morning, I removed the standard feeder from each room and exposed one array feeder and the unlit cue above it. After birds had fed several times from the array feeder, its cue was lit and training continued. After several more feedings, all other feeders were exposed, a new feeder was set to provide food and the cue above it was lit. After several feedings from the new cue-feeder pair, typically interspersed with visits to unprofitable feeders, the cue and profitability were reassigned to another new cue-feeder pair. Training lasted until all six cue-feeder pairs had been presented once to each bird (approximately 2 h) with only

one cue-feeder pair profitable at any one time. Testing followed training immediately.

Testing

Each hummingbird was tested on two successive days; each of the two days began with the initial training as described above and was followed by 60 feeding trials during which data were collected. Between testing sessions birds remained in the rooms with the feeder arrays covered and with a standard feeder hanging in front of a central array feeder. Birds were returned to their home cages immediately after they completed their second day of testing.

Feeding trials began with the nearly simultaneous occurrence (i.e. within a few hundredths of a second) of four events: (1) one cue-feeder pair among the six pairs in feeder arrays was selected at random and designated as correct for that trial (the same random sequence, however, was used for all testing sessions); (2) the cue above the correct feeder was lit; (3) the correct feeder was set to provide 2 μl for each visit up to a maximum of 12 visits; and, (4) a soft buzzer was sounded for .5 s. Birds quickly learned to turn their head toward the feeder array when trials started. On their first day, they usually remained on their perches for several minutes or more after the start of feeding trials, but by the end of the second day, most birds flew toward the array within 10 s (70% of all 600 trials for all birds on the latter half of Day 2). A total of 24

μl of sucrose solution, which could be obtained by 12 probes to the correct feeder, was available during each feeding trial. This limit could provide food at slightly more than average ad libitum feeding rates. Birds were free to obtain the limit by any sequence of visits to the one correct and five wrong feeders, i.e. they paid no penalties for visits to wrong feeders other than lost time and energy.

Feeding trials ended when the correct feeder had been visited 12 times, or after at least one feeder had been visited and a bird had returned to its perch. The light cue was then turned off and no more food was delivered by its feeder. Even though no food was available from feeders between trials, birds often visited them, particularly on the first testing day or if they had been unsuccessful during the preceding feeding trial. On the second testing day, successful birds rarely visited feeders between trials, however, they often inspected unlit cues and hovered in front of feeders without probing them. The interval between trials was 2 min or as soon thereafter as a bird had perched.

Data analysis

Hummingbird learning was evaluated by correct choices, i.e. first visits in feeding trials that were to correct (cued) feeders. Individuals performed statistically better than chance (16.7%) on testing days if they scored more than 16 correct choices in 60 trials (>26.7%) by chi-square analysis. On Day 1, bird 8 in Tall-Wide and bird 18 in Short-Wide

completed only 51 and 55 trials, respectively, and their scores were compared to appropriately adjusted chance levels. For all statistical comparisons among treatments, percentage correct choices were first arcsine transformed.

The effects of vertical distance between cues and their feeders and horizontal distance between cue-feeder pairs were evaluated by two-way fixed effects analysis of variance (ANOVA). Individual learning scores were highly variable on Day 1 and for this reason, I used only Day 2 scores in statistical comparisons among treatments. It is not surprising that Day 1 results would be variable. The birds began the experiment with only about two hours of experience with the cue-feeder association and with no experience with the experimental protocol and they were undoubtedly learning both in early trials.

RESULTS

Effects of treatments on learning

The birds in the two treatments with the short vertical separation between cues and feeders (Short-Thin and Short-Wide) learned the cue-feeder association relatively quickly (Fig. 4). Several birds in either treatment made only one or two wrong first choices in all 120 trials and only one bird (on Short-Thin) did not perform perfectly by the end of Day 1. This bird improved dramatically on Day 2, though; it made only four

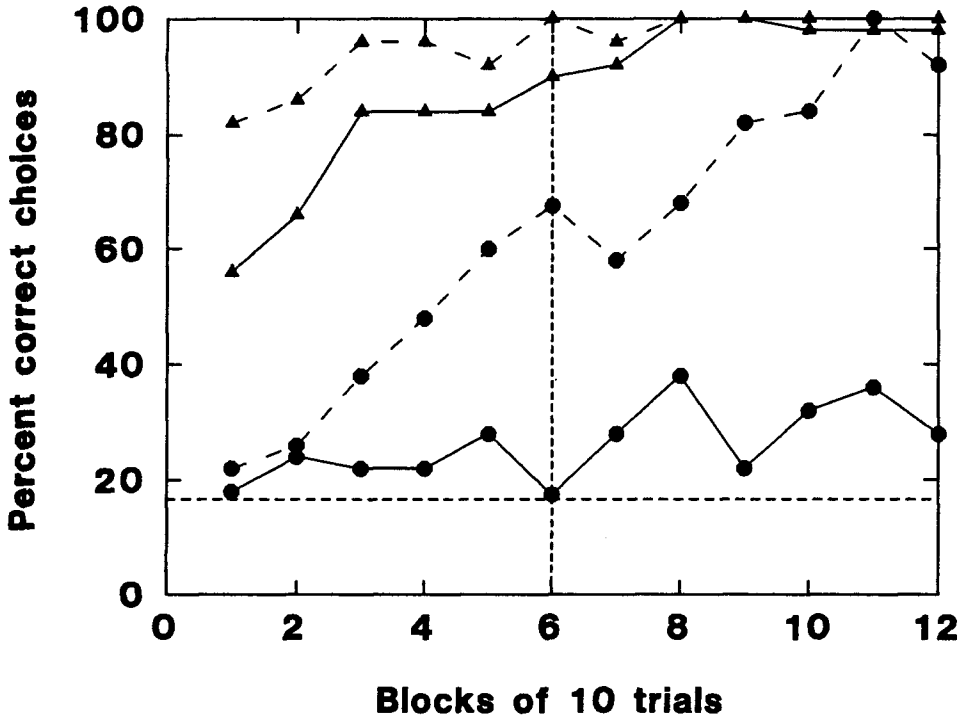


Figure 4. Mean percentage correct first choices in the four experimental treatments of experiment 3 (N = 5 for each treatment). The solid line and circles indicates the Tall-Thin treatment, the dashed line and circles the Tall-Wide treatment, the solid line and triangles the Short-Thin treatment, and the dashed line and triangles the Short-Wide treatment. The vertical dashed line separates Day 1 and Day 2. The horizontal dashed line indicates the level of chance performance.

wrong first choices, all in the first five trials. Despite the relatively poorer performance of that one bird, the Short-Thin and Short-Wide groups did not differ significantly in correct choices even in the first 10 trials on Day 1 when the apparent difference between the groups was greatest (two-tailed t test: $t(8) = 1.89$, $p = .10$; see Fig. 4). Clearly, birds learned both Short treatments with relative ease, and the fact that the Short-Wide treatment was not tested concurrently with the other treatments is unlikely to have had a dramatic effect on the overall results.

The Tall-Wide group learned more slowly on average but they performed as well as birds on the two Short treatments in the last 20 trials of Day 2. Two of them performed almost as well as birds in the Short treatments. These two began Day 1 at chance, well below the birds in the Short treatments, but they reached essentially perfect performance by the end of the day.

The Tall-Thin group performed least well of the four groups. None of these five birds improved beyond chance on Day 1 (range of overall scores: 20.0 - 25.4%) and only two performed better than chance on Day 2 (46.7% for bird 23 and 51.7% for bird 18). Those two birds improved quite suddenly. Bird 18 jumped from zero correct choices in the first 10 trials of Day 2 to 31 correct choices in the remaining 50 trials (62%). Bird 23 jumped from 3 correct choices in the last 10 trials of Day 1 to 7 correct choices in the first 10 trials of Day 2; it then continued to perform well and scored 21 correct choices out of the last 50 trials (42%).

Tests of specific hypotheses

The learning curves for each treatment indicate that both vertical distance between cues and feeders and horizontal distance between cue-feeder pairs strongly influenced how quickly and how well hummingbirds learned the spatial association between cues and feeders (Fig. 4). They also indicate that these two factors interacted in their effects as learning was similar between the two Short treatments but markedly different between the two Tall treatments. A two-way ANOVA of percentage correct choices on Day 2 confirmed all of these results (see Table 1). Thus, this experiment provides clear evidence that hummingbird learning is influenced by both separation of cues from feeders and separation of cue-feeder pairs.

Other responses to the treatments

Not all measures of learning and performance were influenced by both vertical and horizontal distance. One such measure was the number of profitable visits per feeding trial. A two-way ANOVA based on mean values calculated across trials for each individual within groups indicated that this measure was significantly related only to vertical distance between cues and feeders (see Table 1). The birds were free to visit any number and sequence of feeders in feeding trials and it is puzzling that any bird which found the correct feeder would cease probing it before additional probes produced no more food. However, the consequence of ending foraging bouts before all available food was obtained was that birds in the Tall

Table 1. Summary of mean responses to the treatments on Day 2 of experiment 3 and results of two-way ANOVAs.

	Treatment means				Sources of variation in ANOVA		
Measure of performance	S-T	S-W	T-T	T-W	H	V	H x V
Correct 1st choices (%)	97.7	99.3	30.7	80.7	20.45***	80.12***	13.16**
Profitable visits/trial	10.1	9.2	5.1	7.9	1.00	10.73**	3.94
Time to choose 1st (s)	1.03	1.01	1.73	1.49	0.06	7.13*	0.27

Sources of variation in ANOVA: H = horizontal distance between cue-feeder pairs; V = vertical distance between cues and their feeders; H x V = interaction of H and V factors. The values under the sources of variation are F values; df = 1,16 for each factor in each test. The asterisks represent p values: *** $p < .001$; ** $p < .01$; * $p < .05$. Sample size for each treatment is 5 birds. Percent correct first choices were arcsin transformed for the ANOVA. Number of profitable visits per feeding trial and time to choose the first feeder in feeding trials are means of average individual responses in 60 trials on Day 2.

treatments averaged less food per feeding trial out of the total quantity available (Tall-Thin, 43%; Tall-Wide, 66%) than those in the Short treatments (Short-Thin, 84%; Short-Wide, 77%).

Vertical distance between cues and feeders was also the only significant effect in a two-way ANOVA of the mean duration of the flight from the perch to the first feeder visited in feeding trials (Table 1). These flights were about .5 s shorter in the Short treatments (Short-Thin, 1.03 s; Short-Wide, 1.01 s) than in the Tall treatments (Tall-Thin, 1.73 s; Tall-Wide, 1.49 s). This measure was also negatively correlated with mean group percentage correct choices ($r = -.92$, $t(2) = -3.22$, $p = .08$) and the correlation between the two variables explained 84% of the variance in the mean group learning scores. The individual mean flight durations and percentage correct choices were also negatively correlated within treatments, except in the Short-Thin group. However, only in Tall-Thin (i.e. the most difficult treatment) was the correlation significant ($r = -.89$, $t(3) = -3.30$, $p = .05$). I can provide no behavioral or psychological explanation for the variation within and between treatments in the duration of flights from the perch to the first probe but the biological consequence is clear: net energy intake rate would necessarily be lower for birds who flew longer before visiting the feeder array.

Analysis of errors in the Tall-Thin treatment

That two birds in the Tall-Thin treatment performed significantly above chance in correct choices on Day 2 of the experiment shows that hummingbirds can associate cues widely separated from feeders, even under difficult conditions such as with close spacing between cue-feeder pairs. That the other three birds in the treatment performed poorly by this measure, however, does not necessarily mean that they did not learn the cue-feeder association. One possibility is that they learned the association but failed to project correctly between cues and their feeders in the closely packed array. In other words, close packing may have interfered with practical application of what they learned. Such interference could also explain why the two birds who performed better than chance, nonetheless failed to perform perfectly by the end of the experiment, as did birds in the other treatments.

If birds had learned the spatial association between cues and feeders but were unable to perform it well, then wrong first choices should cluster beside correct feeders. It is also reasonable to expect that a high proportion of wrong first choices should be followed by successful second visits. In addition, both of these measures of performance should improve as the experiment proceeds. Support for these predicted effects would provide strong evidence that the birds had indeed learned the cue-feeder association even though their first choices were mainly to wrong feeders.

