

Memory for spatial and object-specific cues in food-storing and non-storing birds

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Abstract. Two storer/non-storer pairs of species, marsh tit (*Parus palustris*)/blue tit (*P. caeruleus*) and jay (*Garrulus glandarius*)/jackdaw (*Corvus monedula*) were compared on a one-trial associative memory task. In phase I of a trial birds searched for a reward in one of four feeders which differed in their trial-unique spatial location and object-specific cues. Following a retention interval, the birds had to return to the same feeder to obtain a further reward. In control trials the array of feeders was unaltered, whilst in dissociation tests it was transformed to separate spatial location and object-specific cues.

In control trials there was no difference in performance between species. In dissociation tests, the two storing species went first to the correct spatial location and second to the correct object-specific cues, whereas the two non-storing species went first with equal probability to the correct spatial and local object cues.

Monocular occlusion was used to investigate differences between the two eye-systems. In control trials there was no effect of occlusion. In dissociation trials, all 4 species preferentially returned to the feeder with the correct object-specific cue when the left eye had been covered in phase I and to the feeder in the correct spatial position when the right eye had been covered in phase I.

These results suggest that (a) food-storing birds differ from non-storers in responding preferentially to spatial information and (b) in storers and non-storers the right eye system shows a preference for object-specific cues and the left eye system for spatial cues.

Key words: Memory – Spatial and object-specific cues – Food-storing birds – Hemispheric specialization

Introduction

Food-storing birds rely on memory to retrieve their caches of stored food (reviews in Sherry 1989; Krebs 1990). Given the importance of an accurate spatial memory for retrieving stored caches, it seems possible that

food-storers may have evolved a memory which may be qualitatively and/or quantitatively different from that used in normal foraging (Krebs 1990; Krebs et al. 1990a,b; Shettleworth 1990, but see Sherry and Schacter 1987). The Paridae and Corvidae are two families of birds which provide an opportunity to test this hypothesis because both contain food-storing and non-storing species. In the parids, for example, marsh tits (*Parus palustris*) and black-capped chickadees (*Parus atricapillus*) store food in the wild and use memory to find their stored caches hours to days later (Hitchcock and Sherry 1990) (see reviews in Sherry 1989; Shettleworth 1990) whereas blue tits (*P. caeruleus*) share similar ecology and feeding habits yet do not store food. In the corvids, jays (*Garrulus glandarius*) store food in the autumn and rely on memory to find these caches in the following spring, after an interval of 6 months (Bossema 1979) whereas jackdaws (*Corvus monedula*) do not store (references cited in Healy and Krebs 1992b).

In order to compare the memory of storing and non-storing species, it is necessary to use a memory task which does not involve storing food. Ideally the task should also contain the essential features of food-storing memory such as the requirement to return to a particular location following a single experience. Several studies have used variants of a task called one-trial associative learning (Brodbeck et al. 1992; Brodbeck 1994; Clayton 1992a; Clayton and Krebs 1992, 1994; Healy and Krebs 1992a). In a typical one-trial associative memory task, each trial consists of two phases separated by a retention interval, the first phase corresponding to storing food and the second phase to retrieving the stored food. In phase I, the bird is trained to search for a piece of peanut in one of several feeders and is allowed to eat it for 30 s. In the second phase of each trial, the food is hidden in the site where it has been seen in phase I and the bird is allowed to search for and eat the remaining piece of peanut. The location of the food reward varies from trial to trial so that the bird has to remember the trial-specific location and/or object-specific cues around the site on the basis of a single experience on each trial. If

the bird has remembered perfectly, it should return immediately to the site where it had partially eaten the peanut in phase I without looking in any of the other sites, whereas if it searches at random it will have an equal probability of visiting each of the feeders. The main difference between food-storing and the one-trial associative learning task is that the bird does not place the food in the site itself; the similarities include the fact that the site is visited once and may be associated with food, some aspect of this site is memorised during the visit and at a later time the bird returns to this site and retrieves food.

Brodbeck (1994) compared black-capped chickadees and non-storing dark-eyed juncos (*Junco hyemalis*) on a version of the one-trial memory task in which the array of trial-unique feeders was transformed on test trials so that the birds had to choose between spatial location and object-specific cues on the feeder. Chickadees went first to the correct spatial location and second to the correct feeder, whereas juncos were equally likely to go first to the correct spatial position and the correct feeder. Brodbeck also found that the chickadees' preference for responding to spatial cues was seen in both food-storing and one-trial associative memory, suggesting that the two tasks utilise similar features of memory.

The first objective of the present study was to test Brodbeck's hypothesis by comparing two other pairs of species in the test procedure in which spatial and object specific cues are dissociated by transforming the array. In Brodbeck's study, the two species came from different families of passerine birds, so his observed differences in behaviour could have been a reflection of a phylogenetic difference between chickadees (Paridae) and juncos (Emberizidae) rather than a difference between storers and non-storers. In the present study each pair of species was from within the same family (two parids: the storing marsh tit and non-storing blue tit and two corvids: the storing jay and non-storing jackdaw), substantially reducing the possibility that differences between storers and non-storers could be confounded with phylogenetic differences.

