Memory for spatial and local cues: A comparison of a storing and a nonstoring species

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Two passerine species, black-capped chickadees (*Parus atricapillus*, a food-storing bird) and dark-eyed juncos (*Junco hyemalis*, a nonstoring bird) were compared in a task in which they inspected four feeders in an aviary. Different feeders and different spatial locations were used on each trial. One of the feeders was baited. The subjects returned after a 5-min retention interval to find the baited feeder. Tests with transformations of the feeder array made it possible to determine what cues controlled the food-finding behavior. Chickadees responded to spatial cues preferentially over local color and pattern cues associated with the feeder (Experiments 2-4). The same ordering of responding was found in Experiment 1, a food-storing version of the food-finding task outlined above. Experiment 5 tested juncos on the food-finding task. Juncos responded to all types of information equally. The results are discussed in relation to the notion that because of their food-storing lifestyle, chickadees may need to rely more heavily on spatial cues than do juncos.

Some birds among the parids (chickadees and tits) and the corvids (nutcrackers and jays) store food items in the wild and recover them for later consumption. The use of memory for cache recovery by these birds has been widely documented (see Shettleworth, 1990, for a review). Food-storing birds cache a large number of food items and recover them hours, days, or months later (Sherry, 1989; Vander Wall, 1982). This reliance on the recovery of remembered caches has led to speculation that memory in food-storing birds may be adaptively specialized—that is, it may be different from or better in some way than memory in nonstoring birds (Krebs, 1990; Shettleworth, 1985, 1990).

If it is to be determined that memory in storing birds is indeed specialized, their performance must be compared with that of nonstoring birds. Comparative experiments must be done because the notion of adaptive specializa-

tion is inherently comparative: determining whether food storers' memory is different from or better than nonstorers' memory requires a comparison of species from both groups. Obviously, a food-storing paradigm cannot be used for such a comparison. Food-finding tasks have been used successfully by numerous investigators to test memory in food storers and nonstorers alike. These tasks share some characteristics of food storing (e.g., locomotion to a food site, brief exposure to the food sites, etc.), but allow for comparisons across species. A food-finding task known as "window shopping" (Shettleworth & Krebs, 1986) has been used to investigate memory in storing birds and it seems that the memory displayed is the same as that used in recovering stored seeds (Shettleworth, Krebs, Healy, & Thomas, 1990).

Brodbeck, Burack, and Shettleworth (1992; see also Clayton & Krebs, 1993; Healy & Krebs, 1992) described a food-finding task that is similar to window shopping. In Brodbeck et al.'s version of this task a chickadee enters an aviary and encounters a number of feeders, all uniquely decorated and in trial-unique spatial locations. One of these feeders is baited with a piece of food (half a peanut). The animal is allowed to consume part of the nut and is then returned to its home cage for a retention interval. After the retention interval, the animal's task is to find the food, which is now hidden by Velcro circles placed over the holes that hold the reward in the feeders. When different feeders are used in different spatial locations each day, chickadees perform better than chance almost immediately (after between 5 and 15 trials).

Many different types of cue may be controlling food-finding behavior. Global spatial information in the room may point the birds to the correct feeder. The spatial relationships among the feeders themselves may be used. Finally, because each feeder is differently decorated, the colors and patterns on the individual feeders could be

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used. One successful method of determining which cues control behavior is to play one set of cues off against another. This has been effective in rats (Cheng, 1986; Suzuki, Augerinos, & Black, 1980), pigeons (Cheng, 1992; Spetch & Edwards, 1988), gerbils (Collett, Cartwright, & Smith, 1986), and honeybees (Cartwright & Collett, 1987). All of these species seem to use redundant information from many sources. Usually each type of information points to the same "place," the food site. However, by changing the task on test trials it is possible to make a given response indicate control of behavior by one type of cue and another response indicate control by some other type of cue. By using such a technique it would then be possible to see whether chickadees use the information available to them in a different way than do other species, whether they encode information differently, or whether they respond to the represented information in a different manner. In other words, one can find out *what* the chickadee remembers.

One possibility is that chickadees rely heavily on spatial cues. Sherry (1992) demonstrated the importance of so-called "global" cues in effective cache recovery by black-capped chickadees. When these cues (various geometric shapes hung on the walls of an aviary) were rotated between caching and recovery, the subjects followed them. Vander Wall (1982) found that Clark's nutcrackers encode the spatial relationship between landmarks and a cached food item. However, these are not the only cues used; Balda and Turek (1984) systematically degraded the cues available to a Clark's nutcracker in an aviary and the bird was still able to recover its caches.

Along with the behavioral data, there has been evidence from neurological studies of the importance of spatial information to hoarding birds. Storing birds have a larger hippocampus relative to brain and body weight than do nonstoring birds (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989). This brain region has been found to be important for spatial and associative tasks in mammals (Mishkin & Apenzeller, 1987; Squire, 1992), and in effective cache recovery in black-capped chickadees (Sherry & Vaccarino, 1989). The hippocampus may not be completely analogous in function in birds and mammals (Reilly & Good, 1987), but the above neuroanatomical evidence combined with the great spatial memory demands of food storing and the behavioral data are consistent with the hypothesis that spatial cues control cache-recovery behavior.

