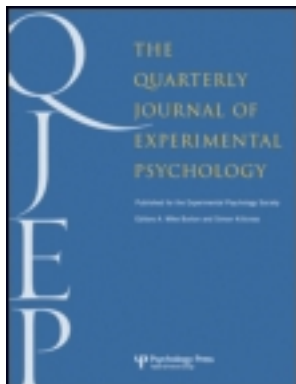


This article was downloaded by: [University of St Andrews]

On: 20 May 2013, At: 07:12

Publisher: Routledge

Informa Ltd Registered in England and Wales Registered Number:
1072954 Registered office: Mortimer House, 37-41 Mortimer Street,
London W1T 3JH, UK



The Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology

Publication details, including instructions for
authors and subscription information:

<http://www.tandfonline.com/loi/pqjb20>

Delayed-matching-to-sample by marsh tits and great tits

Susan D. Healy ^a & John R. Krebs ^a

^a University of Oxford, U.K.

Published online: 29 May 2007.

To cite this article: Susan D. Healy & John R. Krebs (1992): Delayed-matching-to-sample by marsh tits and great tits, *The Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology*, 45:1, 33-47

To link to this article: <http://dx.doi.org/10.1080/14640749208401023>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or

costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Delayed-matching-to-sample by Marsh Tits and Great Tits

Susan D. Healy and John R. Krebs

University of Oxford, U.K.

The ability of two species of tits to remember the location and/or features of an object was tested in a delayed-matching-to-sample procedure. Three values of retention interval between presentation of the sample stimulus and the choice—30 sec, 5 min, and 15 min—were used. Both species performed at above-chance level at all retention intervals, and there was no significant decline in accuracy with increasing interval. A pool of 100 stimulus objects was used, but the results of control trials indicated that the birds responded primarily to location rather than stimulus features of the object itself. Although the food-storing marsh tit tended to perform at a higher level than the non-storing great tit, the only significant difference between the species was in the first 50 trials of the first treatment, when the birds were acquiring the task. The results are discussed in relation to the hypothesized special memory capacity of food-storing birds.

The “synthetic” approach to animal learning and memory (Kamil, 1988) is the combination of psychological method and theory with behavioural and ecological knowledge of the animals being studied. This approach has been used, in particular, during the last few years to study the spatial memory of food storing species belonging to the Corvidae and the Paridae (Kamil & Balda, 1990; Krebs, 1990; Shettleworth, 1990). Within these two families some species store food, either on a long-term basis (food retrieval occurs several months after storage, as in nutcrackers *Nucifraga* spp.) or on a short-term basis (food retrieval occurs after several hours or a few days as in some tits *Parus* spp.). The fact that very large numbers of items are stored in and retrieved from different individual locations suggests the hypothesis

Requests for reprints should be sent to S. Healy, Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, U.K.

We thank St Hilda's College, Oxford (SDH) and St John's College, Oxford (SDH), the Royal Society (JRK), and SERC (SDH & JRK) for financial support. Tim Guilford, Andy Hurly, and Sara Shettleworth made helpful comments. Mark Pagel provided invaluable statistical advice.

that food-storing birds have a specialization of memory associated with their ecological niche.

The clearest evidence in support of this hypothesis comes from neuro-anatomical rather than behavioural work. Krebs, Sherry, Healy, Perry, and Vaccarino (1989) and Sherry, Vaccarino, Buckenham, and Herz (1989) found that food-storing passerines (song-birds) have a larger dorso-medial cortex (hippocampus) relative to the rest of the telencephalon than do non-storers. Lesion experiments by Sherry and Vaccarino (1989) on food-storing black-capped chickadees (*Parus atricapillus*), and Bingman (1990) on homing pigeons (*Columbia livia*), have shown that the avian hippocampus may play a role in spatial memory, although it may also be involved in other kinds of memory (Good, 1989).

The results from the behavioural studies are less convincing. Studies of North American corvid species have looked for differences in spatial memory between species that rely to differing extents on stored food for survival in the wild. The studies on the tit species have looked for memory differences between closely related species, some of which store and some of which do not. Neither of these two lines of research has yet produced conclusive results (summarized in Krebs, 1990). One of the more suggestive results is that of Olson (1989), who compared the performance of an intensive storer, the Clark's nutcracker *Nucifraga columbiana*, a less-intensive storer, the scrub jay *Alphelocoma coerulescens*, and the pigeon in a spatial delayed-non-matching-to-sample task (DNMTS). Nutcrackers appeared to remember over longer intervals than do the other two species, although there was no significant difference between scrub jays and pigeons.

In this paper we use a version of delayed-matching-to-sample (DMTS) to compare the performance of two species of tit: the food-storing marsh tit *Parus palustris* and the non-storing great tit *Parus major*. DMTS and DNMTS have been used to study a variety of problems related to memory including short-term visual memory (e.g. rats: Roitblat & Harley, 1988; pigeons: Roberts & Grant, 1976; monkeys: D'Amato, 1973; Forestell & Herman, 1988; Herman, Hovancik, Gory, & Bradshaw, 1989), object recognition (Aggleton, 1985; Gaffan, 1974; Mishkin & Delacour, 1975), concept learning (e.g. Wright, Cook, Rivera, Sands, & Delius, 1988) and spatial memory (pigeons: Brodbeck, Burack, & Shettleworth, 1992; Roitblat & Harley, 1988; Wilkie, 1989; Wilkie & Summers, 1982).