The second objective of the present study was to test the hypothesis that the two eye systems play distinct roles. Extensive work on young chicks (reviewed in Bradshaw and Rogers 1992) has shown that there are hemispheric asymmetries in visual perception and memory. Most relevant to the present study is the work of Andrew (1988), Rashid and Andrew (1989), Mench and Andrew (1986) and Andrew (1991), showing that the right hemisphere (fed by the left eye) appears to attend to spatial position of a food reward whilst the left hemisphere (fed by the right eye) attends to conspicuous cues which allow an object to be assigned to categories such as food or non-food.

Sherry et al. (1981), Clayton (1992a) and Clayton and Krebs (1992) have used monocular occlusion to show that in marsh tits and blue tits, memories formed by one eye system are not accessible to the contralateral system after short (at least up to 3 h) retention intervals. This presents the possibility of using monocular occlusion combined with dissociation of object-specific and spatial cues to investigate the roles of the left and right eye systems in remembering the two kinds of cue.

Brodbeck's hypothesis that storers rely to greater extent than non-storers on spatial cues and the hypothesis that the right hemisphere stores spatial and the left hemisphere object-specific information were tested in the same experiment by exposing individuals of the four species to three different treatments, no monocular occlusion, left-eye occlusion and right-eye occlusion in a balanced design.

Methods

Birds and housing conditions. The subjects were 24 wild-caught birds with no previous experience of laboratory experiments. All birds were in adult plumage at the time of capture and were caught during a two month period before the start of the experiments. Six marsh tits (mean weight 10.5 g), 6 blue tits (mean weight 11.3 g), 6 jays (mean weight 175 g) (one of which died during the experiment) and 6 jackdaws (mean weight 220 g) were housed indoors in single wire cages (parid cages measuring 0.44 m wide \times 0.77 m long \times 0.44 m high; corvid cages measuring 0.62 m wide \times 0.76 m long \times 0.91 m high). Both the living and experimental rooms were maintained on a 10:14 h light: dark cycle. During the experiment, the birds were deprived of food overnight starting at 17:00 GMT, tested the following morning from 9:00 onwards and given fresh food and water following each trial. As a result of this protocol the parids were deprived of food for at least 3 daylight hours before each trial and the larger corvids were deprived for at least 6 daylight hours before each trial.

Experimental environment. The experiments were done in January and February 1993. The parids were tested individually in a room, 3.5 \times 2.0 \times 2.8 m high, and observed through a one-way Plexiglass window. The room contained four "peanut feeders" (Krebs et al. 1990; Brodbeck et al. 1992) which were hung from plastic mesh screens (1 m \times 2 m, 1.5–2.5 m off the ground) attached to two adjacent walls of the room. Each peanut feeder consisted of a wooden block measuring 9.0 \times 4.0 \times 15.0 cm high with a hole 0.5 cm diameter in the centre of the front of the block which could contain a piece of peanut. The hole was covered by a string knot in phase II of a trial to prevent the birds from seeing the hidden seed (Clayton 1992b; Hampton and Sherry 1994). To ensure that only part of the peanut was eaten in phase I, the peanut was wedged firmly into the hole so that it could not be removed in its entirety and the lights were switched off after 30 s of feeding time. Four cm below the hole there was a perch, 5.5 cm \times 0.9 cm diameter on which the bird could sit and examine the contents of the hole. Each feeder was made visually unique on every trial by the addition and removal of sticky coloured paper shapes. For each trial, the location of the feeders was chosen at random from 400 possible coordinates on the two mesh walls (the array always included both walls) so that both spatial and object-specific site cues were trial-unique (Brodbeck et al. 1992; Brodbeck 1994). The floor was swept between each phase and trial to ensure there were no extraneous pieces of food in the test room.

The corvids were tested individually in a room, 4.24 \times 2.80 \times 2.30 m high, and observed through a one-way Plexiglass window. The room contained four "peanut feeders" placed on the floor. Each peanut feeder consisted of a square metal sand-filled tray measuring 25.5 \times 25.5 \times 7.5 cm deep. In the centre of the tray was the cap of a 35 mm film cannister which could contain a peanut. The film cap was covered with sand in phase II to prevent the birds seeing the peanut. To ensure that only part of the peanut was eaten in phase I of a trial, the lights were switched off after 30 s and one of the two halves of the peanut was held in the film cap with clear adhesive tape so that the two halves could not be removed together. Each feeder was made individually distinct by the presence of a vertical cylindrical landmark inserted into the tray. The landmarks were 30 cm tall and 5.5 cm in diameter and were made visually unique on

every trial by the addition and removal of sticky coloured paper shapes. The spatial locations of the four feeders were also trial-unique, selected from 400 possible coordinates.

Monocular occlusion. In monocular occlusion treatments, the bird's left or right eye was covered with a circular cardboard eye cap 10 min before entering the experimental room for phase I of a trial (treatments referred to as "Left-None" and "Right-None", respectively). In the third treatment the birds did not wear an eye cap on either eye ("None-None" treatment). The eyecap did not touch the eye itself but was glued to a circular strip of cloth which protected the feathers around the eye without impeding vision. The parid eyecap measured 2.2 mm in diam and was attached with Eylure® cosmetic eyelash adhesive to a circular strip of black satin cloth (Clayton 1992). The eyecap for the corvids measured 22 mm in diam and because of its larger size and weight the original method was insufficiently strong to hold the eyecap in place. In order to adapt the technique for the corvids, the inside of the eyecap was covered with velcro. The eyecap was attached to a second piece of velcro which protected the feathers around the eye and was attached using Copydex adhesive glue. In all 3 treatments, the birds spent the 10 min prior to phase I in a cloth bag, to ensure that in the monocular occlusion treatments the eyecap was fixed firmly to the feathers around the eye and that the glue had time to dry. In both eyecap treatments the birds only wore eyecaps in phase I of a trial and the eyecap was removed immediately after completion of phase I.