As noted above, a comparison is necessary to find out if there is something different about what the chickadees remember. Dark-eyed juncos (*Junco hyemalis*) were chosen as the nonstoring comparison species in the present experiments. While the chickadee and junco are not as closely related as are, say, the food-storing marsh tit (*P. palustris*) and the nonstoring great tit (*P. major*) used by Krebs and his colleagues (e.g., Healy & Krebs, 1992; Hilton & Krebs, 1990), the comparison is still useful. Chickadees and juncos are both small passerines, though the juncos weigh more (about 20 g compared with 12 g or

so for a chickadee). Juncos live and breed in an area that overlaps the habitat of the chickadee. The two species have evolved different ways to survive the winter: one species (the chickadee) stores food, while the other does not. If it is believed that storing birds should have better or different memories than do nonstoring birds, many comparisons must be made to test this hypothesis. However, each comparison should be viewed as a single data point, because life history (of storer vs. nonstorer in this case) is the independent variable (Kamil, 1988).

Chickadees (Experiments 1–4) and juncos (Experiment 5) were trained on a food-finding task. For each bird, four trial-unique feeders, one of which was baited, were placed in trial-unique spatial locations. A bird was released into the aviary to eat part of the food. This completed Phase 1 of a trial. After a 5-min retention interval the bird was let back into the aviary for Phase 2 of the trial, in which it had to find the now-hidden food. Once the animals reached a criterion of consistently better-than-chance responding, they were presented with a number of tests. Each test involved some sort of transformation of the feeder array before the start of Phase 2. These changes in the array in Phase 2 of each experiment were chosen to dissociate different types of cues that may have been used in the representation of the baited feeder. This was accomplished by transforming the feeder array in such a way that a visit to a given feeder indicated control by one class of cue (e.g., spatial), while a visit to another feeder indicated control by another set of cues (e.g., those of local color and pattern). Unrewarded tests made it possible to look not only at first choices but also at second and third choices, which can be indicative of memory even though an error has occurred (Brodbeck et al., 1992; Roitblat, 1980; Roitblat & Harley, 1988; Roitblat & Scopatz, 1983). Because a subject was not rewarded for a choice on test trials, it searched through all the feeders, one after the other. The first choice showed what type of cue the subject associated most strongly with the baited site (or alternatively, which class of cues it was biased to respond to), the second choice showed the second strongest association, and so on.

Experiment 1 used a food-storing version of the food-finding task to determine if the same memory processes were being tapped into in the food-finding task as in the food-storing task. This was necessary because the memory used in food storing is the memory that is hypothesized to be specialized, as mentioned earlier. Instead of a single feeder out of four being baited, one feeder out of four was available for the chickadee to store in. On test trials, room position and position in the feeder array were dissociated from color and pattern cues on the feeder. Experiment 2 dissociated these same cues in the same manner, except that food finding was used. Experiment 3 dissociated room position from the array position and the color and pattern cues. Experiment 4 dissociated all three types of information. Finally, Experiment 5 dissociated all three types of cue, but juncos were used as subjects instead of chickadees.

EXPERIMENT 1

Experiment 1 adapted the Brodbeck et al. (1992) paradigm to a food-storing task. The birds were presented with arrays of four trial-unique feeders. They were allowed to store in one of the feeders, chosen by the experimenter, and then recover a small piece of peanut after a retention interval. Test trials were designed to determine what cues were controlling cache recovery—spatial or local. The array of feeders was transformed so that a response to one feeder on each test trial showed control by spatial cues while visits to another feeder showed control by local cues on the feeder itself. This test configuration is shown in Figure 1.

Method

Subjects

Four black-capped chickadees caught at the Erindale campus of the University of Toronto were used in this experiment. All subjects had previous experience in aviary experiments, two birds in food-storing experiments and two birds in food-finding experiments other than those in this paper. In their previous experience the use of either spatial or local cues would have led to correct responding. The subjects were housed in individual cages on a 10:14-h light:dark cycle and were deprived of food overnight plus 2–3 h (for a total of 16–17 h of deprivation).

Apparatus

These experiments took place in an aviary measuring $2.45 \times 3.5 \times 2.27$ m. Three walls and the ceiling were covered with wire mesh. The three walls were divided into 14 columns and 8 vertical rows. Thus, any place on the walls could be described using the lower left corner of the left wall as the origin of a Cartesian coordinate system. An observation window was located in the middle of the fourth wall of the aviary and a small trapdoor was located to the left of this window to allow the chickadees to fly into the room.

Ninety-six wooden blocks (8.3 cm wide $\times$ 15.3 cm tall $\times$ 3.8 cm thick) were used as feeders. Each one had a different pattern and combination of from one to eight colors of acrylic paint; they were made to look different to the experimenters by varying the size, color, number, and position of stripes, spots, splotches, and representational and nonrepresentational designs in an unsystematic way. A hole 0.8 cm in diameter and 4.4 cm from the top of a feeder was available for the subjects to store food in. A dowel protruding out from the feeder 1 cm from its bottom served as a perch. A Velcro ring 1.5 cm in diameter and glued around the hole in each feeder allowed a small piece of Velcro (1 cm in diameter) to be placed over the hole to conceal its contents.

Procedure

Pretraining. Five days before the start of training a randomly chosen feeder baited with half a peanut was placed in each cage. Each day the feeder was checked and if the peanut was eaten the feeder was rebaited. At the end of the 5 days a small piece of Velcro was used to partially cover the peanut. When the bird ate the nut the feeder was rebaited as before and the peanut was again covered by the Velcro. In this way the birds learned to remove the piece of Velcro to get at the reward.