In our experiments, the animal was presented with a rewarded sample and then, after a retention interval, tested for its ability to choose the correct (matching) object using location, appearance, or both. These two kinds of cue were deliberately confounded because in natural food storing we assume the bird has to remember sites that may be characterized both by appearance and by position. We used a pool of 100 different objects,

so that each stimulus was presented on only a few occasions. The birds experienced a maximum of 20 objects per day, so any one object was seen only on every fifth day. In addition to designing the experiment in this way to capture some aspects of natural food storing, the use of a large pool of stimuli has been shown in other studies of memory to enhance performance, presumably because it reduces interference between successive trials (Aggleton, 1985; Brodbeck et al., 1992; Macphail & Reilly, 1989; Overman & Doty, 1980; Wright et al., 1988).

Accuracy of animals solving DMTS problems has been shown to increase with increasing delays between trials (intertrial interval: ITI) (monkeys: Jarrard & Moise, 1971; pigeons: Maki, Moe, & Bierley, 1977), such that in some cases increased ITI has counterbalanced performance decline due to increased retention intervals (Roberts & Kraemer, 1982). In an attempt to minimize the effect of trials interfering with each other, in our experiments the ITI was always at least twice as long as the retention interval.

Method

Subjects. Eight marsh tits and eight great tits were caught in deciduous woodland at Stanton St John, Oxfordshire, 1–6 months before the start of the experiment. Both species were housed individually indoors in wire-mesh cages (77 cm × 44 cm × 44 cm high). The birds were fed daily a commercial insectivorous bird food mixture, supplemented by boiled egg, carrots, peanuts, sunflower seeds, fly pupae (for the marsh tits), and mealworms (for the great tits) and were maintained on a 10:14 hour light:dark cycle. None of the birds had been involved in experiments previously. The experiments were begun in November 1988 and completed in March 1990.

Experimental Design. The apparatus is shown in Figure 1. It consisted of a Perspex box attached to one side of each bird's cage such that the bird could move freely in and out of the box (the side of the Perspex box facing the cage had no wall). The side facing the experimenter was a sliding Perspex door through which the experimental tray could be presented. The two ends and the bottom of the box were black opaque Perspex, with the top and the sliding door made from clear Perspex. The observer presented the tray and recorded data from behind a curtain.

The protocol consisted of presenting a T-shaped tray (see Figure 1) into the Perspex box, with the vertical arm of the T pointing towards the bird's cage. The well in this arm was not used in this experiment. The two wells on the crossed arm were 8 cm apart and separated by a partition (0.3 cm thick × 5.5 cm wide × 5.1 cm high), so that the bird, when at one well, could not see the contents of the adjacent well.

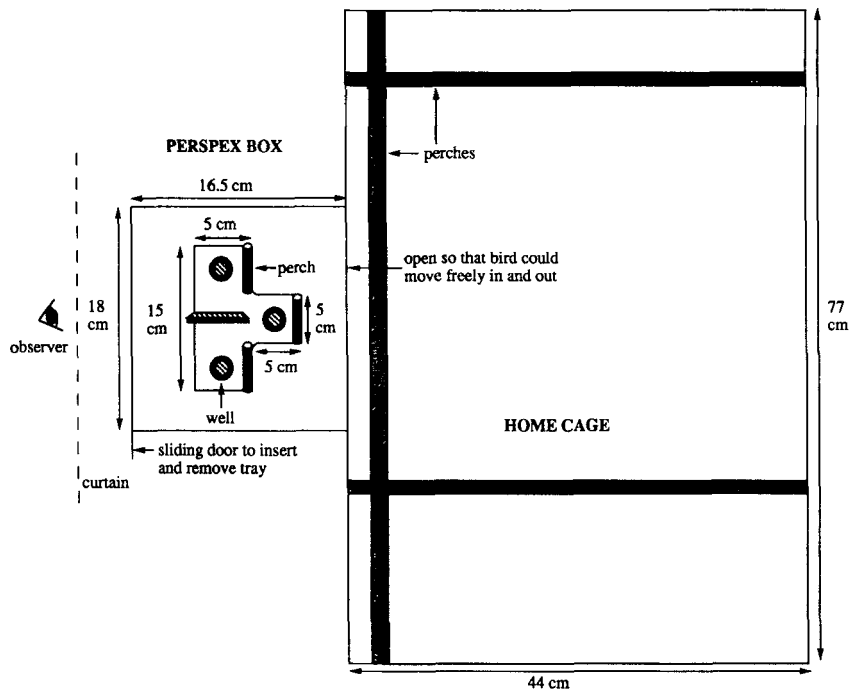


FIG. 1. A scale drawing of the experimental apparatus with the T-shaped tray in place.