The two birds who performed best on Tall-Thin clearly showed each of the predicted effects. Their wrong first visits were randomly distributed with respect to correct feeders early in the experiment before they made many correct first visits, but 83% and 100% of their wrong first visits were beside correct feeders in the last 30 trials of Day 2 (birds 18 and 23, respectively; Fig. 5). These birds also became increasingly more successful on second visits after wrong first choices as the experiment progressed (Fig. 6). Most of their second visits were unsuccessful early in the experiment, but 73% of both birds' wrong first choices were immediately followed by successful second visits in the last 30 trials. It would be difficult to conclude anything other than that these birds demonstrated learning even in their errors because the correct feeder changed location each trial and their errors followed it. The most plausible explanation for their behavior is that they had learned the association between cues and feeders but for some reason were unable to perform as well as birds in the other treatments.

In contrast to the two birds that performed well, I found little evidence that the other three in the Tall-Thin treatment learned much about the spatial association between cues and rewarding feeders. None of these birds made more wrong first choices beside correct feeders than expected by chance in any block of 30 trials (chance = 40%; log-likelihood chi-square tests: all Gs < 3.27, all ps > .05), although bird 15 showed a slightly increasing trend by this measure (Fig. 5). Bird 4 visited the correct feeder just after wrong first choices more often than expected by

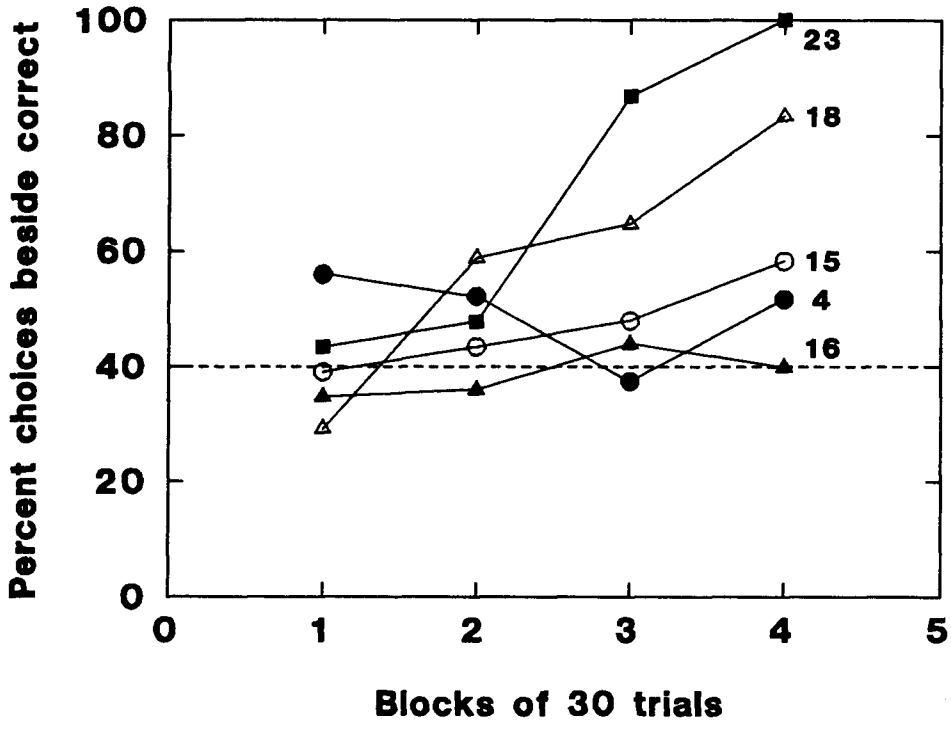


Figure 5. Percentage wrong first choices beside correct feeders for the 5 birds in the Tall-Thin treatment of experiment 3. The numbers to the right of each line indicate individual birds. The horizontal dashed line indicates chance performance (40%). The percentages are based on ratios whose denominators are the numbers of wrong first choices in each block of 30 trials.

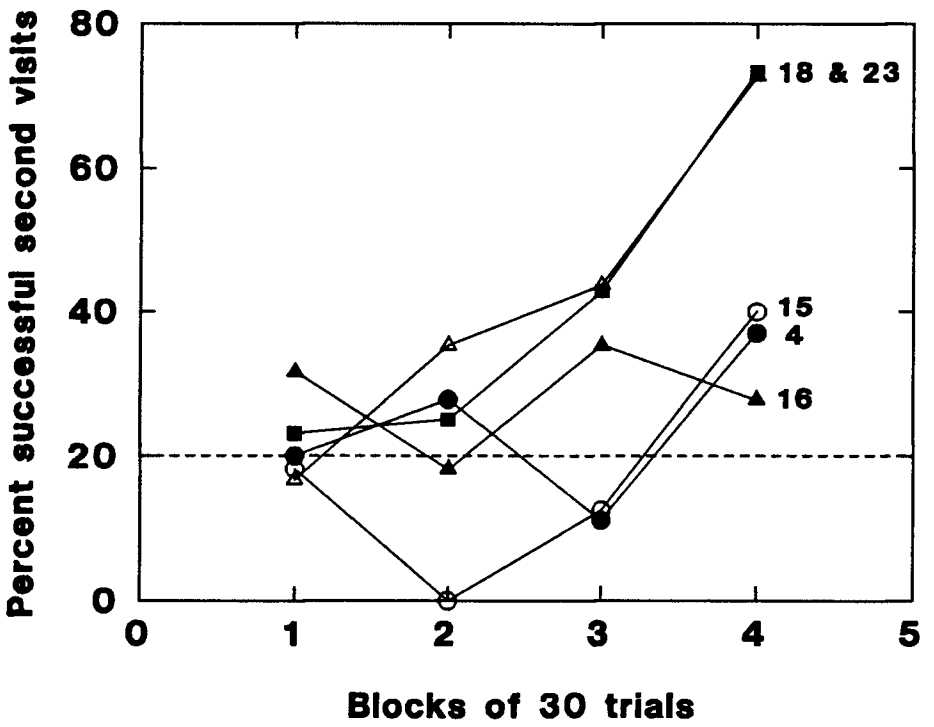


Figure 6. Percentage wrong first choices immediately followed by successful second visits for the 5 birds in the Tall-Thin treatment of experiment 3. Numbers to the right of each line indicate individual birds. The horizontal dashed line indicates chance performance (20%). Percentages are based on ratios whose denominators are the numbers of wrong first choices followed by at least one other visit in each block of 30 trials.

chance during the last 30 trials (chance = 20%; log-likelihood chi-square test: $G = 4.18$, $p < .05$) but its erratic performance overall is not convincing evidence for learning (Fig. 6). Bird 15 showed an increasing trend by this measure as well, but neither it nor bird 16 exceeded chance in any quarter of the experiment.

DISCUSSION

The larger vertical separation between cues and feeders of the Tall treatments clearly inhibited hummingbird learning compared to the smaller separation of the Short treatments. This result was predicted from the Gestalt principle of spatial proximity and expected from the experimental results of previous studies with other animals (McClearn & Harlow 1954; Stollnitz & Schrier 1962; Schrier et al. 1963; Milner et al. 1979; Iwai et al. 1986). Nevertheless, all five birds in the Tall-Wide treatment and two birds in the Tall-Thin treatment learned relatively fast and with less training compared to monkeys tested at a similar separation distance. For example, in one study which showed relatively fast learning, four rhesus monkeys averaged 90% correct responses within 190 trials on a two-choice color discrimination problem with a 10 cm cue-response separation (McClearn & Harlow 1954). However, the 10 cm separation trials were randomly intermixed with smaller separation trials, on which the monkeys performed well, and success on the smaller separations quite possibly transferred to the larger ones (Stollnitz 1965). In another study, rhesus monkeys learned first with contiguous cues and then the distance between cues

and response locations was gradually increased. Under this procedure, one monkey reached criterion (2 consecutive correct responses) by 120 trials with an 8 cm separation (Schrier et al. 1963). In both studies, the monkeys had the benefit of extensive previous experience with discrimination procedures and they also received further training before the experiment.

In contrast to those studies with primates, the experimentally-naive hummingbirds were given only two hours of training immediately before testing and each individual was tested at one separation distance only. With no special training procedures, two birds on the Tall-Wide treatment reached nearly perfect performance within 60 trials and the rest reached it within 100 trials. Even on the Tall-Thin treatment, which I predicted to be difficult because of both separation distance between cues and feeders and interference with the visual association between closely packed cue-feeder pairs, two birds performed well above chance on the second day of the experiment. The birds' success was perhaps even more remarkable considering that the 10 cm separation between cues and feeders was greater than the distance from the tip of their bills to the tip of their tails (approximately 8 cm). No other animal has been tested with a spatial separation between cues and response locations which exceeded their maximum body length. The hummingbirds may have performed well, because as discussed in Chapter 2, they may use spatial associations while foraging in nature and the experimental procedures I used accommodated certain features of the natural foraging situation.

The most significant results of this study are that hummingbird learning was influenced not only by distance between cues and response locations, but also by distance between neighboring cue-response location pairs. In addition, the vertical and horizontal separations interacted in their effects on learning and this result strongly suggests that learning is a consequence of relative, rather than absolute, spacing among stimuli. Thus, the difficulty of associating cues separated from response locations by some absolute distance can be varied markedly by adjusting the proximity of other stimuli in the visual field.

These results are significant because, to my knowledge, they are new to the study of spatial association learning and they are not well predicted by associative learning theory. The associative principle of stimulus similarity (Rescorla 1980; Mackintosh 1983) makes the general prediction that the small, round, red light cues should have been readily associated with the feeders marked by small, florescent-orange circles (which they were), but it does not predict any of the specific results of this study. In contrast, the Gestalt principle of spatial proximity predicted them all.

The successful application of the principle of spatial proximity in this study suggests that the Gestalt principles provide a useful theoretical framework for studying spatial association learning. Numerous principles of grouping were proposed by the Gestalt theorists (e.g. Koffka 1935; Kohler 1947; Wertheimer 1950), none of which have been refuted (Rock &

Palmer 1990), and two new principles have been recently added by Rock and Palmer (1990). Thus, Gestalt theory provides an established set of theoretical principles from which many testable predictions, both general and specific, can be generated. For example, a general prediction from Gestalt theory is that for any geometric configuration of cues and response locations, factors that strengthen visual association among neighboring cues or neighboring response locations should interfere with the visual association, and hence learning of the spatial relationship between cues and their corresponding response locations. Conversely, factors that strengthen the visual association between cues and their response locations should reduce the detrimental effect of cue-response separations and facilitate learning.

Each grouping principle specifies a particular factor which, depending on its application to an array of cues and response locations, predicts facilitation, inhibition, or no effect on learning. Consider the principle of connectedness. It predicts that visible connections among particular elements of stimulus arrays should strongly influence the degree to which relationships between pairs of the stimuli should be perceived and learned (Rock & Palmer 1990). For example, lines connecting cues with cues and response locations with response locations, or cues with noncorresponding response locations, should interfere with visual associations between cues and their corresponding response locations and interfere with learning of associations between them. On the other hand, lines connecting cues with correct response locations (such as the 'nectar

guides' in many natural flowers) should visually enhance the spatial relationship between cues and response locations and facilitate associative learning. They may also promote learning by decreasing any visual confusion among neighboring cue and response location pairs (as could occur among closely spaced flowers).

The Gestalt principles clearly suggest novel hypotheses and generate predictions that are different from those generated by associative learning theory. Other areas of research on learning and memory have also recognized this fact and have advanced by testing alternative hypotheses generated from Gestalt and associative theory (Greeno et al. 1978; Rescorla 1985b). Further testing is clearly necessary to confirm the usefulness of the Gestalt principles to the study of spatial association learning, but the initial indications from the present study are quite promising.

The effects of spatial separation on learning have been known since early studies by Kohler (1925), Lashley (1930) and Gellermann (1933), but have played almost no role in the development of associative learning theory. Instead, associative learning theory is derived mainly from the study of temporal separations between stimuli and responses (Mackintosh 1983; Bowe 1984). One reason that has been given for this historical bias is that spatially separated cues and response locations may result in delays between when cues are observed and responses are made (Mackintosh 1983). Thus, it is possible that the well-known effects of temporal separation could explain variation in learning attributed to spatial separa-

tion. At best, spatial and temporal effects may be unavoidably confounded in spatial association tasks (Rescorla & Cunningham 1979; Mackintosh 1983).