Once the birds were successfully removing the Velcro they were allowed into the aviary for further training. Eight feeders were chosen for each trial and placed in random locations. A small bowl of peanut eighth was placed in the middle of the room, along with a perch. The animals were allowed to consume the pieces of peanut or store them in the holes in the feeders. Once either a subject had stored a piece of nut or 12 min had elapsed, the lights in the aviary

were extinguished. This forced the return of the subject to its lighted home cage. After a 30-min retention interval, if it had stored a peanut the subject was let back into the aviary and was allowed to visit the now Velcro-covered feeders until the peanut was found and eaten. Once storage and recovery were successfully done with eight feeders, only seven feeders were used on the next trial. By removing a feeder after each successful trial the number of feeders in each training array was eventually brought down to four. Once the four-feeder mark was reached a new procedure was used. One feeder was chosen and covered with Velcro in Phase 1 of this new trial. If a subject successfully completed this trial, two feeders were covered in the next trial. This progression of trials continued until only one feeder was left open, for the first training trial.

Training trial. Before each training trial began, four feeders were randomly selected without replacement from the pool of stimuli. For each feeder, a location in the 14×8 grid on one of the three walls was randomly chosen without replacement. One of the four feeders was chosen randomly and left uncovered; the other three were covered with the Velcro circles, as in pretraining. A subject was then allowed into the aviary, where it found a bowl of peanut pieces and a perch as in pretraining. Once either the subject had stored in the uncovered feeder or 12 min had elapsed, the subject was returned to its home cage. The experimenter recorded whenever a subject ate a piece of peanut or whether the subject stored a food item. This completed Phase 1 of the trial. Part of the way through the experiment, the pieces of Velcro used in Phase 1 were replaced with an acetate window held by a Velcro rim. This change took place somewhere between Trials 7 and 26, depending on the subject. Regardless of subject, the change to acetate windows took place before any test trials were given. This change prevented the chickadees from storing in feeders other than the one chosen by the experimenter; they could, however, see that the other feeders were empty. Experiment 1 was thus made more similar to the other experiments reported in this paper in that the contents of "unbaited" feeders could be seen and the two phases of the experiment were made more discriminable. Phase 2 of each trial remained the same throughout the experiment.

After a 30-min retention interval the chickadee was let back into the aviary, where it encountered the same four feeders in the same locations. However, now each hole was covered by a Velcro circle and the food bowl was removed. The bird was allowed to search until it found the stored piece of food. It was then allowed to consume the food. This completed Phase 2 of the trial. The experimenter recorded which feeder was landed on and whether the Velcro was pulled off. If the Velcro was removed, this was termed a "look." One or two trials were run each day 5–6 days per week. If two trials were run, the intertrial interval was 2 h.

If a subject was responding randomly (i.e., not using memory), one would expect an equal proportion of trials during which it took one look, two looks, three looks, and four looks to find the stored peanut. Therefore, chance performance on any given trial is 2.5 looks. Obviously, one look represents perfect performance. Once a subject reached a criterion of 15 trials completed and either 3 of the last 4 trials below chance (< 3 looks) or 2 successive perfect trials (one look), the first test trial was given. (If the birds were performing randomly, the chance of finding the peanut in two looks or fewer on 3 trials out of 4 would be .1; the probability of 2 successive perfect trials by chance is .06.)

Test trials. A test trial began with Phase 1 as outlined above. During the retention interval the open feeder had its contents removed (to allow for unbaited tests) and then had its spatial position exchanged with that of a randomly chosen feeder from the array of feeders (Figure 1). Ten of these tests were given to each subject. In Phase 2 of a test trial, the bird was not let back into its home cage until it had searched through (i.e., pulled off the Velcro) all of the feeders in the array. After each test trial, the subject was given training trials until it found the stored piece of peanut in fewer than three looks in three of the last four trials or until there

Figure 1. Sample test feeder array presented to subjects in Experiments 1 and 2. The top panel shows the configuration during Phase 1, while the bottom panel shows Phase 2. The arrow indicates the open feeder (Experiment 1) or the baited feeder (Experiment 2). In Phase 2 the plain feeder is in the correct spatial position with respect to the other feeders and the walls of the aviary, while the one to the right of it has the correct pattern information.

were two consecutive perfect trials. In this way, each test trial was equated with respect to previous performance.

Data analysis. The data analyzed in this experiment are the distributions of the number of looks to find the stored item (baseline data) or the number of looks to find a given class of stimuli (test trials). An equal frequency of each number of looks would indicate chance performance. These distributions were analyzed using the *G* statistic (Sokol & Rohlf, 1981). This statistic is distributed as chi-squared, but differs from the chi-squared statistic in an important characteristic: results of groups of *G* tests can be summed and degrees of freedom can be partitioned as in an analysis of variance (ANOVA). This allows one to sum the distributions for each subject and look at an overall difference from a chance distribution. Variance in the distributions caused by differences between individual subjects can then be separated from the overall difference from chance and from

any difference between conditions. This summing of distributions to get an overall picture would not be possible using chi-squared. A significance level of .05 was used for all statistical tests.

Results and Discussion

The birds reached the criterion in a mean of 22 trials ($SD = 9.06$). They took a mean of 3.9 trials ($SD = 0.85$) between each test to get back to the criterion. Baseline data—the number of looks to find the stored item in trials immediately preceding a test trial—are shown in Figure 2.