Wells were covered with pale blue plastic discs (1.6-cm diameter) glued to each of which was a coloured bead or button (the experimental objects). These beads and buttons varied in size, shape, and colour: the height of the object glued to the disc ranged from 0.1 to 1 cm, the width of the objects ranged from 0.4 to 1.5 cm. The shapes of the objects included spheres, tubes, cubes, and animals, and the colours ranged from red through yellow, blue, and green to purple, as well as black, silver, white, and gold. There were 100 different objects in all, and they were presented in pairs such that the paired objects were as dissimilar in appearance as possible. The combination of objects into pairs was changed after each trial but not randomized because we wanted to make the pairs as unlike as possible.

Training Procedure. For both training and experiments the birds were deprived of food overnight from 1700 hrs to 0900 hrs the following day, when tests started.

Initial training involved placing the birds' food bowls in the Perspex boxes so that the birds became used to moving in and out of the box and also to acquiring food in the box. The tray was first presented to the bird in

the bottom of its cage and the wells covered with plain pale blue discs. Both wells contained food, and the bird learned to move the disc aside to remove the food hidden underneath. When the bird had learned to do this (2–3 days), the food bowls were removed from the Perspex box and replaced by a tray, again with the plain blue discs covering food in both wells. The bird would then come into the box, move aside one of the discs, and return to a perch in its cage to eat the piece of peanut. When the bird was entering the box to look for food under the discs within two minutes of presentation of the tray (2–3 days), it then had 2–3 days of “training trials”.

Training and subsequent experimental trials were divided into two phases. The first phase of the trial was the presentation of the tray into the bird’s Perspex box. One of the wells, chosen at random, contained a small piece of peanut of about 30 mg, covered by one of the objects (discs with beads), which acted as the sample, whereas the other well remained empty and uncovered. The well covered by the object was chosen such that each of the two wells was used for 50% of each day’s trials, but the order of presentation was randomized. The bird was required to move the object in order to remove the food. This was done easily by both species. The bird would then fly back into its cage to eat the food. Whilst it was eating the food, the tray was withdrawn, and when the bird had finished eating, the tray was presented again [this was the minimal retention interval (RI)]. In phase 2 the well that had contained food and been covered in Phase 1 again contained the food covered by the same object from Phase 1 and the other, empty well was also covered. To locate the food successfully, the bird had to return both to the same position at which it had found food in Phase 1 and to the same object. The bird thus could use both characteristic features of the rewarded object and its spatial location to find the food in Phase 2. Cues emanating from the food itself have been shown in previous experiments not to be used by tit species to locate food (Shettleworth & Krebs, 1982). In addition, as the birds did not remain in front of the wells after finding the food in Phase 1, they could not have used postural changes to solve the problem. For the first day of training only, if the bird chose the wrong object it was allowed to retrieve the food from under the correct object. Thereafter, however, the birds were allowed to displace one object only.

Many previous experiments have found that animals spontaneously perform non-matching-to-sample (NMTS) tasks. The first four birds (two of each species) to finish initial training were tested for their preference to perform either a delayed matching-to-sample task or a DNMTS task. This involved the front well being used to present the sample and the two back wells to present the choices. Food was hidden under both choice objects in Phase 2 and the bird observed as to which of the objects it chose. The birds were each given 10 such trials, and all four birds chose the matching object

in more trials than the non-matching object—great tit one: 7/10; great tit two: 6/10; marsh tit one: 7/10; marsh tit two: 7/10; binomial probability test: p (two-tailed) = 0.038.

Pilot studies, also using these four birds, then tested the birds' performance on a version of the task described above in which the reward in Phase 2 could be obtained only by choosing the correct object and not by position. The front well was used to present the sample and the two back wells to present the choices, with the correct (matching) object randomly assigned to one of these wells. After 50 trials per bird, none of the birds was performing better than at random, and all of them had developed preferences for one or other of the wells. These 50 trials were followed by 10 trials of a purely spatial DMTS task in which the sample was presented over one of the side wells and the choice consisted of two identical objects, the one in the same position as the sample being rewarded. The performance of the birds over these 10 trials was better than random—one-sample t -test, $t(3) = 8.66$, $p = 0.003$.

The results from these two pilot studies suggested both that the birds spontaneously performed matching-to-sample, and, when spatial information was available in addition to object-specific cues, the birds did not show preferences for one or other of the wells. Thus the subsequent experimental procedure used a DMTS task with both spatial and object cues available for making the correct choice.

Training and experimental trials were performed between 8 am and 12 noon, with a maximum of 10 trials run per day. Training ended when the birds were able to perform 5 trials in half an hour (2–3 days for both species). Trials were always at least five minutes apart.

Test Procedure. The experimental procedure consisted of two-phase trials (as in training). The phases of each trial were separated by a predetermined RI, and trials were separated by an ITI dependent on the RI. The number of trials per day was also dependent on the RI.

Experiment 1 consisted of 15 days of 10 trials per day (150 trials in total), with a RI of 30 sec and an ITI of 5 min.

Experiment 2 consisted of two treatments: a RI of 5 min with an ITI of 15 min and a RI of 15 min with an ITI of 30 min. Each bird experienced 15 days of each treatment.