One-trial associative memory task. For both experiments, each trial consisted of two phases. In phase I, the bird was allowed to enter the experimental room and spend 30 s eating from a piece of peanut in one of the four feeders. In this phase the peanut was not hidden from view so that the bird usually found it on the first visit to a feeder. If a bird did not take the peanut within five minutes the trial was stopped and repeated the following day. The bird was allowed back into the room for Phase II of a trial following a retention interval of 5 min. The remainder of the partially eaten peanut was in the same site as in phase I, but hidden, by placing the pieces of string knot in front of the holes in the feeders for the parids or covering the site with sand for the corvids. The order of visiting the four feeders in phase II provided a test of the bird's ability to remember the location of food seen previously. Perfect performance would be to return immediately to the site with the partially eaten peanut, whereas by random without revisiting the bird should take a mean of 2.5 looks to find the peanut (Brodbeck et al. 1992; Brodbeck 1994). In other words, perfect performance would be visiting the correct feeder on the first look in 100% of the trials and random performance would be visiting the correct feeder on the first look in 25% of the trials.

Training. For both experiments the training and testing protocols were essentially the same. During initial training, all 4 sites contained pieces of peanut and the rewards were visible. Once the birds had learned to visit sites containing food, only one site was rewarded on each trial and then this reward was only visible during phase I so that the bird had to search in phase II for the feeder where it had partially eaten peanut in phase I. Following Brodbeck (1994), the criterion performance for proceeding to the test trials was for each bird to have completed at least 15 trials in which three of the last 4 were below chance (< 3 looks on 3/4 trials) or two successive perfect trials (1 look on 2/2 trials). Birds were given no more than 3 trials per day, with an inter-trial interval of at least 1 h. In the first experiment, marsh tits required a mean and standard error of 22.16 ± 1.00 trials and blue tits required 22.50 ± 0.50 trials of training. In the second experiment, jays required a mean and standard error of 20.33 ± 1.0 trials and jackdaws required 21.67 ± 1.33 trials of training. Once birds had reached criterion they were given a further 3 training trials for each of the 3 eyecap treatments (None - None, Left - None and Right - None) to provide a baseline control.

Dissociation test trials. Test trials differed from training trials only in phase II of the experiment. Immediately after phase I, in the eyecap

treatments Left - None and Right -None, the eyecap was removed and the bird returned to its home cage; in the None - None treatment the bird simply remained in its home cage. During the retention interval of 5 min, the contents of the baited feeder were removed and the feeder was swapped with one of the other 3 feeders used in phase I (chosen at random). The feeders were adjusted by covering the holes with string knots (parids) and the site of the peanut with sand (corvids), and the bird was allowed back in the room. Thus, phase II test trials differed from training and baseline control trials in two ways: (1) there was no reward; (2) the spatial location of two of the feeders had been exchanged so that the previously baited feeder had the correct object-specific decoration but incorrect spatial location with respect to phase I of the trial. Therefore, in test trials the bird was forced to choose between spatial and object-specific cue. The order in which the four feeders were visited in phase II of each trial was recorded. Birds that relied on spatial information should have returned to the feeder in the correct spatial location first whereas those that relied more heavily on object-specific cues around the feeder should have looked first in the feeder with the correct object-specific cues. If the birds did not remember which feeder contained peanut in phase I they should search randomly in the 4 feeders.

All individuals of the 4 species were given 15 test trials, consisting of 5 replicates for each eyecap treatment (None - None, Left - None, Right - None) in a randomised block design. After each test trial the bird was given training trials until it reached criterion again so that the test trials were equated with respect to previous performance. In each of these retraining trials, the birds wore an eyecap on either the left or right or on neither eye during phase I as in the test trials and baseline control trials. Each bird received the eyecap treatments during retraining trials in a randomized block design. Marsh tits required a mean and standard error of 3.45 ± 0.22 trials, blue tits required 3.20 ± 0.55 , jays 3.50 ± 0.50 and jackdaws 3.84 ± 0.38 to reach criterion again after a test trial.

Results

Baseline control trials

Figure 1a and b shows the results of the 3 control trials at the end of training, in which the feeder array was not transformed to dissociate spatial and object-specific cues. The data shown are the mean and standard error of the percentage of trials for each treatment in which birds visited the correct feeder on the 1st, 2nd, 3rd and 4th look (excluding revisits, which were rare) in phase II. Figure 1a shows the results for parids and Fig. 1b for the corvids.

In all 3 eyecap treatments, all 4 species performed significantly better than chance, tending to visit the correct feeder on the first look more often than the 25% random expectation (horizontal line in Fig. 1) (G-tests all $P < 0.001$ for total G; heterogeneity G non-significant and pooled G < 0.001 in all cases). Performance in phase II was further analysed using a repeated measures analyses of variance. Within the parids and corvids, species were compared by calculating the mean percentage (arcsin square root transformed) of visits that each bird made to the correct feeder on the 1st look. The three eyecap treatments were repeated measures and species was a between subjects factor.