Spatial and temporal effects have proven difficult to disaggregate experimentally in other studies of learning (Rescorla & Cunningham 1979) but one simple approach to this problem is to ask whether temporal effects alone can account for observed results. Based on the results of many conditioning and short-term memory studies (Rescorla & Holland 1982; Mackintosh 1983), poorer performance should result when longer delays occur between observation of cues and performance of responses. In addition, similar performance should result from similar delays. In my study, birds in the Tall treatments delayed significantly longer in making first choices compared to birds in the Short treatments. Delays in making choices were also statistically similar in the two Short treatments and in the two Tall treatments. From these results, one should expect poorer performance on the Tall treatments and similar performance in both of the Short treatments and in the Tall treatments. Neither of these expectations was well supported. First, performance was poor only in the Tall-Thin treatment; in the Tall-Wide treatment it reached the same near perfect level that it did in the Short treatments. Second, performance was highly similar in the two Short treatments but it was dramatically different in the two Tall treatments. Clearly, temporal effects alone cannot account for the results of this study.

Why hummingbirds delayed in making choices in the treatments with the larger cue-response separation, or what they did during the delay, are interesting questions which remain to be answered. One factor that should be kept in mind is that the delays observed in this study were not determined by experimental procedure as they are in most studies of conditioning and short-term memory. Delays in choices were part of the responses of individual birds to the experimental treatments, and consequently, the delays are probably best interpreted as correlates, rather than determinants, of performance.

In the Tall-Thin treatment, two birds learned the cue-feeder association but they did not reach perfect scores as did birds in the other three treatments. It is unclear why they did not perform perfectly after they learned the association, but several explanations, not necessarily exclusive, are possible: 1) their knowledge of the cue-feeder association was imperfect; 2) they did not observe cues before they chose feeders; or, 3) their knowledge of the association was perfect but their ability to project between the correct cue and response location was not. The first two explanations are difficult to assess. The third explanation, however, would be strongly supported if the birds made increasingly more of their wrong first choices closer to correct feeders. This is exactly what they did. Early in the experiment their errors were distributed randomly with respect to correct feeders, but by the end, nearly all their errors were immediately beside correct feeders. The best interpretation for the birds' behavior is that the birds learned the association but were able to

locate the correct feeder only approximately. This is possibly the first explanation for poorer performance at larger spatial separations that proposes difficulty in performance of a learned association rather than difficulty in learning an association (see Iwai et al. 1986).

In conclusion, the results of this study with hummingbirds are consistent with predictions based on the Gestalt principle of spatial proximity and suggest that associative learning is profoundly influenced by interacting spatial relationships among stimuli. The extent to which this is true awaits further testing of the principle of spatial proximity and other Gestalt principles as well. The Gestalt principles were intended to apply across sensory systems and animal species and thus they could provide both a useful and a general theoretical framework for the study of spatial association learning.

CHAPTER 4

EFFECTS OF VISIBLE CONNECTIONS ON SPATIAL ASSOCIATION LEARNING

INTRODUCTION

The general consensus from studies of spatial association learning is that learning is determined by distance between cues and response locations (Davis 1974; Milner et al. 1979; Iwai et al. 1986; Butter et al. 1982). Experiment 3 reported in the previous chapter, however, showed that learning at a particular separation could be influenced significantly by changing the relative proximity of neighboring cues and neighboring response locations. Thus for rufous hummingbirds, and perhaps other animals as well, learning is not determined solely by absolute separation distance. I used the Gestalt principle of grouping by spatial proximity (Wertheimer 1950) to predict that particular result, but other Gestalt principles predict this as well.

Consider, for example, the newly proposed principle of grouping by connectedness (Rock & Palmer 1990). The hypothesis it generates is that continuous visible connections between discrete cues or objects should strongly influence the extent to which relationships between particular stimuli are perceived and learned. As applied to spatial association

learning, this principle suggests that connections such as 'lines' leading from cues to their corresponding response locations should facilitate learning of the relationship between cues and response locations.

Another Gestalt principle, that of closure (Wertheimer 1950), predicts that visible connections need not be complete to promote visual associations, and hence, learning of functional relationships between components of stimulus arrays. Broken or dotted lines, for example, can also promote visual associations (Koffka 1935; Boucart & Bonnet 1991). Studies of visual processing have shown that the human visual system extracts the overall orientation of similarly aligned elements and in effect, ignores gaps between them (Boucart & Bonnet 1991; Pomerantz 1981). A practical application of this grouping principle is illustrated by the ability of humans to use broken or dotted lines to convey functional relationships among points in graphical displays. As applied to spatial association learning, the principle of closure predicts that interrupted, or broken, connections should promote learning of relationships between cues and response locations.

Both Gestalt principles, connectedness and closure, predict that visible extensions between cues and response locations, even if interrupted, should reduce the detrimental effects of separation distance. I tested this prediction in experiment 4. As in my previous experiments, I tested hummingbirds foraging from arrays of spatially separated cues and feeders. An outcome in favour of the prediction would provide additional

support for the idea I proposed in Chapter 3, that spatial association learning is not determined by absolute distance between cues and response locations. It would also provide encouragement for continued application of the Gestalt principles to the study of spatial association learning.

If visible connections facilitate hummingbird learning, there are at least two mechanisms by which hummingbirds could respond to them. The first mechanism, derived from Gestalt theory, involves spatial association learning but the second, derived from associative learning theory, does not. Gestalt theory suggests that visible connections serve primarily to delineate the spatial relationship between cues and response locations and that learning consists of acquiring knowledge of the spatial relationship (Kohler 1947). This hypothesis predicts that removal of the visible connections should result in little disruption of performance of a previously learned spatial association. In contrast, associative learning theory suggests that visible connections unite each cue and response location into a single contiguous stimulus and that learning consists of association of this stimulus complex with reinforcement (Williams 1991). According to this hypothesis, visible connections eliminate the necessity of learning spatial relationships between cues and response locations, and it predicts that removal of the connections should disrupt performance of the learned association.

In two experiments following experiment 4, I examined the role of visible connections in spatial association learning. In experiment 5, I

first determined the likelihood with which hummingbirds learn spatial associations in the absence of visible connections between cues and feeders. This experiment consisted of testing birds with a diagonal relationship between cues and feeders. Such a relationship would require the use of distance and direction in selection of correct feeders and successful performance would suggest that hummingbirds can learn spatial relationships. In experiment 6, I then tested whether hummingbirds learn spatial associations in the presence of connections between cues and feeders by removing the connections after birds had learned to select feeders correctly with them.

EXPERIMENT 4

In this experiment, I tested the prediction derived from the Gestalt principles of connectedness and closure that visible extensions between cues and response locations should facilitate spatial association learning. They suggest that both continuous and interrupted connections should facilitate learning, and I therefore tested hummingbirds on two different arrays with one or the other type placed between spatially separated cues and feeders. On one array, a narrow bar of colored tape extended between each cue and its feeder. In the other, a bar of colored tape also extended between each cue and its feeder, but two sections were removed from each bar to give them the appearance of broken lines. I also tested birds on a control array with no connections between cues and feeders.

Hummingbirds may be particularly appropriate subjects for testing the effects of visible connections on learning because in their natural environments they forage from many wild flower species which present some form of 'nectar guide' (Meeuse 1961; Waser & Price 1983). Nectar guides vary between species of flowers, ranging from patterns of lines, spots or concentric circles, but in each case, they provide a striking visual contrast against the general color of a flower and are used by foragers to direct them to nectar sources within flowers (Manning 1956; Meeuse 1961; Waser & Price 1983). Given the use of such visible aids in the natural foraging behavior of hummingbirds, there is a good basis for expecting them to respond to visible connections between cues and feeders in laboratory experiments.

Method

Subjects

Thirty experimentally-naive adult rufous hummingbirds (Selasphorus rufus) were tested in this experiment. Eighteen of the birds (10 females and 8 males) were captured and tested in one summer; the other 12 (7 females and 5 males) were captured and tested in the next. The same training and testing procedures were used in both years. When not being tested in this experiment, birds had free access to food in their home cages at all times.

Apparatus and procedures

The birds were randomly assigned and tested in one of three treatments, 10 birds per treatment. I call the two treatments using visible connections the Solid Guides and the Broken Guides treatments. Performance in these treatments was compared to performance in a third treatment, No Guides, in which nothing extended between cues and feeders. For each treatment, the cue-feeder array was similar to those used in my previous experiments in that each of six feeders in a horizontal row had a small, red light cue (an LED) positioned directly above it. In this particular experiment, the horizontal spacing between cue-feeder pairs was 3 cm and the vertical separation between cues and their feeders was 12 cm.

A 9 mm wide bar of florescent orange 'Dymo' tape connected each cue with the feeder directly below it in the Solid Guides treatment, contacting the florescent orange Avery label surrounding feeders and enclosing and extending 1 cm above the LED cues (see Fig. 7). The Broken Guides treatment was identical but the bars of tape had two 3 cm long sections removed at regularly spaced intervals. A 2 cm long section contiguous with each feeder projected upwards toward its cue; another 2 cm long section contiguous with each cue projected downwards toward its feeder. A third 2 cm long section was centered between the other two sections. In total, 50% of the distance between cues and feeders was covered by tape in the Broken Guides treatment.

The solid or broken bars of tape for each treatment were pasted to transparent plastic masks which were positioned over the cue-feeder arrays in the testing rooms. A transparent mask was also used for the No Guides treatment. These masks enabled easy transfer of the treatments among the testing rooms and each time testing was begun for a new set of three birds, the three treatments were assigned randomly among the three testing rooms. Birds were tested for 60 trials on each of three successive days. All testing days began with a brief training period as described for the experiment 3 of Chapter 3.

The responses of hummingbirds to the treatments were assessed by statistical comparison of mean percentage correct choices on the final day (Day 3) of the experiment. Percentage scores were arcsine transformed for statistical analyses. Mean scores of correct choices in consecutive blocks of 10 trials were also calculated to allow visual comparison among the learning curves for each treatment.

Results and Discussion

General responses to the treatments

Based on results from studies with other animals (Milner et al. 1979; Davis 1974; Stollnitz 1965), and the overall results from the Tall-Thin treatment of Chapter 3, I expected hummingbirds to learn slowly or not at all in this experiment in which cues and feeders were relatively

far apart and cue-feeder pairs were quite close together. However, most of the birds in each treatment performed significantly better than chance (16.7%) in correct first choices by the end of the experiment (Fig. 7). Even in the No Guides treatment, 8 of 10 birds performed above chance on Day 3 and two of them exceeded 80% (Fig. 8). Most of the improvement in the No Guides treatment occurred on Day 2 and average performance leveled off around 46% on Day 3.

The birds on the Solid Guides treatment learned more quickly and performed better on average than those in either of the other two treatments (Fig. 7). All of them performed better than chance, four on Day 1. As a group they averaged 81.5% correct first choices on Day 3 and eight of them scored 85% or more. Performance of the Broken Guides group was intermediate between the Solid Guides and No Guides groups (Fig. 7) and the mean percentage correct choices on Day 3 was 64.1%. The overall trajectory of the mean learning curve for the Broken Guides group suggests that they were still improving by the end of the experiment and may have attained the nearly perfect performance level of the Solid Guides group if the experiment had been continued. The individual (bird 26) who performed best of all 30 birds in this experiment was in the Broken Guides group; this bird performed well above chance on Day 1 (43.3%) and made not a single error from trial 69 to trial 180 at the end of the experiment.