On test trials, the birds overwhelmingly chose the spatially correct feeder first and the feeder with correct color and pattern second (Figure 2). The distribution of the

Figure 2. Distribution of the number of looks to find the stored item on trials preceding test trials (baseline) and to visit the spatially correct or locally correct feeder (pattern/color) on test trials in Experiment 1; the solid line indicates chance performance.

number of looks taken to the spatially correct feeder on test trials differed from chance [$G(3) = 41.05$], while there was no significant intersubject variation [$G(9) = 16.70$], which shows that each subject had the same pattern of choices. This difference from chance was in the direction of a first choice of look to the spatial location. When the distribution was examined of the number of looks to the feeder with the correct pattern and color on test trials, a significant difference from chance [$G(3) = 23.68$] and no intersubject variation [$G(9) = 13.23$] were found. When the data from the correct spatial location on tests were compared with the baseline trials, no difference was found between the two distributions [$G(3) = 3.22$]. Between-subject variation was not significant [$G(18) = 19.59$]. These results indicate that spatial location was treated as the correct cue by the birds.

A different picture emerges when the baseline and local cue distributions are compared. These distributions do differ significantly [$G(3) = 53.5$], indicating that the correct individual feeder was not treated in the same way as the correct feeder in the baseline trials was. Again, intersubject variation was not significant [$G(18) = 16.12$].

One concern, given the importance of space demonstrated in the experiment, is that the feeder that was originally baited may have been switched to a position systematically closer to the spatial location it previously occupied (i.e., the correct spatial location) than some other

feeder was. This might bias the subject to choose the previously baited feeder rather than some other feeder. On average, however, the correctly colored feeder was 25.82 cm farther ($SD = 117.82$) from the spatially correct feeder than the next closest feeder was; this is not a significant difference [$t(39) = 1.59$].

In summary, it seems that in a storing task the representation of the cache site contains information about both spatial and local cues. The spatial information is responded to first, followed by local information. This is shown by the fact that once the bird responded to the spatial information, it next chose the feeder that matched the color and pattern of the originally baited feeder.

EXPERIMENT 2

Experiment 2 was the first of a sequence of experiments (2-4) that were designed to determine which cues controlled chickadees' behavior in a food-finding task similar to the food-storing task in Experiment 1. The eventual goal of these experiments was to compare what cues control behavior in chickadees and juncos and, by extension, to discover whether the memory used by chickadees in food storing and recovery is somehow special. It was therefore first necessary to find out whether the same cues that control food storing (Experiment 1) also control food finding, since the juncos' memory could not

be tested in a food-storing experiment. As a result, Experiment 2 was identical to Experiment 1, except that a food-finding task was used.

Method

Subjects

Four black-capped chickadees caught at the Erindale campus of the University of Toronto served in this experiment. They all had previous experience in memory experiments in an aviary. Like the subjects in Experiment 1, these subjects had not been trained to respond preferentially to one set of cues over another in their previous experience—that is, both spatial and local cues could be used to solve the tasks they had been required to do. All other conditions were the same as in Experiment 1.

Procedure

Pretraining. Subjects were trained to pull Velcro in their home cages as in Experiment 1. Once the birds were successfully removing the Velcro they were allowed into the same aviary as that used in Experiment 1 for further training. This training involved placing one baited feeder at a randomly chosen location on one of the three mesh-covered walls. A bird was let in through the trapdoor and allowed to eat the peanut for 30 sec, after which it was returned to its home cage. The subject was immediately let back into the aviary to finish the reward. The same method of partially covering the reward with Velcro was used here. Training trials began once the subjects had completed at least 5 pretraining trials with the peanut fully covered in less than 1 min for each trial.

Training trial. Before a training trial began, four feeders were randomly selected from the pool of stimuli, with the constraint that over trials all the feeders should be used once before any was used again. For each feeder, a location in the 14×8 grid on one of the three walls was randomly chosen without replacement. One of the

four feeders was randomly chosen and baited. A bird was then allowed into the aviary to find the peanut. Once the subject had found the baited feeder, it was allowed to eat for 30 sec and was then returned to its home cage. This completed Phase 1 of the trial. After a 5-min retention interval, the chickadee was let back into the aviary, where it encountered the same four feeders in the same locations. However, now each hole was covered by a small piece of Velcro. The bird was allowed to search until it found the baited feeder and then consume the rest of the reward. This completed Phase 2 of the trial. The experimenter recorded which feeder was landed on and whether the Velcro was pulled off. Up to 3 trials a day were given to each bird, with an intertrial interval of about 1 h. The same criterion as used in Experiment 1 had to be met by a subject before a test trial was given.

Test trials. The same test given in Experiment 1 was given here. Before Phase 2 began the baited feeder was emptied and switched with a randomly chosen second feeder from the array (Figure 1). Once again, the subject was required to remove the Velcro from all four feeders in Phase 2 of a test trial before it was returned to its home cage.

Results and Discussion

The subjects reached the criterion in a mean of 23.5 trials ($SD = 4.04$). On average, the subjects had 3.69 trials ($SD = 0.97$) between successive tests.

The pattern of behavior on the test trials was nearly identical to that in Experiment 1 (Figure 3). The distribution of looks to the feeder that was in the correct spatial position differed significantly from chance [$G(3) = 42.45$], while intersubject variation was not significant [$G(9) = 6.26$]. The difference from chance is accounted for by the large proportion of first looks to the spatial position. The

Figure 3. Distribution of the number of looks to find the peanut on trials preceding test trials (baseline) and to visit the spatially correct or locally correct feeder (pattern/color) on test trials in Experiment 2; the solid line indicates chance performance.

distribution of the number of looks to the correct feeder with respect to local (color/pattern) cues on test trials did differ from chance [$G(3) = 8.72$]. There was also significant intersubject variation [$G(9) = 19.42$]. This distribution differed from chance because most of the time (50%) the birds chose the correctly patterned/colored feeder second, indicating that the pattern cues did indeed play a role in the representation of the baited feeder.