Four individuals of each species had the 5-min RI followed by the one of 15 min, and three individuals of each species experienced the treatments in the reverse order (only seven individuals of each species completed Experiment 2). For the 5-min RI, 10 trials per day were run, but with the 15-min RI it was possible to run only 6 trials per day, so that the birds had a total of 90 trials at this RI.

Results

As trials within a day are less likely to be independent than averages between days, the data were analysed as the proportion of each day's trials that were successful; thus there were 15 data points per bird for each RI. The data were arcsine square root transformed. All *p*-values are two-tailed unless specified otherwise.

Experiment 1

1. Effect of Acquisition. To determine whether there was any improvement in the birds' performances over the 15 days, regression lines were calculated through each bird's data. The slopes for two of the eight great tits were significantly different from zero—Great tit 1: $F(1, 14) = 17.09$, $R = 0.75$, $p = 0.001$; Great tit 2: $F(1, 14) = 8.18$, $R = 0.62$, $p = 0.013$. The performances of both of these birds improved with increasing sessions. None of the slopes of individual marsh tits differed significantly from zero (0/8 birds). The average slope of each species was also compared against a slope of zero. The great tits differed significantly from zero, $F(1, 14) = 9.64$, $R = 0.65$, $p = 0.008$, and the marsh tits were close to significance [$F(1, 14) = 3.42$, $R = 0.46$, $p = 0.087$]. *T*-tests were used to compare the slopes and intercepts of the two species. The slopes were not significantly different [$t(14) = 1.02$, $p = 0.33$], but marsh tits had a significantly higher intercept than great tits, $t(14) = 2.21$, $p = 0.045$ (Figure 2), suggesting that they performed at a higher level in the first few days of Experiment 1. This was confirmed by comparing the species in the early and late part of the experiment: Marsh tits performed significantly

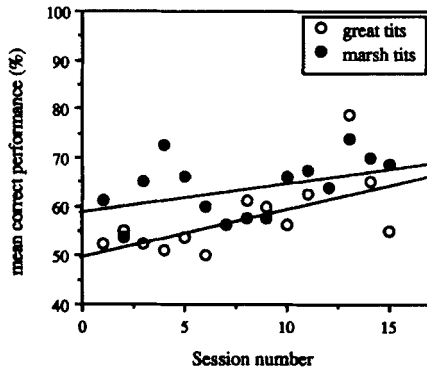


FIG. 2. Experiment 1: acquisition. The improvement in performance with experience. Data are daily means for $n = 8$ individuals per species. Marsh tits are significantly better than great tits for the first five trials but not the last five.

better than great tits on the first five sessions, $t(1, 14) = 2.37, p = 0.032$, but there was no difference between the species on the last five sessions [$t(14) < 1, p = 0.75$].

2. *Performance Relative to Random.* One-sample t -tests were used to compare each bird's performance to a random expectation of 50% correct per day. The p -values reported are one-tailed, as the hypothesis is that the birds should perform better, and not worse, than random. Four birds, one marsh tit [Marsh tit 6: $t(14) < 1, p = 0.248$] and three great tits [Great tit 3: $t(14) < 1, p = 0.237$; Great tit 6: $t(14) = 1.72, p = 0.054$; Great tit 7: $t(14) < 1, p = 0.392$] did not perform better than at random, but the other individuals were above chance (Figure 3). Mean values for each bird were used in one-sample t -tests to determine whether the species performed better than at random: both species performed better than at random—great tits: $t(7) = 2.34, p = 0.026$; marsh tits: $t(7) = 3.86, p = 0.003$.

3. *Differences Between the Species.* A repeated measures analysis of variance (ANOVA) was used to test for differences between the species over the whole 15 days. There were no differences between the species [$F(1, 14) = 1.12, p = 0.307$], a significant effect of session number, $F(14, 196) = 3.03, p = 0.0003$, and no significant species \times session number interaction, [$F(14, 196) = 1.47, p = 0.125$].

Experiment 2

1. *Effect of Acquisition.* To test whether the birds' performance improved over the course of this experiment, regression lines for each bird were calculated across the sessions from each retention interval. None of the birds improved or declined significantly with increasing session number

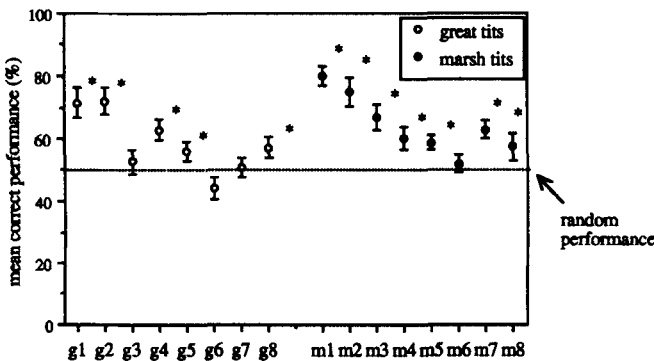


FIG. 3. Experiment 1. The mean performance (percentage correct) \pm SE of each individual over 15 days. * indicates that individual was above chance.