There was no significant difference between marsh tits and blue tits in the mean percentage of trials in which the correct feeder was visited on the first look ($F_{1, 10} = 0.50$, $P = 0.827$) nor was there a significant effect of eyecap

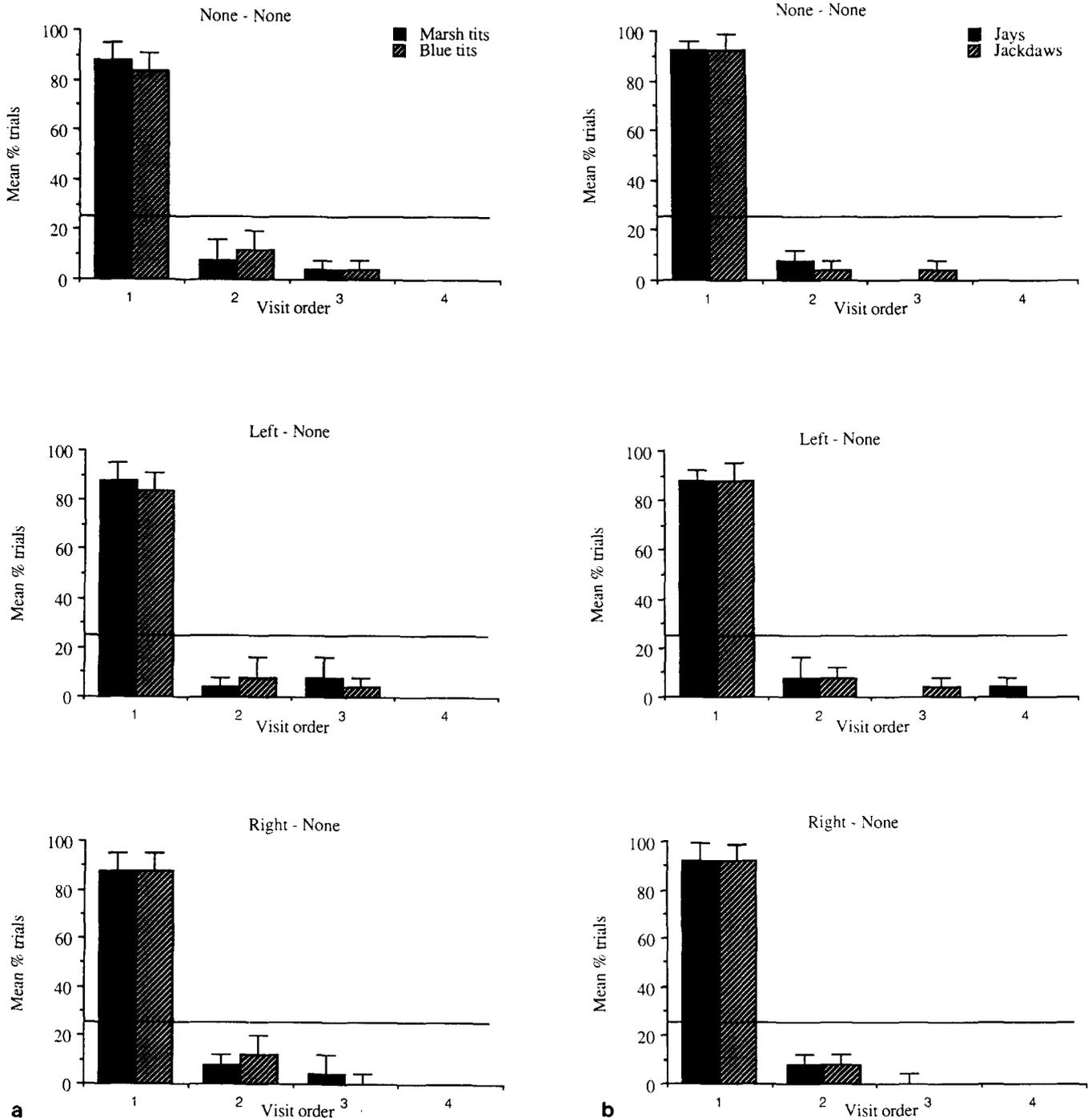


Fig. 1a, b. Baseline control trials in which spatial and object-specific cues were not dissociated and birds were tested in the 3 eyecap treatments: *None - None* (no eyecaps worn), *Left - None* (birds wore an eyecap over the left eye in phase I but neither eye was covered in phase II), *Right - None* (birds wore an eyecap over the right eye in phase I but neither eye was covered in phase II). The data shown are mean and standard error of the percentage of trials in which birds

visited the correct feeder (baited in phase I) on the 1st, 2nd, 3rd and 4th look (discounting revisits) in phase II of each trial. The horizontal line represents the values predicted if the birds were visiting the 4 feeders at random without revisits. **a** Comparison of marsh tits and blue tits; **b** comparison of jays and jackdaws. There are no significant differences between pairs of species and between eyecap treatments

treatment ($F_{2, 20} = 0.042$, $P = 0.959$) or interaction between eyecap \times species ($F_{2, 20} = 0.096$, $P = 0.909$). In the corvids, there was also no significant difference between species in the mean percentage of trials in which the correct feeder was visited on the first look ($F_{1, 9} = 0.110$, $P = 0.748$) nor was there a significant effect of

eyecap treatment ($F_{2, 18} = 0.109$, $P = 0.897$) or interaction between eyecap \times species ($F_{2, 18} = 0.050$, $P = 0.952$). These results show that there were no differences between the pairs of species in baseline performance in any of the 3 eyecap treatments; nor were there differences among treatments.