When the data from the correct spatial location were compared with those of the baseline trials, no difference was found between the two distributions [$G(3) = 3.22$]. Between-subject variation was also not significant [$G(18) = 13.89$]. On the two trials where the correct spatial location was not chosen first, it was chosen second. These results indicate that the spatial location was treated as the correct location by the birds.

A different picture emerges when the baseline and local-cue distributions are compared. These distributions do differ significantly [$G(3) = 18.61$], indicating that the correct individual feeder was not treated in the same way as the correct feeder in the baseline trials was. Again, intersubject variation was not significant [$G(18) = 26.97$].

The concern on test trials about placement of the previously baited feeder after the switch was examined here as well. On average, the feeder was 45.69 cm farther away ($SD = 131.27$) from the correct spatial position than was the next closest feeder. These distances did not differ significantly [$t(19) = 1.56$]. Therefore, the feeder that the originally baited feeder was exchanged with did not end up significantly farther from the correct spatial location than did the originally baited feeder.

In sum, this experiment shows that spatial cues are heavily relied upon in this task. However, once the bird found that the spatial information did not lead it to the partially consumed peanut, it utilized the local pattern and color information, rather than a random search. This was the same pattern that was obtained in Experiment 1. These results support those of Shettleworth and Krebs and their colleagues (Shettleworth & Krebs, 1986; Shettleworth et al., 1990), in indicating that the same memory processes are tapped into by food finding as by food storing. Since this is the case, the present task is suitable for use in comparisons between storers and nonstorers.

EXPERIMENT 3

Experiments 1 and 2 showed the importance of spatial information, but this information was of two types. The feeder chosen first on tests occupied the same position in the array and in space with respect to the aviary as did the storage site (Experiment 1) or the baited feeder (Experiment 2) in Phase 1. In Experiment 3 spatial location with respect to the aviary was dissociated from local color and pattern cues and array-position cues to test how important absolute spatial information was on its own. In the tests, the array of feeders was moved along the wall of the aviary so that the originally baited feeder occupied a new position in the aviary but the same position with respect

to the other feeders. A second feeder was now closest to the original position of the baited feeder on the aviary wall—that is, it was correct with respect to global spatial cues, but not necessarily with respect to array position.

Method

Subjects

The four chickadees used in Experiment 2 were used in this experiment as well.

Procedure

Test trials. The attempted dissociation of cues in this test was accomplished by moving the entire feeder array over either one (44.5 cm, Condition M1) or two (89 cm, Condition M2) horizontal coordinates. Only the back wall was used for this test, to avoid moving around corners. Four trials of each type were given. The baited feeder was in the same place in the array as it was in Phase 1, but the closest feeder to the absolute spatial position did not have to be the previously baited feeder. This test configuration is shown in Figure 4.

Results and Discussion

On average, the subjects took 2.80 trials ($SD = 0.78$) to get back to the criterion after a test.

Correct absolute spatial location was defined as the feeder that was closest to the absolute location on the aviary wall occupied by the baited feeder before the shift. In the absolute spatial location distribution of Condition M1 (Figure 5), the subjects did not differ [$G(18) = 12.08$]. The M1 distribution did not differ from its baseline [$G(3) = 4.60$]. In Condition M2 (Figure 6), subjects again did not vary [$G(18) = 12.82$], but all other effects were significant [condition, $G(3) = 9.92$; difference from chance, $G(3) = 17.75$]. These differences in effect are due to the fact that the M1 distribution on its own did differ from chance [$G(3) = 12.87$], being shifted toward one look, while the M2 distribution did not [$G(3) = 2.60$].

Unlike the case in Experiments 1 and 2, for Experiment 3 the originally baited feeder was left in its original array position. G tests on the array-position distributions revealed similar effects to those found above. M1 showed no between-subject variation [$G(18) = 8.40$] and did not differ from its baseline [$G(3) = 4.86$]. The M2 feeder distribution did differ from its baseline [$G(3) = 18.00$]. Again, subjects did not vary significantly [$G(18) = 11.04$]. Once more, the M2 distribution was not different from chance [$G(3) = 7.16$], while the M1 distribution was [$G(3) = 16.15$].

When the array was shifted over one coordinate (44.5 cm), the birds still used information from Phase 1 of the trial in an attempt to find the baited feeder. However, when the array was shifted 89 cm, they responded at chance. This indicates that they no longer used the information from the baited feeder. It seems that if the array were far enough away from its original position, the subjects treated it as a new trial.

In this experiment the feeder nearest the correct absolute spatial location was the most common first choice. The feeder that was correct with respect to array position and local pattern and color cues was also a common

Figure 4. Sample test feeder array presented to subjects in Experiment 3. The top panel shows the configuration during Phase 1, while the bottom panel shows Phase 2. The arrow indicates the baited feeder. In Phase 2 the plain feeder is closest to the correct spatial position, while the one to the right of it has the correct pattern information and is in the correct array position.

first choice and the most common second choice. However, in this experiment it was possible for all three types of information to converge (i.e., the spatially correct feeder could be the previously baited feeder). This happened on seven occasions (this was possible since the array that was shifted on a given test varied from bird to bird). On these trials, the first choice was to the feeder associated with all three types of cue seven times. In other words, when all three types of information converged the subjects always chose these feeders. If these cases are ignored, nine test trials remain. On these occasions, the second choice was to the correct individual feeder eight times. It seems that absolute spatial information is most important, followed by the convergence of array position and pattern cues. Experiment 4 dissociated all three types of information.