for either retention interval [RI = 5 min: F values ranged from 0.005 to 2.19, R values ranged from 0.02 to 0.38, p values ranged from 0.163 to 0.944 (great tits); F values ranged from 0.03 to 1.67, R values ranged from 0.05 to 0.34, p values ranged from 0.219 to 0.866 (marsh tits); RI = 15 min: F values ranged from 0 to 1.97, R values ranged from 0 to 0.36, p values ranged from 0.184 to 1.00 (great tits); F values ranged from 0.006 to 2.13, R values ranged from 0.07 to 0.37, p values ranged from 0.182 to 0.809 (marsh tits)]. The average slope of both species did not differ from zero at either retention interval. Neither the slope nor the intercept of the two species differed at either retention interval [Slopes: RI = 5 min: $t(12) = 1.64$, $p = 0.128$; RI = 15 min: $t(12) < 1$, $p = 0.824$; intercepts: RI = 5 min: $t(12) = 1.78$, $p = 0.103$; RI = 15 min: $t(12) < 1$, $p = 0.662$].

2. *Performance Relative to Random.* One-sample t -tests were used to test each bird's performance relative to random. One marsh tit and two great tits did not perform better than at random over the 5-min sessions [Marsh

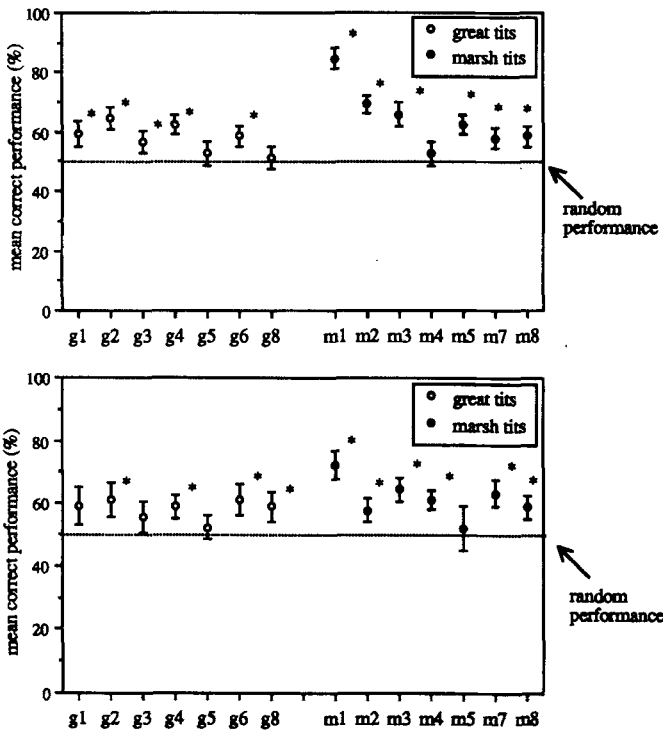


FIG. 4. Experiment 2. The mean performance (percentage correct) \pm SE of the seven individuals of each species at (a) 5-min RI (top panel) and (b) 15-min RI (bottom panel), averaged over 15 days for each treatment. * indicates that individual was above chance.

tit 4: $t(14) < 1$, $p = 0.510$; Great tit 5: $t(14) < 1$, $p = 0.519$; Great tit 8: $t(14) < 1$, $p = 0.695$] (Figure 4a) and over the 15-min session one marsh tit and three great tits did not perform better than at random [Marsh tit 5: $t(14) < 1$, $p = 0.569$; Great tit 1: $t(14) = 1.542$, $p = 0.145$; Great tit 3: $t(14) = 1.087$, $p = 0.296$; Great tit 5: $t(14) < 1$, $p = 0.524$] (Figure 4b). As two of the three birds that performed at random in the 5-min sessions and three of the four birds that performed at random in the 15-min sessions had these retention intervals second, it seemed possible that there was some influence of order on performance. However, a nested ANOVA with repeated measures showed that there was no significant effect of order on performance accuracy [$F(1, 12) < 1$, $p = 0.35$], no effect of retention interval [$F(1, 12) < 1$, $p = 0.56$], and no Order \times Retention Interval interaction [$F(1, 12) = 2.95$, $p = 0.002$].

At both RI both of the species on average performed better than at random: RI = 5 min: great tits: $t(6) = 4.33$, $p = 0.005$; marsh tits: $t(6) = 3.18$, $p = 0.019$; RI = 15 min: great tits: $t(6) = 6.19$, $p = 0.001$; marsh tits: $t(6) = 5.15$, $p = 0.002$.

3. Differences Between the Species. A repeated measures ANOVA was used to test for differences in performance between the species and for differences between performances on the different retention intervals. There was no significant difference between the species [$F(1, 12) = 3.01$, $p = 0.108$], between the retention intervals [$F(1, 12) < 1$, $p = 0.728$], nor a significant Species \times Retention Interval interaction [$F(1, 12) = 2.18$, $p = 0.165$].

A similar analysis was used to compare all three retention intervals from both experiments, and again there were no significant effects of species [$F(1, 12) = 2.62$, $p = 0.132$], retention interval [$F(2, 24) < 1$, $p = 0.437$], nor of an interaction [$F(2, 24) < 1$, $p = 0.477$] (Figure 5).