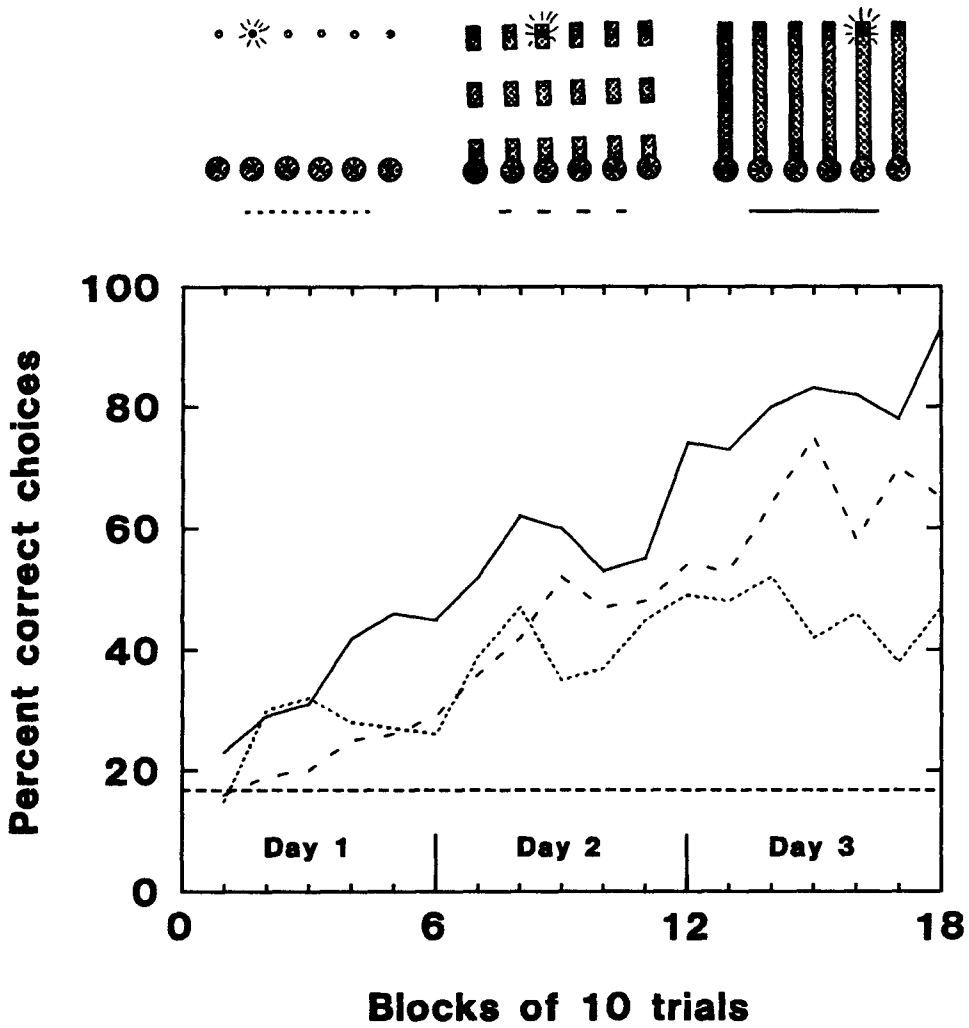


Figure 7. Mean percent correct first choices in the three treatments of experiment 4 (N = 10 birds for each treatment). The dotted, dashed, and solid lines indicate, respectively, the No Guides, Broken Guides, and Solid Guides treatments. The horizontal dashed line indicates chance performance (16.7%). The figures above the graph represent the 3 treatments and are drawn to actual scale.

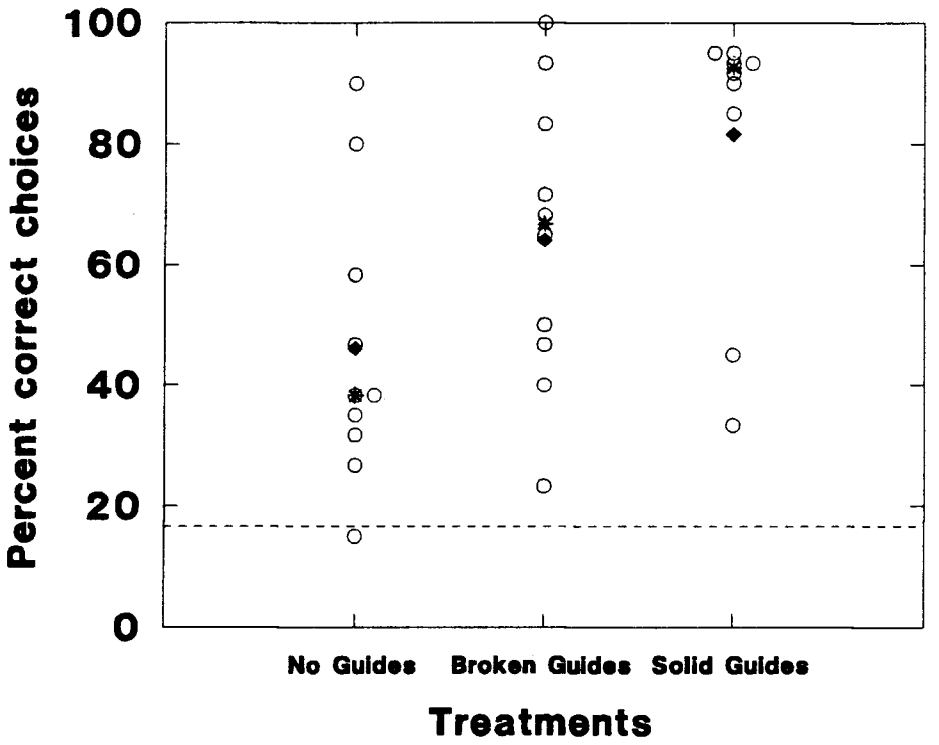


Figure 8. Percent correct choices in the 60 trials on Day 3 for each individual in the three treatments of experiment 4. The unfilled circles represent individual scores. The filled diamonds represent the mean for each treatment. The stars represent the medians. Repeated scores are shown beside each other. The horizontal dashed line indicates chance performance (16.7%).

Test of the prediction

To test my hypothesis that continuous and interrupted visible connections between cues and feeders should each facilitate spatial association learning, I compared mean performance of the three groups of birds on Day 3 in a one-way fixed effects analysis of variance. This analysis indicated that there was a significant difference in performance among the treatments, $F(2, 27) = 3.791$, $p = .035$, and I subsequently performed a Tukey test to determine which treatments differed from each other. Only the No Guides and Solid Guides groups differed significantly from each other ($p = .029$); performance of the Broken Guides group differed from neither of those two groups (both ps > .228).

These analyses indicate that the Solid Guides treatment clearly improved learning and performance compared to the No Guides treatment. They also suggest that the Broken Guides group reached a level of performance intermediate between the other two groups. This, in turn, suggests that the Broken Guides treatment did have some positive effect on learning, but not as much as the Solid Guides treatment. Further evidence that Broken Guides improved learning is that 9 of 10 birds in that treatment achieved higher than the median score of the birds in No Guides treatment in percentage correct choices on Day 3 (38.3%). In contrast, only two birds in the No Guides treatment scored above the median value for the Broken Guides treatment (Fig. 8).

I conclude overall that visible connections, particularly continuous ones, markedly improve how quickly hummingbirds learn spatial associations. The results of this experiment also provide added support for the conclusion of Chapter 3, that spatial association learning is not determined solely by absolute distance between cues and response locations. The two types of visible connections considerably reduced the inhibitory effects of one relatively difficult spatial separation. Visible connections effectively resulted in more birds achieving higher levels of performance in the Solid and Broken Guides treatments compared to the No Guides treatment.

EXPERIMENT 5

Studies of spatial association learning presume that animals learn by discovering the geometry of the spatial relationships between particular cues and response locations (Davis 1974; Butter et al. 1982). This assumption, however, has never been adequately tested because in all but one recent study of spatial association learning, subjects could have performed well by learning only one simple rule: "select the response location nearest the cue" (for examples, see Stollnitz 1965; Davis 1974). In the one study that is the exception (Rumbaugh et al. 1989), rhesus monkeys successfully learned to move computer-generated cues to specific places on video screens by manipulating joysticks. While that study has provided one of the best examples of rapid spatial association learning in nonhuman primates, it is unclear at present why the computer-video technology was

so easy for the two rhesus monkeys to learn and whether other species would learn as successfully as they did.

In studies that have used standard discrimination learning procedures, successful performance has not necessarily required learning of spatial relationships. Any procedure that requires only selection of the response location nearest the correct cue for successful performance does not necessarily require that animals employ spatial concepts such as distance or direction. In fact, simple attraction toward highly salient cues could effectively result in what would appear to be perfect performance of a learned spatial association.

The purpose of experiment 5 was to determine whether hummingbirds can learn a spatial relationship in which the correct feeder is not the one nearest the cue. The cue-feeder array I used was a slanted parallelogram in outline and the relationship between cues and their corresponding feeders was a diagonal one. The diagonal relationship was created by displacing the separate horizontal rows of the cues and the feeders in opposite directions. In this array, the feeder nearest the cue was unrewarding and successful performance required that birds avoid it. If birds had succeeded in all my other experiments only by approaching the feeder nearest the cue, then they should perform poorly with a diagonal relationship between cues and feeders. To determine how well birds learned the diagonal relationship, I compared their success with a second group that learned with the vertical relationship.

Method

Subjects

Eleven naive adult wild-caught rufous hummingbirds were tested in this experiment. Care and housing were the same as for the birds in previous experiments.

Apparatus and procedures

The three testing rooms used in this experiment were the same as those used in experiment 4. One room was outfitted with the vertical cue-feeder array of experiment 4. The other two were each outfitted with diagonal arrays. For the diagonal arrays, the row of feeders was shifted exactly one feeder position with respect to the row of cues. Thus, the cue at one end of each array had no feeder below it and the feeder at the other end had no cue above it. In one array, the feeders were displaced leftward of the cues and henceforth, I refer to it as the 'left' array. In the other, the feeders were displaced rightward and I refer to it as the 'right' array.

In all three arrays, 3 cm separated adjacent cues and adjacent feeders and 12 cm separated each cue from its feeder. In the vertical array, the distance between the row of cues and the row of feeders was 12 cm. In the diagonal arrays, however, the vertical distance between the rows was

reduced by .5 cm to maintain the separation distance of 12 cm between each cue and its feeder.

Five birds (all females) were tested in the Vertical treatment. Six birds (5 females and 1 male) were tested in the Diagonal treatment, three on the left diagonal and three on the right diagonal. Each bird was trained and then tested for 60 trials a day for three successive days. The training and testing procedures were as described in Chapter 3.

Results and Discussion

Overall responses to the treatments

The Vertical group improved consistently over the course of the experiment and averaged well above chance in percentage correct choices by the end of it (Fig. 9). Only one bird of the five tested did not show any evidence of learning by any measure. The Vertical group of this experiment achieved higher average Day 3 percentage correct choices (60.6%) compared to the birds in the identical No Guides treatment of experiment 4 (46.0%; compare Fig. 7 and Fig. 9). Both groups of birds were trained and tested by the same procedures and thus, I have no explanation for the difference in performance between them.