EXPERIMENT 4

Experiments 1, 2, and 3 established the importance of spatial information, be it absolute or that of array position. Experiment 3 suggested that absolute position in the aviary is more important. This final test dissociated all three types of cues—absolute spatial, array information, and pattern—by combining the tests of Experiments 2 and 3. This allowed for a final comparison among the three types of cue in the food-finding task.

Method

Subjects

Four chickadees caught at the Erindale campus of the University of Toronto were used in this experiment. Two were experimentally naive and 2 had previous experience in memory experiments

Figure 5. Distribution of the number of looks to find the peanut on trials preceding test trials (baseline) and to visit the feeder that was spatially correct with respect to the aviary or correct with respect to pattern/color and array position on test trials in Experiment 3, Condition M1; the solid line indicates chance performance.

Figure 6. Distribution of the number of looks to find the peanut on trials preceding test trials (baseline) and to visit the feeder that was spatially correct with respect to the aviary or correct with respect to pattern/color and array position on test trials in Experiment 3, Condition M2; the solid line indicates chance performance.

Figure 7. Sample test feeder array presented to subjects in Experiments 4 and 5. The top panel shows the configuration during Phase 1, while the bottom panel shows Phase 2. The arrow indicates the baited feeder. In Phase 2 the light gray feeder is in the correct spatial position with respect to the aviary, the black feeder is in the correct array position, and the blank feeder has the correct pattern information.

not reported in this paper. Those experiments did not involve being trained to respond to a certain type of cue—the subjects could have responded to spatial or local cues and in either case would have performed correctly. All other conditions were the same as those in the previous experiments.

Procedure

Training trials. Training trials proceeded as in Experiment 2.

Test trials. This test combined the two previous tests. The entire array was shifted over one horizontal coordinate and the baited feeder was switched with a randomly selected second feeder. This test configuration is shown in Figure 7. The choice of the feeder to be switched with the baited feeder was constrained: it could not be the feeder in the correct array position, as that would defeat the purpose of this experiment; furthermore, the feeder to be switched could not be too far from the spatial position occupied by the baited feeder in Phase 1 of a test trial, since the first three experiments outlined here indicate that this feeder would often be chosen first because of the importance of absolute spatial information. In this way, the choice of feeder would not be biased against the one that had the pattern information consistent with the Phase 1 baited feeder.

As in Experiment 3, only the back wall was used on test trials. Ten tests of this type were given to each subject.

Results and Discussion

The birds took a mean of 18.5 trials ($SD = 3.51$) to reach the criterion. On average, the subjects had 3.67 trials ($SD = 0.72$) between successive tests.

The baseline distribution for this experiment was similar in shape to those from the previous two experiments (Figure 8). The distributions of the number of looks to the correct spatial position, array position, and feeder are also presented in Figure 8. The first two distributions showed no significant intersubject variation, while the third did [$G(9) = 3.84$, $G(9) = 5.01$, and $G(9) = 15.41$, respectively]. All three did differ from chance [$G(3) = 51.9$, $G(3) = 24.8$, and $G(3) = 25.05$, respectively]. These differences from chance were for different reasons. The spatial location distribution difference was due to the

Figure 8. Distribution of the number of looks to find the peanut on trials preceding test trials (baseline) and to visit the correct feeder with respect to the aviary, the correct feeder with respect to the feeder array and the feeder with the correct pattern/color on test trials in Experiment 4; the solid line indicates chance performance.

preponderance of first choices of looks to the correct spatial location. Array position was usually the second choice, while the correct feeder was usually the third choice.

Further evidence of this ranking of types of cues is given by comparing these distributions with the baseline. The spatial distribution did not differ from the baseline [$G(3) = 4.09$], but the array-position distribution [$G(3) = 45.92$] and the feeder color/pattern distribution [$G(3) = 90.02$] did differ from it. Between-subject variation was not significant in any of the comparisons with baseline [$G(18) = 4.42$, $G(18) = 5.59$, and $G(18) = 15.98$, respectively].

The fact that the birds chose feeders with respect first to absolute spatial location, then to array position, and finally to pattern cues is also shown by the number of times this search order was used—on 19 of the 40 test trials, or 47.5% of the time. By chance this should only happen on 4.2% of the trials.

This experiment clearly demonstrated the importance of absolute spatial information. There was a definite rank-

ing of the types of information utilized by the chickadees in this task. First the absolute spatial location was tried. If this did not point to the reward (as it never did, since these were unbaited trials), then array position was used. Finally, the birds used the pattern on the previously baited feeder.

EXPERIMENT 5

In the test trials in the previous experiments, chickadees responded to spatial information first and to local information second. The overwhelming dominance of control by spatial cues is consistent with the suggestion outlined in the introduction that food-storing species should be especially responsive to spatial cues. Experiment 5 addressed this issue by testing dark-eyed juncos—nonstoring birds—in the same way as the chickadees were tested in Experiment 4. The hypothesis that strong control by spatial cues is part of the chickadee's possible adaptive specialization for food-storing predicts that juncos

should show less control by spatial cues relative to other cues than did the chickadees. The test used in Experiment 4 was used here because it dissociated all three types of cue (those of absolute spatial position, array position, and local pattern and color). Each junco was given 10 tests of this type.