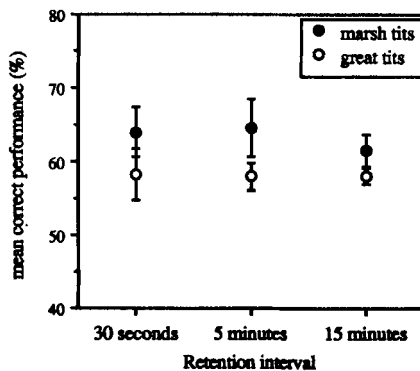


FIG. 5. Summary of results of Experiments 1 and 2 showing mean species performance (percentage correct) \pm SE at three retention intervals.

Discussion

The main results of the experiment are as follows: (1) both species were able to respond at above-chance level after retention intervals of 30 sec, 5 min, and 15 min; (2) performance did not decline significantly with increasing retention interval; (3) there was some improvement of performance over the first 150 trials (Experiment 1), but not thereafter; (4) although marsh tits tended to perform slightly better than great tits at all three retention intervals, the only significant difference was in the first 5 sessions (50 trials) of Experiment 1.

1. Comparison with Previous Studies. In comparison with the results of most other studies, the species we studied appear to remember over much longer retention intervals. Aggleton (1985) reported that rats recall trial-unique objects (independent of location) for up to 120 sec, and Olson (1989) showed that Clark's nutcrackers remember locations for up to 80 sec. In our study, both species were above chance after 15 min. It is possible that this reflects a genuine difference in memory between species, but it seems more likely that the difference is related to experimental procedure. Indeed, even pigeons can recall locational events after unusually long delays if given the right delayed alternation procedure (Olson & Maki, 1983). The fact that we used a large pool of stimuli, allowed the animals to use both spatial and stimulus-specific cues, and had a relatively long ITI all contributed to good performance even with a long RI. Although the birds could have used either spatial or non-spatial (stimulus-specific) cues, the results of our preliminary trials (see Method section) strongly suggest that they use spatial cues. However, further experiments would be necessary to determine whether or not spatial cues are used preferentially when in conflict with object cues.

Two previous studies have used methods somewhat related to ours in comparative studies of avian memory. Wilson, Mackintosh, & Boakes (1985) compared the performance of pigeons with two corvids, jackdaws *Corvus monedula* and jays *Garrulus glandarius*, in matching or non-matching to sample tasks (with no delay between sample and choice). The aim of their work was to compare the abilities of the species to transfer the matching or non-matching response learned with one set of stimuli to a novel set. Both jackdaws and jays were better able to transfer than were pigeons, suggesting that the corvids, unlike the pigeons, had learnt the rule rather than the individual stimuli. However, jackdaws learned the initial task at a slower rate and reached a lower level of performance than the pigeons. Furthermore, differences in performance might be attributable to difference in the kind of reward use for the species (dog food for corvids and grain for pigeons). As Macphail (1982) has emphasized, comparative studies in which differences are attributed to memory must consider

whether other factors, such as motivation or motor skills, might influence the results (Krebs, Healy, & Shettleworth, 1990). Wilson and colleagues did not compare the two corvids, one of which, the jackdaw, is a non-storer, whereas the other, the jay, is a food storer: this comparison would have been interesting in the context of differences in hippocampal volume within the corvids (Healy, 1990).

Olson (1989) used a spatial DNMTS design to compare memory in two food-storing species, Clark's nutcrackers (*Nucifraga columbiana*) and scrub jays (*Aphelocoma coerulescens*) and a non-storing species, pigeons (*Columbia livia*). In one experiment, she used a titration procedure. A peck to the correct (non-matching) key resulted in a 0.1 sec increment in delay from sample to choice for the next trial, and an incorrect response led to a 0.3 sec decrease in delay. The nutcrackers reached a significantly longer delay (50–80 sec) than did either scrub jays (7–44 sec) or pigeons (0.5–25 sec); the latter two did not differ significantly. As the nutcracker is a more intensive storer than is the jay, this could be taken as supporting the view that food-storing is associated with good memory; on the other hand, the storing jay was not significantly better than was the pigeon. Thus the results are inconclusive. A potential difficulty with the design of this titration experiment is that by performing well, the animal drives its rate of reinforcement down. If the animals were capable of detecting the change in delay, they might learn to make errors to keep the delay short.

Two studies have used an open-field design related to DMTS. Brodbeck et al. (1992) showed that black-capped chickadees are able to return correctly to the site where food had been eaten 30 minutes earlier when given a choice of three possible sites. Healy and Krebs (in press) similarly showed that blue tits *Parus caeruleus* (a non-storing species) and marsh tits return to the "correct" site, out of a possible seven sites, above chance after after 30 min, with some individuals still performing above chance after a retention interval of 24 hr. In the Brodbeck et al. study performance was above chance only when the objects were trial-unique, and in the study of Healy and Krebs identical objects were used in all trials.