The Diagonal group also improved during the experiment, averaging 51.7% correct choices on Day 3. As in the Vertical treatment, only one bird failed to perform above chance by the final day. Comparison of the

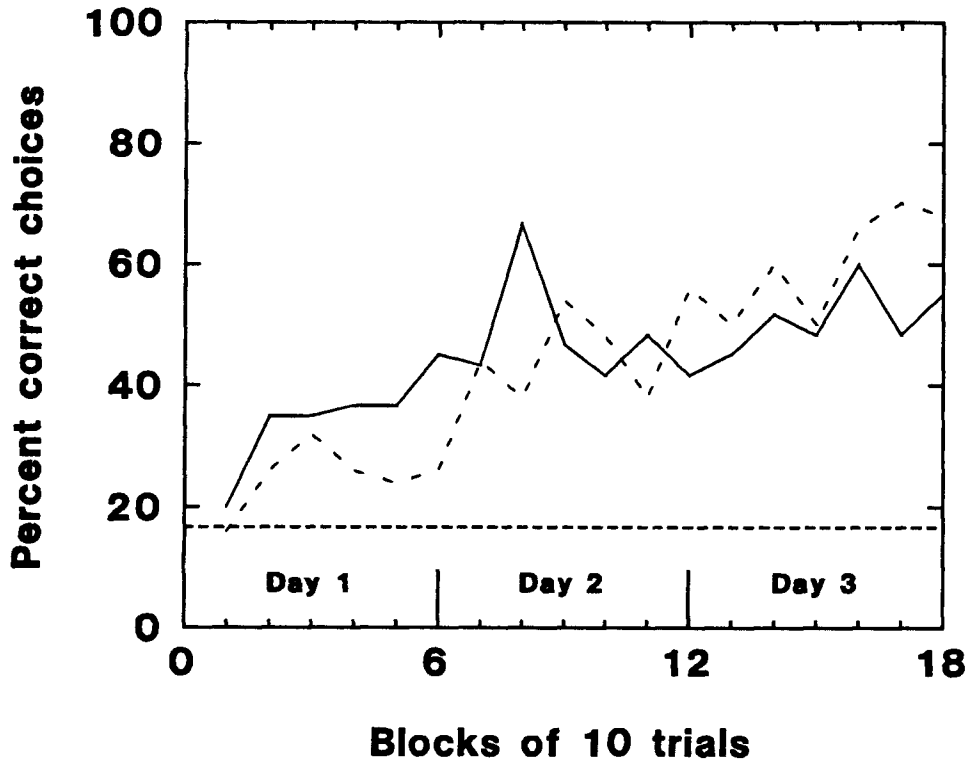


Figure 9. Mean percent correct first choices for the Vertical (dashed line) and Diagonal (solid line) treatments of experiment 5 (N = 5 and N = 6, respectively). The horizontal dashed line indicates chance performance (16.7%).

mean learning curves for the Diagonal and Vertical treatments showed that they learned at similar rates and that they performed equally well by the end of the experiment (Fig. 9). In the last 30 trials of Day 3, the Vertical and Diagonal groups averaged 20.4 and 16.3 correct choices, respectively, and these scores were not statistically different (Mann-Whitney U test, $U = 21.5$, $p = .117$).

Evidence for learning of spatial relationships

The birds in the Diagonal treatment averaged well above chance in first choices and performed as well as the birds in the Vertical treatment. These results show clearly that hummingbirds can learn a cue-feeder relationship in which the correct feeder is not simply the one nearest the cue. The birds tested in all my other experiments could have performed well by simply visiting the feeder nearest the cue, but this experiment demonstrates that the birds are not limited to such a learning mechanism.

On Day 3, the five birds which performed better than chance in first choices also made most of their errors immediately beside correct feeders (mean = 78.9%). This provides further evidence that they were attempting to visit correct feeders and that they had learned the spatial association. Nevertheless, closer examination of their errors suggests that their choices were influenced by lit cues. Consider a 3-feeder target which has the correct feeder at its center. On one side of this target is a feeder below the lit cue and on the other is a feeder two positions away

from the lit cue. If the birds were 'aiming' for the correct feeder, 'misses', or errors, should be distributed symmetrically on either side of it. However, if the birds were biased toward the cue, errors should occur mostly at the feeder below the cue.

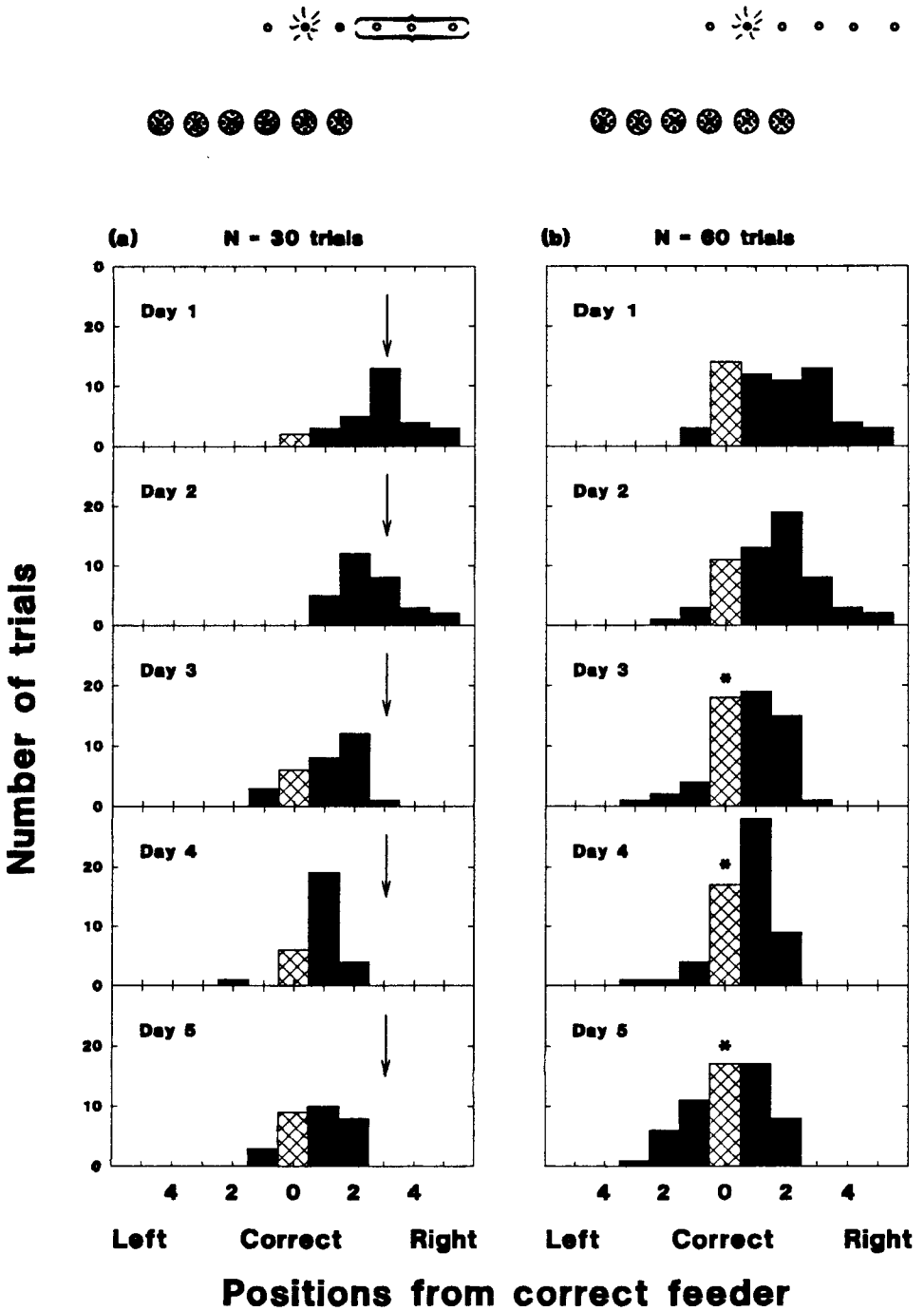
Of the errors made beside correct feeders, two birds made no more on the side nearest the cue than on the side opposite the cue (bird 18, 10 vs 10 errors; bird 24, 12 vs 6 errors; log-likelihood chi-square tests, both Gs < 2.03, ps > .10). These two were clearly aiming for the correct feeder. The other three birds, however, were significantly biased toward the feeder nearest the cue (bird 33, 11 vs 3 errors; bird 3, 16 vs 0 errors; bird 15, 21 vs 3 errors; all Gs > 20.43, ps < .001). The first choices of bird 3 are particularly puzzling; this bird made the most correct choices of the Diagonal group (44 of 60 trials) and regardless of which cue-feeder pair was correct on any trial, he made errors (16) only at the feeder below the lit cue.

Such consistent bias in the errors of several birds suggests that a tendency to choose the feeder nearest the cue, either learned or unlearned, could have interfered with their application of the diagonal cue-feeder relationship. If this were true, birds should find more exaggerated diagonals extremely difficult to learn. I explored this possibility in a pilot study with one bird and one exaggerated diagonal relationship. In this cue-feeder array, the row of feeders was shifted exactly three positions to the left with respect to the row of cues. The array was thus a

'left' diagonal; cues on the right half had no feeders below them and feeders on the left half had no cues above them (see Fig. 10). The distance between cues and their corresponding feeders was kept at 12 cm.

No naive birds were available for this pilot so I used bird 20 which had participated in the Diagonal Guides treatment of experiment 6. She performed well in that treatment but her experience was with a 'right' diagonal array and mainly with guides between cues and feeders. Immediately after she finished experiment 6, she was retrained on the exaggerated left diagonal and tested for five consecutive days. On Days 1 and 2, she performed at chance in correct choices (23.3% and 18.3%, respectively) but on the remaining three days she performed slightly better than chance (30%, 28.3%, and 28.3% for Days 3 to 5, respectively; chi-square values > 5.07, ps < .025). More convincing that she learned the cue-feeder association was the change in distribution of her errors relative to correct feeders (Fig. 10a). Figure 10a includes only trials in which the three cue-feeder pairs on the left half of the array (i.e. those in which cues had a feeder directly below them) were correct (30 trials each day), however, bear in mind that first choices could occur at any feeder. On Day 1, the bird made most of her first choices to the feeder below the lit cue and made no choices on the other side of the correct feeder. This initial bias could have been due to her recent experience with the moderate diagonal array in which the correct feeder was nearer the cue than in the exaggerated diagonal array. It could not have been due to a fixed bias because on each successive day she shifted more of her first choices closer to the correct

Figure 10. Frequency distribution of first choices relative to the location of correct feeders for each of the 5 days that Bird 20 was tested on the extreme left diagonal cue-feeder array. The figures above the 2 columns of panels represent the exaggerated diagonal treatment and are drawn to actual scale. (a) These panels include only trials (30 on each day) in which the signalling cue had a feeder below it, i.e. the correct feeder was one on the left half of the cue-feeder array. The brackets enclosing the cues on the right half of the cue-feeder array indicate that those cue-feeder pairs were excluded from the analysis. The arrows in each panel indicate the relative feeder position that was below the lit cues. (b) These panels show the distribution of first choices in all 60 trials of each day. The asterisk above the '0' position of the x-axis on Days 3 - 5 indicates significantly better than chance performance in correct choices. The 0 position on the x-axis indicates the correct feeder independent of its actual location in the feeder array. All other values on the x-axis, marked either left or right, indicate the number of feeders the birds' choice was from the correct feeder. For example, if the correct feeder in a trial was #1 at the left hand side of the feeder array but the bird chose #3 to the right of it, a score of '2-right' was recorded.


(a)
N = 30 trials
(b)
N = 60 trials
Day 1
Day 2
Day 3
Day 4
Day 5
Number of trials
0
10
20
4
2
0
2
4
Left
Correct
Right
Positions from correct feeder

feeder and chose correct feeders increasingly more often.

This same pattern of change was also apparent in the distribution of first choices for all six cue-feeder pairs (Fig. 10b). Considering the extreme conditions of this pilot, the nearly symmetrical distribution of bird 20's errors about correct feeders on Day 5 (Fig. 10b) and above chance performance in first choices is good evidence that she was attempting to apply a learned spatial relationship.

Overall conclusions

The most important result of this study is that hummingbirds can learn a spatial relationship that requires a more complex response than simply visiting the feeder nearest the cue. Five birds showed they could do so when one unrewarding feeder intervened between the cue and correct feeder and one bird showed it could do so when there were three. This experiment does not isolate the mechanism by which birds learned spatial associations, and indeed, it is possible that they could use different mechanisms with different spatial relationships or even at different stages of progress with one spatial relationship. What this experiment does show is that birds are not limited to the single mechanism of visiting the feeder nearest the cue.

EXPERIMENT 6

In experiment 4, visible connections strongly influenced how well hummingbirds learned a difficult spatial association. A plausible interpretation for the positive effects of the connections is that they facilitated associative learning of the spatial relationship between cues and their feeders (Rescorla 1985b). An alternative explanation, however, is possible. Each light cue, its column of tape, and corresponding feeder could have been perceived and learned by the hummingbirds as a single stimulus and it was this stimulus complex, rather than just the light cue, that became associated with food rewards. In effect, the columns of tape could have simplified the learning task by making cues contiguous with their feeders and thereby eliminated any need for learning spatial associations (Williams 1991). If this were the case, the associative principle of contiguity could account for the facilitative effect of visible connections and Gestalt principles need not be invoked (Williams 1991).