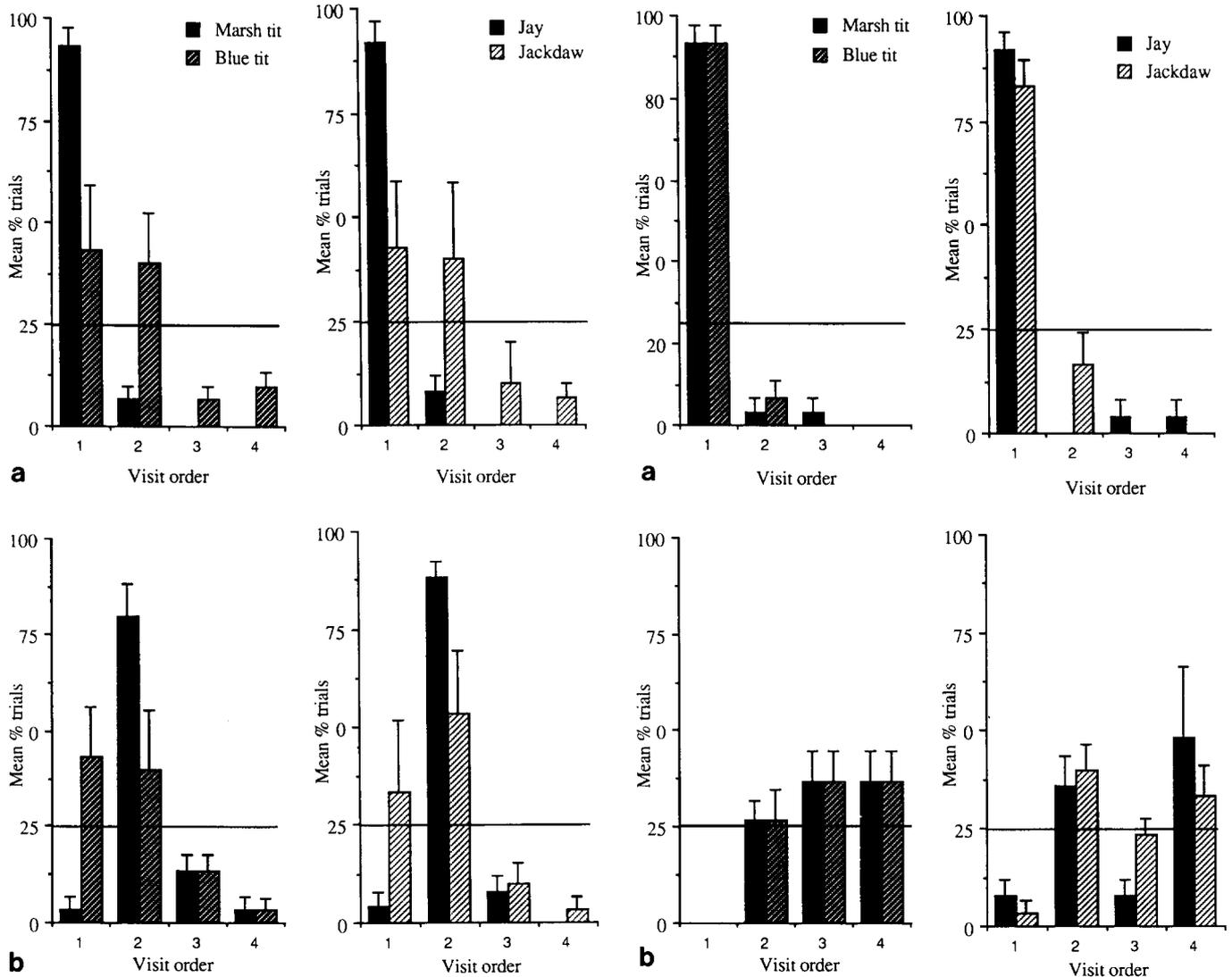


Fig. 2a, b. Dissociation tests with no eyecaps. Mean and standard error of the percentage of trials in birds which visited the feeder that was in **a** the correct spatial location and **b** with the correct object-specific cues on the 1st, 2nd, 3rd and 4th look (discounting revisits) in phase II of each trial. *Left hand column* shows the results of comparison of marsh tits and blue tits and *right hand column* the comparison of jays and jackdaws

Fig. 3a, b. Dissociation tests with the right eye covered in phase I of each trial. Details as in Fig. 2

Dissociation of spatial and object-specific cues

In the 3 test treatments the birds were tested in the 3 eyecap conditions (no eyecap, left and right eye covered in phase I) and the array of feeders was transformed in phase II to dissociate spatial and object-specific cues. Memory performance is shown in Figs. 2–4 as the mean and standard error of the percentage of the five trials of each eyecap treatment in which birds visited the feeder that was in (a) the correct spatial location and (b) of the correct object-specific cue on the 1st, 2nd, 3rd and 4th look (excluding revisits) in phase II of each trial. Random search is indicated as the horizontal line at 25%.