Method

Subjects

Four dark-eyed juncos caught at the Erindale campus of the University of Toronto were used in this experiment. All 4 subjects were experimentally naive. They were housed in individual cages in a room with a 10:14-h light:dark cycle. Since these birds are larger than chickadees, they were deprived for a further 3–4 h after the normal overnight fast (17–18 h total deprivation), compared with the further 2–3 h for the chickadees.

Procedure

Pretraining. The juncos preferred feeding on the ground over feeding from feeders hung on the walls. The method of training for the juncos was therefore somewhat different from that used for the chickadees. A single bird was let into the aviary where four feeders were hanging on the wall. At the start of training, two of the feeders—one of which was hung on the wall low enough so that it touched the floor—were each baited with half a peanut. Once the

subject ate readily from this feeder, it was raised until it was well off the floor, as any feeder would be in a training or test trial. During the next phase of training, one of the four feeders was baited. The junco was let into the aviary, where it was allowed to eat for 30 sec. The lights were extinguished and the bird returned to its home cage. The subject was let back into the aviary immediately to finish the peanut. The Velcro circle was introduced in the second phase of pretraining trials. As with the chickadees, at first the circle was placed over the nut so that it only partially covered it: in subsequent trials, the Velcro circle was moved so that it eventually completely covered the peanut. Once the juncos were successfully completing both phases of the pretraining trial (including removing the Velcro) in under 1 min, training trials began. The training trials followed those mentioned previously. The same criterion that was used with the chickadees was used in this experiment.

Test trials. Each junco was given 10 of the tests outlined in Experiment 4 (Figure 7).

Results and Discussion

The subjects took a mean of 22.5 trials ($SD = 6.66$) to reach the criterion. They needed an average of 3.64 trials ($SD = 1.11$) to get back to the criterion between tests.

The baseline distribution for the juncos in this experiment mirrored that for the chickadees in the previous ex-

Figure 9. Distribution of the number of looks to find the peanut on trials preceding test trials (baseline) and to visit the correct feeder with respect to the aviary, the correct feeder with respect to the feeder array, and the feeder with the correct pattern/color on test trials in Experiment 5; the solid line indicates chance performance.

periments, but the test distributions differed dramatically (Figure 9). In no case was the intersubject variation significant [$G(9) = 14.94$, $G(9) = 15.44$, and $G(9) = 14.74$, respectively]. All three distributions did differ significantly from chance [$G(3) = 9.87$, $G(3) = 11.90$, and $G(3) = 9.32$, respectively]. All of these distributions seem to have differed from chance for the same reason: the given type of cue was responded to first, second, or third about an equal amount of time; it was very rarely chosen fourth. This indicates that the juncos did remember the cues but did not order them in a particular way as the chickadees in Experiment 4 did.

The absolute spatial, array-position, and pattern cue distributions did differ from the baseline distribution [$G(3) = 37.09$, $G(3) = 24.80$, and $G(3) = 9.32$, respectively]. This was different from the result found in Experiment 4, where the absolute spatial position distribution was indistinguishable from the baseline distribution. There was no bias to choose a particular type of cue to which to respond for the juncos. Intersubject variation was not significant when the distributions were compared with the baseline for any of the distributions [$G(18) = 21.38$, $G(18) = 21.88$, and $G(18) = 21.88$, respectively].

While there was no clear-cut ordering of the choices of the different cues, it can be said that the juncos remembered as well as the chickadees. During test trials, the juncos rarely chose the feeder that had no cue associated with it before it chose any of the others. If they were just responding by chance, one would expect that this feeder would be chosen first, second, and third 25% of the time. However, all of the distributions did differ from chance. The juncos were responding to the cues, but not in the rigid order the chickadees showed.

The juncos performed as well as the chickadees in acquiring the task. Acquisition data from the 8 chickadees used in Experiments 2–4 and the 4 juncos used in this experiment are presented in Figure 10. The numbers of

looks in the first three 5-trial blocks were analyzed with a two-factor ANOVA. Only these three blocks were used because none of the subjects had received a test trial before Trial 15 (Block 3). No main effect of species [$F(1,10) = 1.32$] or interaction of species $\times$ block [$F(2,19) = .95$] was found. The only significant effect was that of block [$F(2,19) = 5.68$], indicating that regardless of species, the subjects' performance improved over time. However, these findings should be interpreted cautiously because the methods used for pretraining and the number of pretraining trials required differed between the species, and the data in Figure 10 come from different experiments.

GENERAL DISCUSSION

Two passerine species, black-capped chickadees (a food-storing bird) and dark-eyed juncos (a nonstoring bird), were tested in a one-trial associative memory task. Both species learned the task and performed well. Test trials were given in which certain types of cue were dissociated from each other to determine what the animals were representing in the task. In addition, the chickadees were tested in a food-storing version of the task to see whether the pattern of data obtained from the food-finding task was similar to that obtained from the food-storing task.

When the first two experiments (food-finding vs. food-storing) are compared, it is evident that the chickadees are using the same memory processes in both tasks. During both experiments, the test results indicate that spatial information is responded to first, followed by local pattern and color information. This finding is important, because it allows one to use the food-finding task to examine the memory processes used in food storing in the chickadee (see also Shettleworth et al., 1990).