Experiment 6 was designed to discriminate between these two hypotheses concerning the facilitative effect of visible connections on hummingbird learning. In this experiment, hummingbirds learned for three days with continuous connections between cues and feeders and then on the fourth, the connections were removed. If the birds' performance dropped to chance after removal of the connections, this result would strongly indicate that they had not learned the spatial association between cues and feeders. If, on the other hand, the birds continued with better than chance performance after the connections were removed, this result would

suggest that they had learned the spatial association. It would also be consistent with the Gestalt interpretation of the effects of connectedness on learning.

Method

Subjects

Eleven naive adult wild-caught hummingbirds were tested in this experiment.

Apparatus and procedures

The birds were randomly assigned to one of two treatments, Vertical Guides (five birds) and Diagonal Guides (six birds). Half of the birds in the Diagonal Guides were tested on a 'right' diagonal array and half on a 'left' diagonal array (see experiment 5 for description of right and left arrays). These cue-feeder arrays and the testing rooms were the same as those used in experiment 5. The guides were similar to the Solid Guides used in experiment 4. Both the vertical and diagonal arrays were used because evidence that birds had learned spatial associations would be stronger if they performed well on two different relationships after removal of the connections.

The birds were trained and tested for 60 trials on each of four successive days. For the first three days they learned with the guides in

place but at the start of the fourth, the guides were removed. After this fourth testing day was completed, birds were returned to their home cages. All training and testing procedures were the same as those used for the two previous experiments.

Results and Discussion

Performance before guide removal

All five birds in the Vertical Guides treatment performed virtually perfectly by the end of Day 3 (Fig. 11a; mean correct choices on Day 3 = 92.0%) as had most of the birds in the Solid Guides treatment of experiment 4 (Day 3 mean = 81.5%). Two birds in this experiment exceeded 90% in a block of 10 trials by the end of Day 1 and the other three reached this level by the end of Day 2. In the Diagonal treatment (Fig. 11b), two birds did not perform significantly better than chance by the last day of testing with guides. The other four birds, however, performed at 90% or more correct choices (one on Day 1, one on Day 2, and two on Day 3). In addition, they performed better than the birds of experiment 5 which learned on the diagonal relationship without guides on the identical cue-feeder arrays (mean correct choices on Day 3 of this experiment = 85.5%, N = 4; experiment 5 = 58.7%, N = 5). This result adds support to my conclusion from experiment 4, that visible connections between cues and feeders facilitate learning of spatial associations.

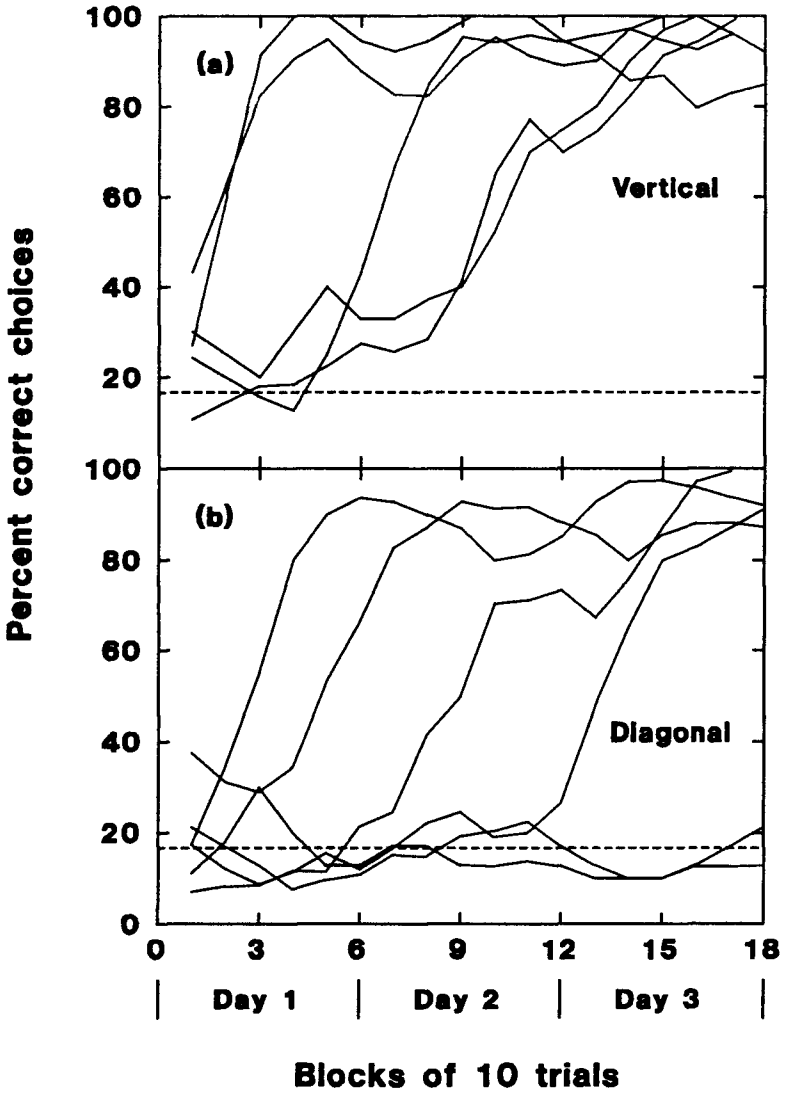


Figure 11. Individual learning curves before removal of guides for the birds in the Vertical Guides and Diagonal Guides treatments of experiment 6 (N = 5 and N = 6, respectively). The horizontal dashed line indicates chance performance (16.7%). The curves were subjected to lowess smoothing to make their individual forms easier to distinguish from each other.

Performance after guide removal

For the birds who performed well with guides (all 5 in the Vertical treatment and 4 of 6 in the Diagonal treatment), performance in percentage correct choices dropped on Day 4 when the guides were no longer in place (Fig. 12). The mean Day 4 scores for the Vertical and Diagonal treatments were 47.0 and 51.7%, respectively. None of the nine individuals, however, performed worse than expected by chance without the guides and some performed much better (chi-square analysis; all 9 chi-squares > 8.67, all ps < .005). The change in performance was least for bird 23 in the Diagonal treatment: she made 85.0% correct choices on Day 3 and 75.0% on Day 4. All birds made more errors after removal of the guides, but the location of their errors also clearly reflected their knowledge of the spatial relationships. Both on the day before and on the day that the guides were removed, most errors in both treatments were immediately beside correct feeders (Fig. 13, a and b).

If birds had not learned the spatial relationships with guides in place in the vertical and diagonal arrays, I expected their performance to drop to chance when cues were no longer connected to feeders. The results of this experiment contradicted this prediction. All birds which performed better than chance before guides were removed (9 of 11) continued to do so afterward, and what errors they made were mostly beside correct feeders. Nonetheless, guides strongly influenced learning because on average, birds performed better with them than without them. Consequently,

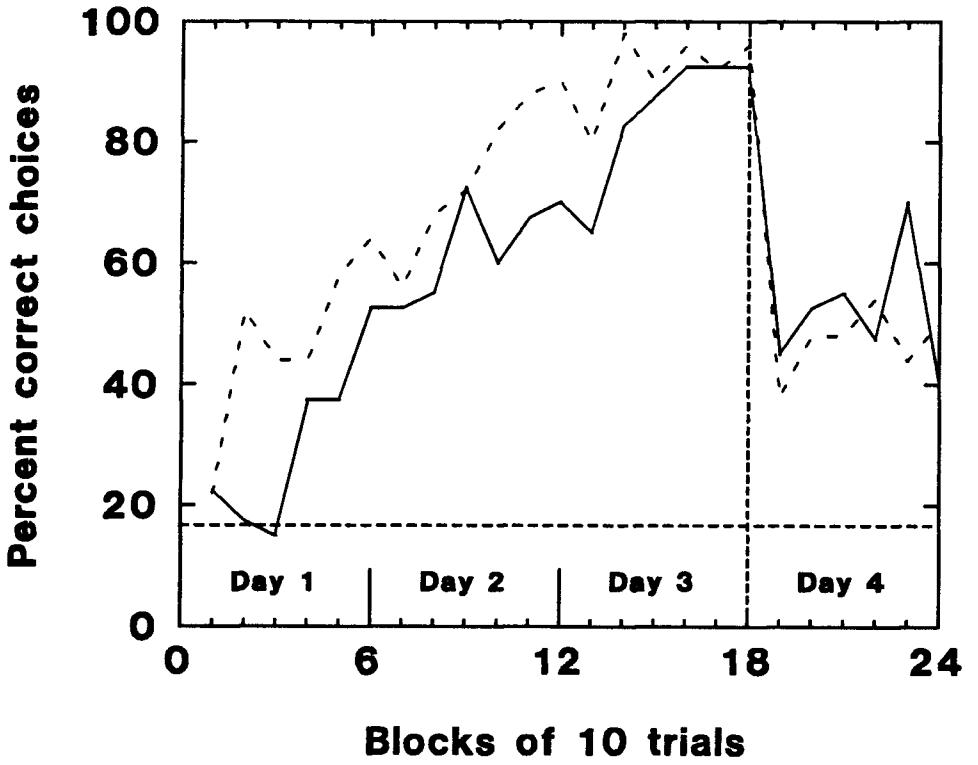


Figure 12. Mean percent correct choices in the Vertical Guides and Diagonal Guides treatments of experiment 6. The solid and dashed lines indicate performance for the Vertical Guides and Diagonal Guides treatments, respectively. Only those birds that performed better than chance were included (N = 5 for Vertical Guides; N = 4 for Diagonal Guides). The vertical dashed line indicates the point at which guides were removed. The horizontal dashed line indicates chance performance (16.7%).

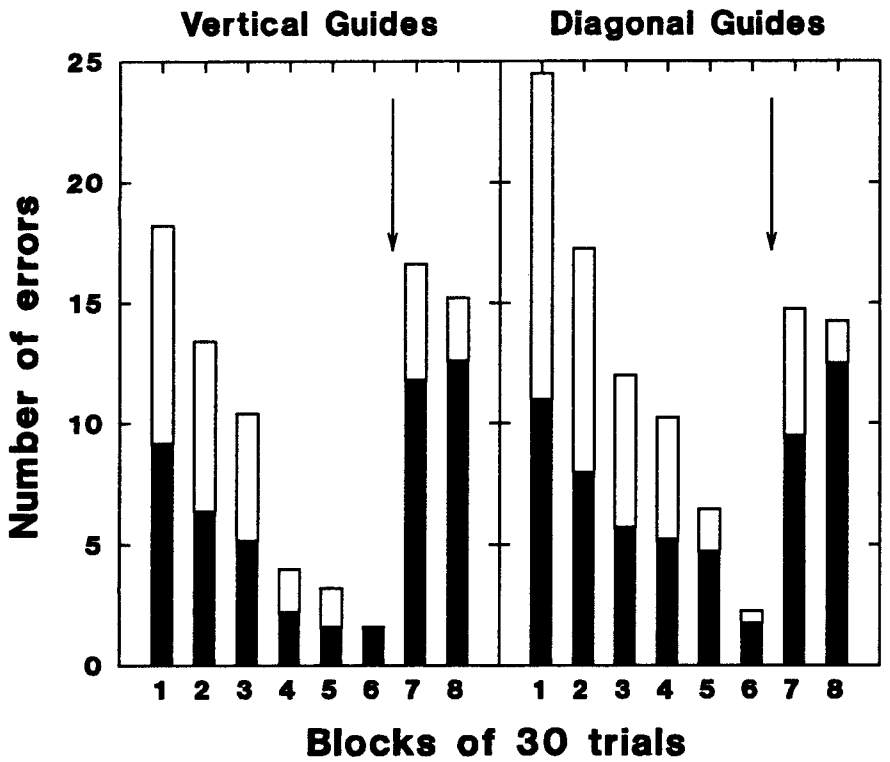


Figure 13. Number of wrong first choices made at feeders beside correct ones (filled portion of bars) out of total wrong first choices in blocks of 30 trials in the 2 treatments of experiment 6. (a) Means for the 5 birds in the Vertical Guides treatment. (b) Means for the 4 birds that performed better than chance in correct choices in the Diagonal Guides treatment. The arrows indicate the point at which guides were removed.

a plausible interpretation for the results of experiment 6 is that guides facilitated the spatial association learning process.