All 4 species differed significantly from random search in the None - None condition, because they visited the feeder in the correct spatial location and the feeder with

the correct object-specific cues before visiting the other two feeders (G tests for both spatial and object-specific cues all $P < 0.01$ total; heterogeneity G significant only for blue tits with spatial cue and pooled G significant in all cases ($P < 0.01$)). This suggests that all 4 species remembered both the location and the specific cues associated with the feeder that had contained peanut in phase I. However, as the Fig. 2 shows, the two food-storing species, marsh tits and jays, tended to go back to the feeder in the correct spatial location first, and the one with the correct object-specific cues second, whereas for the non-storers, blue tits and jackdaws, in about half the trials the feeder in the correct spatial location was visited first and that with the correct object-specific cues second, and in the other half the two feeders were visited in the reverse order. Although it appeared that individual blue tits and jackdaws were either, object or position “specialists” subsequent work in which individuals were tested on a larger number of trials suggests that this may be an artifact of small sample sizes (Clayton, unpublished data).

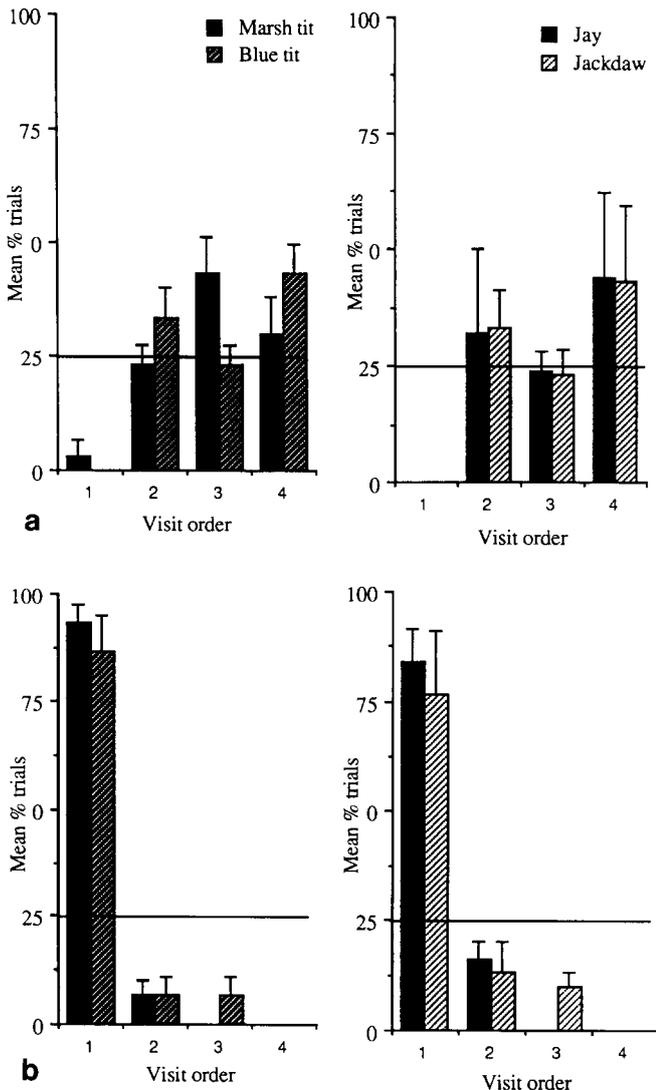


Fig. 4a, b. Dissociation tests with the left eye covered in phase I of each trial. Details as in Fig. 2

Figure 3 shows the results of the treatments in which the right eye was covered in phase I. All 4 species visited the correct spatial location first (total and pooled G , $P < 0.01$ in all tests, in none was heterogeneity G significant). The probability of visiting the feeder with the correct object-specific cues on the second, third and fourth look did not differ from chance (total G not significant). In contrast, when the left eye was covered in phase I, the birds returned to the feeder which had the correct object-specific cues (total and pooled G significant and heterogeneity G non-significant in all cases) but was in the wrong spatial location. The probability of visiting the feeder in the correct place on the second, third and fourth look did not differ from chance (G tests), showing that with the left eye covered birds did not remember spatial cues (Fig. 4).

Comparison between species

Performance in phase II was further analysed using repeated measures analyses of variance for each pair of

species. The two species pairs were compared by calculating the mean percentage of visits that each bird made to the feeder that was in the correct position and had the correct object-specific cues on the 1st look and 2nd look (i.e. correct position on the first look, correct position on the second look, correct object-specific cue on the first look, correct object-specific cue on the second look). Thus in total there were 8 ANOVAS, in each of which the 3 eyecap treatments were repeated measures and species was a between subjects factor.

The analysis on the marsh tit-blue tit pair showed that there was a significant difference between species in the mean percentage of trials in which the feeder in the correct spatial position was visited on the first look and second look ($F_{1,10} = 10.492$, $P < 0.01$ 1st look; $F_{1,10} = 6.957$, $P < 0.05$ 2nd look). However, when the analyses were repeated for the visits to the feeder with the correct object-specific cues there was no significant effect of species ($F_{1,10} = 2.941$, $P = 0.1171$ 1st look; $F_{1,10} = 4.416$, $P = 0.0619$ 2nd look). This result can be explained by the fact that marsh tits differed from blue tits mainly in the way they performed in the None - None eyecap treatment: marsh tits visited the feeder in the correct spatial location first and the feeder with the correct object-specific cues second, whereas blue tits relied more or less equally on spatial and object-specific cues for the first and second look (Fig. 2). However, Figs. 3 and 4 suggest that there were no differences between the two species on the Left - None and Right - None eyecap treatments.