The first four experiments show that the chickadees possess a rich representation of a unique food site after only a 30-sec exposure (in the food-finding experiments) or a brief storing episode (Experiment 1). This representation includes spatial information relative to distant objects (the walls of the aviary in this case) as well as to closer objects (the position in the feeder array) and local features of the food site (in this case, the color and/or pattern on the feeder). Acquisition of such a rich representation is interesting in its own right, but even more interesting is the rigid order in which the chickadees respond to the various cues encoded. In Experiment 4, when all three types of cue were dissociated, the chickadees almost invariably responded in the order space, array, color. All three types of information seem to have been remembered well. Responding to any of the cues was almost always done before choosing the feeder associated with no cue.

In the field, spatial relationships may be much less fleeting than are local cues such as color. All of these types of information usually converge, so responding to one or the other is not an issue. However, if the cues do not converge, spatial information seems to be responded to first,

Figure 10. Percentage of trials on which the peanut was found in the first look of Phase 2, for both chickadees and juncos.

and it seems likely to be the least likely to have changed. The line of trees 50 m away is less likely to have changed position than the twig 3 m away, which, in turn, is less likely to have changed than the pattern in the snow next to the storage site. Indeed, Haftorn (1956) reported that tits could recover stored food after a snowfall, which obviously would change the patterns in the snow. Bossema (1979) found that European jays, a species that stores food, preferred to store the items close to trees and natural "edges" where one type of vegetation gives way to another. Similarly, Vander Wall (1982) reported that Clark's nutcrackers use spatial relationships between a cached item and various landmarks.

The comparison of storers and nonstorers is addressed by the results of Experiment 5. The juncos in this experiment also built up a rich representation in a short period of time. As was the case with the chickadees in Experiment 4, in the tests the nonstoring juncos responded first to the feeders that had features in common with the originally baited feeder. Indeed, this is the reason for the significant difference from chance in all of the data analyzed in Experiment 5, even though each type of cue was chosen roughly equally on the first, second, and third look. The juncos and chickadees differed in the way they solved the food-finding task; however, the juncos solved the problem of finding the correct feeder as well as the chickadees did [compare the baseline results from Experiments 4 and 5 (Figures 8 and 9) and the acquisition data (Figure 10)].

Preferential responding to spatial cues is by no means a rare occurrence. Tinkelpaugh (1932) allowed chimpanzees, monkeys, human adults, and human children to watch as he covered a reward under various boxes or cups. The "feeders" were set out in pairs in a circle around the subject. Each item in a pair was different. The subjects almost always chose the item in the correct spatial position, even if two members of a pair were switched with each other (as they were in Experiments 1 and 2 reported here). More recently, numerous investigators have focused on memory for compound stimuli in matching-to-sample procedures. The subjects (usually pigeons) are presented with a compound stimulus (e.g., color and line orientation, or color and location) and then presented with two alternatives from which to choose. The alternatives test memory for only one element of the compound on any given trial (e.g., sample is a red line at 45°, alternatives are red and green keys, or white lines at 45° or 60°). Experiments such as these have found that space is nearly always remembered better than color (Wilkie, Jacobs, & Takai, 1985). With the above results in mind it is interesting to note that the species that is "different" in this experiment is the dark-eyed junco, because it did not respond to space preferentially. If the speculation is correct about the chickadees responding in the rigid order because of the relative consistency of space, then one could extend the hypothesis to say that the juncos do not rely so heavily on space because space is not so uniquely advantageous as a cue for them; indeed, other types of cues are usually just as effective. This is not to say that juncos

do not encode spatial information. Such ability is necessary in virtually any animal (Gallistel, 1990). They may even be remembering space as well as the chickadees do; they are just not, however, biased to always respond to it first when many types of information diverge. It may be that three-dimensional space is more difficult for them, since they commonly feed on the ground, whereas chickadees do not (Smith, 1991).

Although these experiments clearly establish a species difference in the use of spatial and local cues, further research will be necessary to discover the mechanisms responsible for the difference and how these differences relate to the species' ecology. There may be a difference in the strength of memory for the cues, or a performance/response bias. For example, if both species remember spatial cues equally well but differ in response bias, they should perform equally accurately when tested with plain, undecorated feeders after exposure to the compound of spatial and local cues. However, if they differ in memory, differences in performance would be expected in tests with single cues. A difference in memory might have been found here; if a shorter retention interval was used, the juncos might have responded in the same fashion as the chickadees. In other words, the strength of memory of the spatial location may have decayed over 5 min in the juncos and not by as much in the chickadees over the same period.

Chickadees and juncos were chosen for this research because one species stores food and one does not. Over the past 5 years or so, various investigators have been searching for quantitative differences in brain and behavior between storing and nonstoring birds. Some of their experiments have been quite successful (e.g., Clayton & Krebs, 1993; Olson, 1991). However, one is always left with the possibility that the difference found may be due to some sort of contextual variable, such as motivation (MacPhail, 1987). The results of the research reported here suggest that the adaptive specialization in the chickadee and perhaps other food-storing birds may be qualitative rather than quantitative. However, chickadees and juncos differ in many other ways besides in their tendency to store (or not to store) food. They come from different families and have different feeding ecologies. Specifically, juncos prefer to feed on the ground rather than in trees. They required more pretraining than the chickadees did to eat from feeders on the walls of the aviary. Further research should test both species in a ground-feeding version of the tasks used here.

In any case, any attempt to relate cognitive processes to ecological or life-history variables must include more than one pair of species. Recent comparisons between storing and nonstoring parids and corvids have revealed the same pattern of species differences as that reported here (N. S. Clayton, personal communication, April 1993). Clayton's results support those reported here in indicating that one way in which food-storing birds differ from nonstorers consists in how they process, store, or respond to spatial as opposed to other types of information.

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