2. Differences between the Species. Our results do not show convincing differences between the storing and non-storing species. Two hints that marsh tits were better than great tits are (1) that marsh tits were significantly better than great tits in the first five sessions of Experiment 1 and (2) that 6 out of 8 individual great tits performed at chance level during at least one of the treatments (two individuals were at chance for two treatments), but only 3 out of 8 marsh tits were at chance level in one treatment each. The appropriate conclusion may be that there are only very slight differences in memory between great tits and marsh tits, in which case their differences in hippocampal volume would have to be

interpreted as not being associated with memory, or that the task presented to the birds in this experiment did not reveal the differences. Possible lines for future work would be to increase the difficulty of the task, either by extending the retention interval, or by presenting intervening objects between the sample and the choice, as in running recognition experiments (Steele & Rawlins, 1989).

REFERENCES

- Aggleton, J.P. (1985). One trial object recognition by rats. *Quarterly Journal of Experimental Psychology*, 37B, 279–294.
- Bingman, V.P. (1990). Spatial navigation in birds. In D. Olton & R. Kesner (Eds.), *Neurobiology of comparative cognition* (pp. 423–447). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Brodbeck, D.R., Burack, O., & Shettleworth, S.J. (1992). One trial associative memory in black-capped chickadees. *Journal of Experimental Psychology: Animal Behavior Processes*, 18, 12–21.
- D'Amato, M.R. (1973). Delayed matching and short term memory in monkeys. In G.H. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory*, Vol 7 (pp. 227–269). New York: Academic Press.
- Forestell, P.H., & Herman, L.M. (1988). Delayed matching of visual materials by a bottlenosed dolphin aided by auditory symbols. *Animal Learning and Behavior*, 16, 137–146.
- Gaffan, D. (1974). Recognition impaired and associated intact in the memory of monkeys after transection of the fornix. *Journal of Comparative and Physiological Psychology*, 86, 1100–1109.
- Good, M. (1989). *The role of the avian hippocampus in learning and memory*. Unpublished Ph.D. thesis. University of York.
- Healy, S.D. (1990). *A comparative study of brain and behaviour in food storing animals*. Unpublished DPhil thesis, University of Oxford.
- Healy, S.D., & Krebs, J.R. (in press). Comparing spatial memory in two species of tit: Recalling a single location. *Animal Learning and Behavior*.
- Herman, L.M., Hovancik, J.R., Gory, J.D., & Bradshaw, G.L. (1989). Generalization of visual matching by a bottlenosed dolphin (*Tursiops truncatus*): Evidence for invariance of cognitive performance with visual and auditory materials. *Journal of Experimental Psychology: Animal Behavior Processes*, 15, 124–136.
- Jarrard, L.E., & Moise, S.L. (1971). Short-term memory in the monkey. In L.E. Jarrard (Ed.), *Cognitive processes of nonhuman primates*. New York: Academic Press.
- Kamil, A.C. (1988). A synthetic approach to the study of animal intelligence. In D.W. Leger (Ed.), *Comparative perspectives in modern psychology. Nebraska Symposium on Motivation*, 35 (pp. 257–308). Lincoln, NE: University of Nebraska Press.
- Kamil, A.C., & Balda, R.P. (1990). Spatial memory in seed-catching corvids. In G.H. Bower (Ed.), *The psychology of learning and motivation: Vol. 26* (pp. 1–25). San Diego, CA: Academic Press, Inc.
- Krebs, J.R. (1990). Food-storing in birds: Adaptive specialization in brain and behaviour? *Philosophical Transactions of the Royal Society of London*, B, 329, 153–160.
- Krebs, J.R., Healy, S.D., & Shettleworth, S.J. (1990). Spatial memory of Paridae: comparison of a storing and a non-storing species, *Parus ater* and *P. major*. *Animal Behaviour*, 39, 1127–1137.