The analyses also showed that there was a significant effect of eyecap treatment when the results were analysed in terms of the feeder in the correct position and correct object-specific cue (for position: $F_{2,20} = 79.77$, $P < 0.001$ 1st look; $F_{2,20} = 6.655$, $P < 0.01$ 2nd look; for object specific cue: $F_{2,20} = 120.204$, $P < 0.001$ 1st look; $F_{2,20} = 18.971$, $P < 0.001$ 2nd look). This result can also be seen clearly in Figs. 3 and 4: in the Left - None treatment both species responded to object-specific cues whilst in the Right - None treatment both species responded to spatial cues.

The analyses of the pair of corvid species showed a similar pattern. There was a significant difference between jays and jackdaws in the mean percentage of trials in which the feeder in the correct spatial position was visited on the first and second look ($F_{1,9} = 13.962$, $P < 0.01$ 1st look; $F_{1,9} = 7.818$, $P < 0.05$ 2nd look). However, with correct object-specific cues there was no significant effect of species ($F_{1,9} = 0.1821$, $P = 0.6797$ 1st look; $F_{1,9} = 2.384$, $P = 0.1611$ 2nd look).

There was a significant effect of eyecap treatment (for position: $F_{2,18} = 59.048$, $P < 0.001$ 1st look; $F_{2,18} = 1.646$, $P = 0.2206$ 2nd look; for object-specific cue: $F_{2,18} = 33.662$, $P < 0.001$ 1st look; $F_{2,18} = 12.786$, $P < 0.01$ 2nd look).

Discussion

The main results are as follows. (a) In baseline control trials there were no significant differences between the species, nor was there any significant effect of eyecap

treatment. The performance of all four species differed significantly from chance. (b) When spatial and object-specific cues were dissociated, the two storing species (marsh tits and jays) returned first to the feeder in the correct spatial position and to the correct object-specific cue second, whereas the two non-storing species (blue tits and jackdaws) returned with equal probability to the correct position and the correct object-specific cues. (c) When the right eye was covered in phase I, all four species returned to the feeder that was in the correct position and appeared not to remember object-specific cues. (d) When the left eye was covered in phase I, all four species returned first to the feeder with the correct object-specific cues and appeared not to remember spatial location.

Storers and non-storers

The results of the baseline control trials and the dissociation test with no eyecaps support the findings of Brodbeck (1994). In the baseline control trials there was no difference in performance between storing and non-storing species, as found by Brodbeck (1994) and Clayton and Krebs (1994). The results of the dissociation trials with no eyecaps, combined with Brodbeck's data, suggest that there may be a difference between storing and non-storing birds in their response to spatial versus object-specific cues. The two pairs of species tested in the present study represent independent evolutionary origins of food storing in the Corvidae and Paridae: this strengthens the argument that the difference reported here and by Brodbeck is associated with food-storing. The tendency to respond to spatial in preference to other cues is, however, not a unique feature of food-storers: parallel results have been obtained with primates (Tinkelpaugh 1932) and with pigeons (Wilkie et al. 1985), although the different experimental protocols used do not permit direct comparison with the present results. One possible adaptive explanation for the emphasis of storers on spatial position is that object-specific cues are more prone to change (e.g. due to snowfall or dieback of vegetation in winter) between storage and retrieval of food than is spatial location. By relying on spatial position, storers are able to retrieve their hoards even when object-specific cues have changed (Bennett 1993; Brodbeck 1994).

The present experiments do not attempt to analyse the nature of the spatial cues to which the birds respond, but Brodbeck (1994) studied the response of food-storing black-capped chickadees to double a transformation in which spatial location and object specific location were dissociated, as in the present experiments, and in addition the total array was moved 44.5 cm horizontally within the room. The chickadees went first to the feeder in the correct absolute position, second to the feeder in the correct array position and third to the correct object-specific cues. Therefore in Brodbeck's experiments, spatial location was defined by the birds with respect to the global cues in the room rather than the local spatial position within the array (see also Sherry (1992) for evidence that chickadees respond to global cues). In a further experiment, Brodbeck found that if the array was shifted by 89 cm horizontally the birds performed at chance level.

This suggests that the spatial position is remembered accurately and that a deviation of 89 cm is sufficient for the bird to treat the array as a new trial.

The tendency of storers to respond preferentially to spatial cues is consistent with the findings of Olson (1991) who showed that food-storing Clark's nutcrackers (*Nucifraga columbiana*) are able to remember for longer retention intervals than are pigeons in spatial delayed non-matching-to-sample task. However, the results reported here do not show that food-storers have a superior performance, rather that they differ from non-storers, perhaps in the way in which memory is encoded (see below for alternative hypotheses). The difference in response to spatial and object-specific cues is one of a number of features in which the memory of storers may differ from that of non-storers. Clayton and Krebs (1994) report a difference in accuracy of spatial discrimination in a one-trial associative learning task and Clayton and Krebs (1992) show that hemispheric transfer of memory differs between marsh tits and blue tits (see below). It is not yet clear how these various differences between storers and non-storers are interrelated and how, in turn, they are related to the anatomical specialisation of the hippocampus of storers (Krebs 1990).

Memory or response bias?

The difference between storers and non-storers, assuming confounding factors such as motivation or motor skill are excluded (Macphail 1982), could be explained by two hypotheses. Either there is a difference in storage and/or retrieval of memory or there is a difference in the way the two kinds of species respond to their memories ("response bias"). Within the first of these alternatives two possibilities may be distinguished. (a) Spatial and object-specific cues "compete" with one another at the time of memory formation (akin to overshadowing in learning theory - Mackintosh 1983) and in storers spatial cues outcompete object-specific cues whilst in non-storers the two compete equally. (This competition could also take place at the level of attention to cues before memories are formed). (b) After initial processing, spatial memories persist longer than object-specific memories in food storers but not in non-storers. The available evidence does not distinguish between these alternatives.