GENERAL DISCUSSION

Two results of this study are particularly important. The first is that it provides evidence that visible connections between cues and response locations reduce the detrimental effects of spatial separation on associative learning. In all three experiments, a total of 16 out of 21 birds tested with continuous connections made at least 80% correct choices on the third day of testing whereas only 2 of 21 birds tested without any connections reached this level. This leaves little doubt that visible connections between cues and their feeders improved how quickly hummingbirds learned a difficult spatial association, and Gestalt theory suggests that they should for other animals as well.

Experiment 4 also showed that interrupted connections promoted learning, although not as much as continuous connections. Performance with the interrupted connections reached a level approximately half-way between performance with no connections and with continuous connections (Fig. 8), and since they covered exactly half of the gap between cues and feeders, it is possible that learning scales with the degree of completeness of connection. Comparison of the results of experiments 5 and 6 shows that continuous connections improved learning of a second spatial relationship between cues and feeders: a diagonal one. This is a

promising indication that visible connections may promote learning of any spatial relationship regardless of the orientation of cues with respect to feeders.

Consideration of two Gestalt principles suggested the hypothesis tested in experiment 4 that connections between cues and corresponding response locations should facilitate spatial association learning. This hypothesis has not been considered in any other study of spatial association learning and the results of this study are not predicted by any other theoretical perspective of learning. The successful application of the Gestalt principles of connectedness and closure in this study and the principle of spatial proximity in Chapter 3 suggest that they provide a useful theoretical approach which generates novel hypotheses and testable predictions.

Nectar guide patterns in wild flowers frequently consist of patterns of lines or spots which foragers use to direct them to sources of nectar (Manning 1956; Meeuse 1961; Lunau 1990). The results of my treatments with continuous connections, or 'guides', between cues and feeders are consistent with this well-demonstrated function of floral nectar guides and they suggest some additional functions as well. Naive bees foraging on flowers for the first time are slower to locate nectar pools compared to experienced bees (Laverty & Plowright 1978) and frequently abandon morphologically-complex flowers before discovering nectar. Nectar guides could speed initial associative learning between flower types and their

nectar rewards by decreasing the delay between when naive bees land on flowers and locate and consume nectar. They could also promote learning of flower species and the particular rewards they offer (i.e. pollen, nectar, or nothing) by reducing confusion among closely spaced flowers and consequently, increasing the speed with which rewards are located.

The form of nectar guides varies considerably both among flower species and between flowers of the same species. Little is known about the functional consequences of either source of variation for foragers except that flowers with nectar guides are visited more frequently and their floral rewards are located significantly faster compared to when nectar guides are naturally absent or artificially concealed (Manning 1956; Waser & Price 1983). The variation in performance on the Guide treatments of experiment 6 suggests the possibility that differences in guide forms more subtle than absolute presence or absence could also effect the efficiency with which foragers locate floral rewards. If foragers experienced greater energetic profit from flowers with certain guide forms compared to others, perhaps those with guides that are more highly patterned or that provide a more continuous pathway to nectar, foragers may visit them preferentially if they could discriminate among guide forms. A consistent preference by foragers could result in selection for flowers with superior guides and hence, provide a mechanistic explanation for the existence of nectar guides in many flower species.

The second important result of this study is that it provides evidence that visible connections promote learning of associations between spatially separated cues and feeders. Comparison of the results of experiments 5 and 6 show that birds learned vertical and diagonal relationships faster when cues and feeders were connected by a strip of tape compared to when they were not (Fig. 9 and Fig. 12), and this suggests that the connections facilitated learning. However, connections could have facilitated learning by another mechanism. They could have served to make cues contiguous with feeders and consequently, they could have eliminated the necessity for learning spatial associations. By this explanation, the connections are learned as an integral component of the stimulus associated with reinforcement (Williams 1991), and removal of the connections predicts disruption in performance. Performance should not suffer much disruption if connections mainly facilitate or serve as a 'catalyst' (Rescorla 1982) for learning.

Removal of guides from vertical and diagonal cue-feeder arrays in experiment 6 resulted in some disruption in performance for all birds but each one continued to perform significantly above chance. For some, performance changed little. For example, bird 23 in the Diagonal treatment made 85.0% correct choices on the day before removal of the guides and 75.0% on the day they were removed. These results clearly favour the possibility that visible connections promote spatial association learning.

In conclusion, this study provides preliminary support for application of the Gestalt principle of connectedness and closure to the study of

spatial association learning. The evolutionary history of the hummingbirds with respect to their use of nectar guides in natural flowers, however, may have prepared them to take advantage of visible guides between cues and feeders in this laboratory study (Kamil 1982; Shettleworth 1983; Gould 1986). The extent to which the Gestalt principles are generally applicable to spatial association learning will be determined by testing with a variety of other animals. Potentially useful stimuli in the natural world, even when separated from locations of response and reinforcement, are often linked to them by recognizable connections. For example, the entrances of animal burrows could indicate to predators that prey may be nearby, and the tunnels leading to the burrow resident could provide the associative link between cue and prey for the predator. The Gestalt principles reflect fundamental properties of objects in the environment and their application to the study of learning in general could provide a needed bridge between learning theory and learning in the natural world.

CHAPTER 5

GENERAL CONCLUSIONS

Rescorla and Holland (1982, p. 265) propose that the study of any learning process involves attention to three basic questions: (1) What are the conditions that produce learning? (2) What is it that is actually learned? (3) And how is that learning revealed in the performance of the organism? I have provided some answers for each of these questions in this experimental examination of the process of spatial association learning by foraging hummingbirds.

Conditions That Produce Learning

In chapter 1, I demonstrated that at least one animal species, rufous hummingbirds, can learn spatial associations rapidly and nearly as quickly as when cues and response locations are contiguous. In the experiments of that chapter, the spatial separation between cues and feeders was relatively small but one which has nevertheless resulted in inhibition of learning in studies with other animals (Elias & Warner 1970; Iwai et al. 1986; Yaginuma & Iwai 1986). I argue that the success of the hummingbirds in my experiments was due mainly to a combination of their biological characteristics and to aspects of my experimental procedures which permitted them much of their natural foraging behaviors. I expect that

other animals should show similarly rapid spatial association learning if tested with experimental procedures and apparatus which allow them their natural foraging behaviors.

In chapters 3 and 4, I demonstrated that hummingbirds learn what would normally be considered difficult spatial associations based on the results of studies with other animals (Meyer et al. 1965; Stollnitz 1965). The main objective of those chapters, however, was to test several hypotheses concerning the role of certain visual factors in learning. The result of those tests revealed the significant influence of several factors new to the study of spatial association learning. Chapter 3 showed that learning was strongly influenced by the interaction of distance between cues and feeders and distance between cue-feeder pairs. Thus, the detrimental effects of cue-response separation can be dramatically affected by either decreasing distance between cues and response locations or by increasing separation between cue and response location pairs. This study was the first to test this possibility and the results challenge the consensus reached from other studies that the speed of spatial association learning is inversely related to absolute separation distance (Milner et al. 1979; Butter et al. 1982; Cowey 1968).

Experiment 4 of chapter 4 demonstrated the strong influence of another factor new to the study of spatial association learning. The simple addition of visible connections between cues and their feeders significantly improved how quickly hummingbirds learned a spatial association in

which the separation distance was approximately 1.5 times their total body length. Interrupted connections facilitated learning as well, but not as much as continuous connections. These results provided further support for my conclusion of chapter 3 that spatial association learning is not determined solely by absolute distance between cues and feeders.

While the results of that experiment are new to the study of spatial association learning, they are not new to the study of other learning processes. Several studies have shown that learning with temporal separations between cues and responses is much faster when the temporal gap between them is bridged by another, different stimulus (Rescorla 1985b; Hearst 1991; Williams 1991). The results of my study extend the generality of the hypothesis that 'gap fillers' (Hearst 1991) facilitate learning of relationships among particular stimuli and they are also consistent with the results of the other studies that connections convert difficult learning problems into simpler ones (Rescorla 1985b). The fact that gap-filling stimuli have facilitated learning by other animals indicates that the rapid learning of the hummingbirds with visible connections between cues and feeders may not be just a consequence of their analogous use of nectar guides in natural flowers. Instead, this study, together with the others previously mentioned, suggest the possibility that learning processes of animals may be guided by common mechanisms for recognition of particular kinds of linkages among stimuli. Gestalt theorists proposed this idea some time ago (Kohler 1925; Koffka 1935).

The hypotheses I tested in chapters 3 and 4 were developed primarily from consideration of Gestalt theory in general, and several Gestalt principles of perceptual grouping in particular. The principles of spatial proximity, connectedness, and closure each successfully predicted specific results of particular experiments. Other areas of research on learning and memory have also achieved recent advances by testing hypotheses developed from Gestalt principles and have begun to reevaluate their virtually exclusive reliance on associative learning theory as the dominant theoretical approach (Greeno et al. 1978; Rescorla 1985b). Thus, Gestalt theory, which fell into disfavor with the rise in popularity of the philosophical perspective of Behaviorism (Greeno et al. 1978; Kaniza 1979), should be reconsidered as a powerful heuristic in the general study of learning.

Contents of Learning

Experiments 5 and 6 of chapter 4 were designed to determine what hummingbirds had learned when they performed successfully on the cue-feeder arrays. In all of the arrays with a vertical relationship between cues and feeders, correct feeders were always the ones nearest cues and birds could have performed well if cues simply elicited approach toward them. Performance based on such behavior need not involve learning of spatial relationships between cues and feeders. Hummingbirds, however, successfully learned diagonal relationships between cues and feeders and this suggested that they could at least learn relationships in which the correct feeder was not nearest the cue. This is only an initial step in

determining the mechanism(s) by which hummingbirds learn spatial relationships between cues and feeders, but it has ruled out the possibility that they are limited by simple unlearned responses to salient and attractive cues.

Experiment 6 examined the role of visible connections in facilitating hummingbird learning. It tested two opposing possibilities, derived from associative learning theory (Williams 1991) and Gestalt theory (Rescorla 1985b), respectively. According to the first possibility, connections improved learning by making cues and feeders contiguous with each other; in effect, they reduced spatial separations to zero distance. According to the second possibility, connections improved learning of the relationship between cues and feeders. I predicted that if the birds learned by the first mechanism, their performance should drop to chance after connections were removed. On the other hand, I predicted that if they learned by the second mechanism, their good performance should continue with little change.

Removal of connections did decrease performance, but all individuals who performed significantly above chance before removal, continued to do so afterward. Although some disruption could be expected simply because of the suddenly altered appearance of the cue-feeder arrays, birds continued to choose correct feeders more often than expected by chance without connections to guide them. This result supports the idea that connections between cues and feeders served somehow to facilitate learning of the spa-

tial association between cues and feeders and it adds support to a similar conclusion reached from an earlier experiment by Rescorla (1982). In that experiment, pigeons learned temporal relationships faster when a tone, rather than silence, filled the gap between cues and responses. Evidence is accumulating from diverse sources that in general, 'gaps' among stimuli disrupt a variety of cognitive sources (Hearst 1991).

Learning Revealed in Performance

In this study, hummingbirds demonstrated their learning by choosing correct feeders on the first visit in feeding trials more often than expected by chance. However, the location and overall pattern of their errors was also a good indicator of the extent to which they had learned spatial associations. There were a number of individual cases in the treatments with large separations between cues and feeders where birds performed poorly or inconsistently according to the criterion of correct choices, yet their errors clustered immediately beside correct feeders. In addition, they made few errors at feeders more than one or two positions away from correct feeders and also visited the correct feeder immediately following wrong first choices significantly more often than expected by chance. The good performance of birds by these measures of behavior is difficult to interpret other than that they had learned the cue-feeder association but were not able to accurately locate correct feeders.

Poor performance has been mainly interpreted as evidence of poor learning in other studies of spatial association learning (Meyer et al. 1965; Stollnitz 1965), but this study demonstrates that this is not necessarily always the case. The analysis of errors was possible in this study because I used more cue and response location pairs than the two pairs typically used in other studies. Great benefit has been derived from the analysis of errors in many studies of spatial learning and memory in which the locations of errors are used to infer how information about important locations in the environment is acquired, stored and later recalled (e.g. Roberts & Dale 1981; Balda et al. 1986; Wilkie 1989). Studies of spatial association learning could similarly benefit from adoption of experimental paradigms in which animals are provided a greater range of possibilities for exhibiting learning, but suitable data collection methods must be employed as well.