- Krebs, J.R., Sherry, D.F., Healy, S.D., Perry, V.H., & Vaccarino, A.L. (1989). Hippocampal specialization of food-storing birds. *Proceedings of the National Academy of Sciences (U.S.A.)*, *86*, 1388–1392.
- Macphail, E.M. (1982). *Brain and intelligence in vertebrates*. Oxford: Clarendon Press.
- Macphail, E.M. (1987). The comparative psychology of intelligence. *Behavioral and Brain Sciences*, *10*, 645–656.
- Macphail, E.M., & Reilly, S. (1989). Rapid acquisition of a novelty versus familiarity concept by pigeons (*Columba livia*). *Journal of Experimental Psychology: Animal Behaviour Processes*, *14*, 71–82.
- Maki, W.S. Jr., Moe, J.C., & Bierley, C.M. (1977). Short-term memory for stimuli, responses and reinforcers. *Journal of Experimental Psychology: Animal Behaviour Processes*, *3*, 156–177.
- Mishkin, M., & Delacour, J. (1975). An analysis of short-term visual memory in the monkey. *Journal of Experimental Psychology: Animal Behaviour Processes*, *1*, 326–344.
- Olson, D. (1989). *Comparative spatial memory in birds*. Unpublished doctoral dissertation, University of Massachusetts.
- Olson, D., & Maki, W.S. (1983). Characteristics of spatial memory in pigeons. *Journal of Experimental Psychology: Animal Behaviour Processes*, *9*, 266–280.
- Overman, W.H., & Doty, R.W. (1980). Prolonged visual memory in macaques and man. *Neuroscience*, *5*, 1825–1831.
- Roberts, W.A., & Grant, D.S. (1976). Studies of short-term memory in the pigeon using the delayed match to sample procedure. In D.L. Medin, W.A. Roberts, & R.T. Davies (Eds.), *Processes of animal memory* (pp. 79–112). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Roberts, W.A., & Kraemer, P.J. (1982). Some observations of the effects of intertrial interval and delay on delayed matching to sample in pigeons. *Journal of Experimental Psychology: Animal Behaviour Processes*, *8*, 342–353.
- Roitblat, H.L., & Harley, H.E. (1988). Spatial delayed matching-to-sample performance by rats: Learning, memory and proactive interference. *Journal of Experimental Psychology: Animal Behaviour Processes*, *14*, 71–82.
- Sherry, D.F., & Vaccarino, A.L. (1989). Hippocampal aspiration disrupts cache recovery in black-capped chickadees. *Behavioural Neuroscience*, *103*, 308–318.
- Sherry, D.F., Vaccarino, A.L., Buckenham, K., & Herz, R.S. (1989). The hippocampal complex of food-storing birds. *Brain Behaviour and Evolution*, *34*, 308–317.
- Shettleworth, S.J. (1990). Spatial memory in food storing birds. *Philosophical Transactions of the Royal Society of London, B*, *329*, 143–151.
- Shettleworth, S.J., & Krebs, J.R. (1982). How marsh tits find their hoards: The role of site preference and spatial memory. *Journal of Experimental Psychology: Animal Behaviour Processes*, *8*, 354–375.
- Steele, K.S., & Rawlins, J.N.P. (1989). Rats remember long lists of nonspatial items. *Psychobiology*, *17*, 450–452.
- Wilkie, D.M. (1989). Evidence that pigeons represent euclidean properties of space. *Journal of Experimental Psychology: Animal Behaviour Processes*, *15*, 114–123.
- Wilkie, D.M., & Summers, R.J. (1982). Pigeons' spatial memory: Factors affecting delayed matching of key location. *Journal of the Experimental Analysis of Behaviour*, *37*, 45–56.
- Wilson, B., Mackintosh, N.J., & Boakes, R.A. (1985). Transfer of relational rules in matching and oddity learning by pigeons and corvids. *Quarterly Journal of Experimental Psychology*, *37B*, 313–332.

Wright, A.A., Cook, R.G., Rivera, J.J., Sands, S.F., & Delius, J.D. (1988). Concept learning by pigeons: Matching-to-sample with trial unique video picture stimuli. *Animal Learning and Behavior*, 16, 436-444.

Revised manuscript received 12 July 1991

L'appariement retardé chez les Nonnettes et les Mésanges charbonnières

La capacité de deux espèces de mésanges à se souvenir de l'emplacement et/ou des caractéristiques d'un objet a été testée avec une procédure d'appariement retardé. Les intervalles de rétention entre la présentation du stimulus-échantillon et le choix pouvaient être de 30 sec, 5 min, et 15 min. Chez les deux espèces, les performances sont au-dessous du niveau du hasard pour tous les intervalles de rétention et il n'y a pas de diminution significative des performances corrélatives de l'augmentation des intervalles. Un ensemble de 100 objets-stimulus a été utilisé mais les résultats des essais-contrôle montrent que les oiseaux répondent essentiellement à leur emplacement plutôt qu'à leurs caractéristiques propres. Bien que la nonnette, qui est un oiseau qui stocke sa nourriture, tende à avoir de meilleures performances que la mésange charbonnière (qui ne stocke pas sa nourriture), la seule différence significative entre les espèces se situe pendant les 50 premiers essais du premier traitement, quand les oiseaux apprennent la tâche. Les résultats sont discutés en relation avec les capacités mnésiques particulières des oiseaux stockeurs de nourriture.

Igualación demorada de la muestra en carbonero palustre (*Parus palustris*) y carbonero mayor (*Parus major*)

La capacidad de dos especies de carboneros para recordar la ubicación y/o características de un objeto fue estudiada en un procedimiento de igualación demorada de la muestra. Se usaron tres valores de intervalo de retención entre la presentación del estímulo y la elección: 30 segundos, 5 minutos y 15 minutos. Ambas especies se desempeñaron por encima del nivel de azar en todos los intervalos de retención y no hubo una declinación significativa en exactitud con el aumento en el intervalo. Un grupo de 100 objetos-estímulo fue usado pero los resultados de los controles indicaron que las aves respondieron primariamente a la ubicación mas que a las características del objeto en sí. A pesar de que el carbonero palustre (que almacena alimento en la naturaleza) tendió a desempeñarse a un mayor nivel que el carbonero mayor (que no almacena alimento), la única diferencia significativa entre las especies fue en los primeros 50 ensayos del primer tratamiento, cuando las aves estaban adquiriendo la rutina. Los resultados se discuten en relación con la hipótesis de que las aves que almacenan alimento poseen una capacidad especial de memoria.