The fact that storing and non-storing species were equally good at remembering spatial or object-specific cues when one eye was covered in phase I is consistent either with the response bias hypothesis or with competition in memory formation. The former hypothesis would explain the lack of difference between storers and non-storers by proposing that response bias is eliminated by allowing only one kind of memory to be stored. The competition hypothesis would propose that monocular occlusion reduces or excludes competition between hemispheres for memory establishment and hence eliminates the difference between species (see also Andrew 1991 for a similar interpretation of interhemispheric competition in chicks). In the monocular occlusion treatments, unlike the controls, only one cue was remembered (there was no significant preference for the alternative cue in the second

choice), suggesting that any potential competition between memories for position and object was prevented.

One way to distinguish between competition and response bias would be a treatment in which the birds wore no eyecaps in phase I but searched with one eye covered in phase II. In this treatment, competition has occurred in phase I, so that storsers should do better than non-storsers when the right eye is occluded (so that only the "spatial hemisphere" is accessible) and worse when the left eye is occluded (the "object-specific cue hemisphere" is accessible) in phase II. The response bias hypothesis predicts no difference between species, because only one cue is available in phase II (position or object, according to which eye is occluded) and hence there is no opportunity for storsers to respond preferentially to spatial cues when the object-specific cue hemisphere is tested.

The possibility of a longer term difference in memory processing is suggested by the results of Clayton and Krebs (1992). They showed that in both marsh tits and blue tits, the right hemisphere acts as a short term store and the left hemisphere as a long-term store (see also Horn 1985; Rose 1991). More importantly for the present discussion, they found that information is transferred from the right to the left hemisphere after about 7 h in marsh tits but not in blue tits. This leads to the prediction that after retention intervals longer than 7 h, spatial information should be inaccessible to blue tits (because it has decayed in the right hemisphere and not been transferred to the left), whilst it should persist in marsh tits. If this hypothesis were extended to storsers and non-storsers in general, it would imply a difference after retention intervals of greater than 7 h in the ability to recall spatial cues. An even more dramatic prediction is that in storsers, but not non-storsers, the ability of birds to remember spatial location should actually *increase* with retention interval (as spatial information is transferred from the right to the left hemisphere) in a treatment with right eye occlusion in phase I and left eye occlusion in phase II.

Lateralization

Studies on the nature of behavioural lateralization in chicks and pigeons (reviewed in Bradshaw and Rogers 1992) show some parallels with the present findings. Rashid and Andrew (1989) studied a reference memory task in which chicks (aged from 7–15 days) were trained to look for hidden food in a sawdust-filled tray and then distant and local spatial cues were dissociated by rotating the tray through 180°. Chicks with the left eye occluded searched at random, whereas chicks with the right eye occluded searched in both the place indicated by distant cues in the room but outside the tray and the place indicated by local cues on the walls of the tray. There was some suggestion that at days 13–15, the right eye occluded group attended increasingly to distant cues whilst the left eye occluded chicks increased their response to local cues. This suggests that, as in the present experiments, the right hemisphere encodes spatial information. In young male chicks, the left hemisphere is able to learn more rapidly than the right to discriminate food from similar

non-food objects (grains of chick mash from pebbles) (Mench and Andrew 1986; Zappia and Rogers 1987), a result interpreted by Andrew (1991) as indicating that the left hemisphere attends to conspicuous cues and assigns stimuli to categories. The response of the left hemisphere in the present experiments to object-specific cues would be consistent with the chick results if one defined the object-specific cues as conspicuous features used to categorise food and non-food. In chicks, hemispheric asymmetries in visual performance are age- and sex-dependent, and arise from the fact that in the egg the chick lies with its left eye covered and right eye exposed to light (Rogers 1990). Although in chicks, the asymmetries are thought to disappear by the age of 3 weeks, in adult pigeons there is an asymmetry, the left hemisphere being superior in visual discrimination learning (von Fersen and Güntürkün 1985). No data testing the preference of right and left hemisphere in pigeons for spatial and object-specific cues have been reported, but Bradshaw and Rogers (1992) summarise data on albino rats (in which there is almost complete cross-over of visual information) showing that, as in the present study, the right hemisphere responds to spatial information. Hemispheric specialisation in humans also parallels the present findings: the right hemisphere is predominant in analysis of spatial relations (De Renzi 1982) and the left hemisphere in recognition of particular stimuli (Goldberg and Costa 1981).

Bradshaw and Rogers (1992) suggest that the functional significance of lateralisation is to prevent conflicts of information arising from visual input of two laterally placed independent (largely monocular) eyes. Whilst this hypothesis may account for some overall aspects of laterality, it does not specifically explain why the right hemisphere should be biased towards spatial cues. One possibility is that exposure to light in the egg leads the right eye to respond to the first visual stimuli to which the young bird is exposed. These are conspicuous non-spatial stimuli (e.g. sight of parent): hence the left hemisphere develops a preference for these kinds of stimuli whilst the right hemisphere takes on the role of responding to other visual stimuli including spatial cues. This hypothesis would predict that reversing the position of the head in the egg would not only reverse hemispheric dominance in visual discrimination (Rogers 1986) but also the asymmetry in response to spatial and object-specific cues.

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