Future Directions

Landmark learning, in which animals learn spatial relationships among prominent features of their environments and other important locations such as food sources (Schone 1984), could be considered as one of the best cases of spatial association learning. Animals clearly use them in their natural environments (e.g. Tinbergen 1972; Dyer & Gould 1983) and they also use them readily in laboratory situations (e.g. Vander Wall 1982; Collett et al. 1986; Cheng 1989). And, the readiness with which animals appear to notice and use landmarks in laboratory studies, and the

distances that often exist between them and the spatial location of interest, contrasts strikingly with the difficulty exhibited by many animals with what seems like trivial distances between cues and response in spatial association studies. Landmark learning may indeed be a case of spatial association learning, but I have refrained from any discussion of landmark learning in this thesis because I believe there are a number of important distinctions between the two. These distinctions should be explored experimentally before comparisons are made between the two forms of learning. Following is a discussion of the distinctions because I believe a comparison of how animals learn spatial relationships using landmarks and how they learn them using the cues of spatial associations could prove especially beneficial for the study of spatial association learning.

In both landmark learning and spatial association learning, the landmark or cue presumably represents a spatial relationship with a location. However, objects that are used as landmarks to represent that relationship are selected by individual animals and they are probably selected because they have particular characteristics that make them salient and memorable. Selected landmarks are also likely to be relatively permanent features of the environment and fixed in a particular location. Thus, the spatial relationship they signify is also constant.

In contrast, the cues of spatial associations are not selected by animals and consequently, they may not be particularly salient or memorable to them. Spatial associations exist independently of whether an an-

imal learns any relationship between cues and the locations of opportunity for reinforcement they signal. For example, vultures circle over dying prey regardless of whether other animals use this habit to locate the prey for themselves. In spatial association learning, the spatial location of interest is relative to the location of the cue and thus neither the location or the cue are fixed to one, constant place in the environment.

Experimental procedures used for studying landmark learning and spatial association learning also differ considerably and the differences may be critical. Perhaps one of the biggest differences is that in studies of spatial association learning, cues and correct response locations vary randomly in location from trial to trial (although the same relation between them is maintained), whereas in the landmark learning, landmarks and rewarded locations remain in the same positions for some number of trials. Repeated exposure to the same spatial distribution of stimuli may strongly influence the extent to which relations among them are learned. In landmark studies, the use of landmarks is demonstrated by a sudden unsignalled change in positions of the landmarks, and at this point, landmark studies resemble the trial by trial change of spatial association studies. Landmark studies consistently find that animals apply the relationship that formerly held between a landmark and a goal location even after a change in positions of the landmark and goal locations has occurred (e.g. Cheng 1989). This result demonstrates navigation to a location based on its spatial relation to another feature of the environment and suggests a

similar mechanism underlying landmark learning and spatial association learning.

Procedural and other differences make comparisons between spatial association learning and landmark learning difficult. Experimental examination of the importance of active selection of cues by animals to represent spatial relationships and repeated exposure to single, unique spatial relationships between landmarks and particular locations should provide promising directions for comparison of the two processes. Such studies could profitably unite the study of spatial association learning with the large and rapidly developing field of landmark learning.

LITERATURE CITED

Abordo, E.J. & Lee, J. 1977. Effects of introducing novel configurational cues on a learned color discrimination in squirrel monkeys. Percept. Mot. Skills Res. Exch., 44, 147-151.

Ali, M.A. & Klyne, M.A. 1985. Vision in Vertebrates. New York: Plenum Press.

Asch, S.E. 1961. Perceptual conditions of association. In: Documents of Gestalt Psychology (Ed. by M. Henle), pp. 187-200. Berkeley: University of California Press.

Balda, R.P., Kamil, A.C. & Grim, K. 1986. Revisits to emptied cache sites by Clark's nutcrackers (Nucifraga columbiana). Anim. Behav., 34, 1289-1298.

Barnett, S.A. 1975. The Rat: A Study in Behavior. Chicago: The University of Chicago Press.

Bartholomew, G.A. & Lighton, J.R.B. 1986. Oxygen consumption during hover-feeding in free-ranging Anna hummingbirds. J. Exp. Biol., 123, 191-199.

Benkman, C.W. 1988. Flock size, food dispersion, and the feeding behavior of crossbills. Behav. Ecol. Sociobiol., 23, 176-175.

Blazek, N.C. & H.F. Harlow. 1955. Persistence of performance differences on discriminations of varying difficulty. J. Comp. Physiol. Psychol., 48, 86-89.

Boucart, M. & Bonnet, C. 1991. A study in the effect of structural information and familiarity in form perception. Quart. J. Exp. Psychol., 43A, 223-248.

Bowe, C.A. 1984. Spatial relations in animal learning and behavior. Psych. Rec., 34, 181-209.

Breland, K. & Breland, M. 1961. The misbehavior of organisms. Am. Psychol., 16, 681-684.

Brown, J.H. & Kodric-Brown, A. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. Ecology, 60, 1022-1035.

Butter, C.M., Kurtz, D., Leiby III, C.C. & Campbell, A, Jr. 1982. Contrasting behavioral methods in the analysis of vision in monkeys with lesions of the striate cortex or the superior colliculus. In: The Analysis of Visual Behavior (Ed. by D.J. Ingle, M.A. Goodale & M.A. Mansfield), pp. 301-334. Cambridge, MA: MIT Press.

Carpenter, F.L., Paton, D.C. & Hixon, M.A. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proc. Natn. Acad. Sci. U.S.A., 80, 7259.

Cheng, K. 1989. The vector sum model of pigeon landmark use. J. Exp. Psychol.: Anim. Behav. Processes, 15, 366-375.

Collett, T.S., Cartwright, B.A. & Smith, B.A. 1986. Landmark learning and visuo-spatial memories in gerbils. J. Comp. Physiol. A. Sen. Neur. Behav. Physiol., 158, 835-851.

Collias, N.E. & Collias, E.C. 1968. Anna's hummingbirds trained to select different colors in feeding. Condor, 70, 273-274.

Collier, G.H. & Rovee-Collier, C.K. 1981. A comparative analysis of optimal foraging behavior: laboratory simulations. In: Foraging Behavior: Ecological, Ethological, and Psychological Approaches (Ed. by A.C. Kamil & T.D. Sargent), pp. 39-76. New York: Garland STPM Press.

Cowey, A. 1968. Discrimination. In: Analysis of Behavioral Change (Ed. by L. Weiskrantz), pp. 189-238. New York: Harper & Row.

Croy, M.I. & Hughes, R.N. 1991. The influence of hunger on feeding behaviour and the acquisition of learned foraging skills by the fifteen-spined stickleback, Spinachia spinachia L. Anim. Behav., 41, 161-170.

Davis, R.T. 1974. Spatial discontiguity. In: Primate Behavior, Vol. 3. Monkeys as Perceivers (Ed. by R.T. Davis), pp. 62-72. New York: Academic Press.

Dyer, F.C. & Gould, J.L. 1983. Honey bee navigation. Am. Sci., 71, 587-597.

Elias, M.F. & Warner, L. 1970. Effect of pattern configuration on the relation between pattern area and pattern discrimination. Percept. Motor Skills, 30, 919-924.

Feinsinger, P. 1983. Variable nectar secretion in a Heliconia species pollinated by hermit hummingbirds. Biotropica, 15, 48-52.

Galef, B.G., Jr. 1976. Social transmission of acquired behaviour: a discussion of tradition and social learning in vertebrates. Adv. Study Behav., 6, 77-100.

Galef, B.G., Jr. 1983. Utilization by norway rats (Rattus norvegicus) of multiple messages concerning distant foods. J. Comp. Psychol., 97, 364-371.

Garcia, J., Hankins, W.G. & Rusiniak, K.W. 1974. Behavioral regulation of the milieu interne in man and rat. Science, 185, 824-831.

Gass, C.L. 1979. Territory regulation, tenure, and migration in rufous hummingbirds. Can. J. Zool., 57, 914-923.

Gass, C.L. 1985. Behavioral foundations of adaptation. In: Perspectives in Ethology, Vol. 6. (Ed. by P.P.G. Bateson & P.H. Klopfer), pp. 63-107. New York: Plenum Press.

Gass, C.L. & Lertzman, K.P. 1980. Capricious mountain weather: a driving variable in hummingbird territorial dynamics. Can. J. Zool., 58, 1964-1968.

Gass, C.L. & Montgomerie, R.D. 1981. Hummingbird foraging behavior: decision-making and energy regulation. In: Foraging Behavior: Ecological, Ethological, and Psychological Approaches (Ed. by A.C. Kamil & T.D. Sargent), pp. 159-194. New York: Garland STPM Press.

Gass, C.L. & Sutherland, G.D. 1985. Specialization by territorial hummingbirds on experimentally enriched patches of flowers: energetic profitability and learning. Can. J. Zool., 63, 2125-2133.

Gellermann, L.W. 1933. Form discrimination in chimpanzees and two-year old children: I. Form (triangularity) per se. J. Genet. Psychol., 42, 3-27.

George, M.W. 1980. Hummingbird foraging behavior at Malvaviscus arboreus var. drummondii. Auk, 97, 790-794.

Gill, F.B. 1988. Trapline foraging by hermit hummingbirds: competition for an undefended, renewable resource. Ecology, 69, 1933-1942.

Goldsmith, T.H., Collins, J.S. & Perlman, D.L. 1981. A wavelength discrimination function for the hummingbird Archilochus alexandri. J. Comp. Physiol. A, 143, 103-110.

Goldsmith, T.H. & Goldsmith, K.M. 1979. Discrimination of colors by the black-chinned hummingbird, Archilochus alexandri. J. Comp. Physiol. A, 130, 209-220.

Gomez-Laplaza, L.M. & Morgan, E. 1991. Effects of short-term isolation on the locomotor activity of the angelfish (Pterophyllum scalare). J. Comp. Psychol., 105, 366-375.

Gori, D.F. 1983. Post-pollination phenomena and adaptive changes. In: Handbook of Experimental Pollination Biology (Ed. by C.E. Jones & R.J. Little), pp. 31-49. New York: Van Nostrand Reinhold.

Gori, D.F. 1989. Floral color change in Lupinus argenteus (Fabaceae): why should plants advertise the location of unrewarding flowers to pollinators? Evolution, 43, 870-881.

Gould, J.L. 1986. The biology of learning. Ann. Rev. Psychol., 37, 163-192.

Grant, K. & Grant, V. 1968. Hummingbirds and Their Flowers. New York: Columbia University Press.

Greene, E. 1987. Individuals in an osprey colony discriminate between high and low quality information. Nature, Lond., 329, 239-241.

Greeno, J.G., James, C.T., DaPolito, F.J. & Polson, P.G. 1978. Associative Learning: A Cognitive Analysis. New Jersey: Prentice-Hall, Inc.

Hainsworth, F.R. & Wolf, L.L. 1979. Feeding: an ecological approach. Adv. Study Behav., 9, 53-96.

Hale, E.B. 1956. Social facilitation and forebrain function in maze performance of green sunfish, Lepomis cyanellus. Physiol. Zool., 29, 93-107.

Hearst, E. 1991. Psychology and nothing. Am. Sci., 79, 432-443.

Hollis, K.L. 1982. Pavlovian conditioning and signal-centered action patterns and autonomic behavior: a biological analysis of function. Adv. Study Behav., 12, 1-64.

Houston, D.C. 1983. The adaptive radiation of the griffon vultures. In: Vulture Biology and Management (Ed. S.R. Wilbur & J.A. Jackson), pp.135-152. Berkeley: University of California Press.

Inman, A., Lefebvre, L. & Giraldeau, L.-A. 1988. Individual diet preferences in feral pigeons: evidence for resource partitioning. Anim. Behav., 35, 1902-1903.

Iwai, E., Yaginuma, S. & Mishkin, M. 1986. Acquisition of discrimination learning of patterns identical in configuration in macaques (Macaca mulatta and M. fuscata). J. Comp. Psychol., 100, 30-36.