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Food-storing birds: adaptive specialization in brain and behaviour?

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SUMMARY

Among the passerine birds, species that store food have an enlarged hippocampal region (dorso-medial cortex), relative to brain and body size, when compared with the non-storers. The volume of one of the major afferent-efferent pathways (the septo-hippocampal pathway) is also greater in food storing species. This specialization of brain structure is discussed in relation to behavioural studies in which the spatial memory of storing and non-storing species has been compared.

INTRODUCTION

The studies described in this paper stem from the observation that certain species of the families Paridae and Corvidae use an accurate, long-lasting spatial memory to retrieve stored food. Although the details vary from species to species, individuals often store thousands or tens of thousands of food items, each one in a separate site. These stored items are retrieved over periods ranging from hours to months after storage. By extrapolation from small-scale field and laboratory experiments, it seems probable that successful retrieval of stored food depends to a very great extent on spatial memory (for a full discussion see Shettleworth (1990)). The suggestion that these birds might be able to keep track of the spatial locations of many thousands of food items over periods of hours to months implies a remarkable feat of memory, especially when one compares this performance with that seen in studies of standard laboratory animals such as rats and pigeons (for review see Roitblat (1987)). The purpose of the work described here is to explore this idea that food-storing species have a specialized memory capability.

In a companion article, Shettleworth (this symposium) discusses in detail what might be meant by a 'specialization of memory' and suggests two methods for studying this question. In brief, the term 'adaptive specialization' refers to the possibility that certain memory features (for example, duration, capacity, discrimination) have become modified during evolution in response to the selective advantage of retrieval of stored food. Further, it is implied that these traits are qualitatively or quantitatively different from those that would be expected from other demands on memory, such as normal foraging, migration and spatial orientation. There are two main ways of identifying an adaptive specialization. One is to look for differences within a food-storing species between memory for stored food and other kinds of memory. Work along these lines is reviewed by Shettleworth. The second approach, and the one adopted here, is to look for

differences in memory between species that do and do not store food. This is an example of the 'comparative method' in which patterns of association between ecological, behavioural, morphological or physiological traits across a range of species are used to infer patterns of adaptation (Harvey & Pagel 1990). In any comparative study, there are two major methodological problems: confounding variables and taxonomic independence. The first of these refers to the fact that differences between species in one trait may be confounded with differences in other traits. For example, to conclude that a difference between storing and non-storing species in spatial memory was really associated with food storing, one would have to examine other possible differences between the species, such as home range size, and migratory behaviour. The problem of taxonomic independence can be summarized as follows: if three very closely related food-storing species were shown to differ from three non-storing species, which were closely related among themselves, but distant from the food-storers, one would, in effect, have made only one comparison. In other words, conclusions from comparative studies are persuasive only when parallel trends can be observed in independent comparisons between taxonomic groups.

The comparative work described in this paper examines the question of adaptive specialization from two perspectives. In the first part, experiments designed to look at differences between storing and non-storing species at the behavioural level are reported, while in the second, differences in the putative neuroanatomical substrates of memory are described.

BEHAVIOURAL EVIDENCE FOR DIFFERENCES IN SPATIAL MEMORY

Comparative studies of memory have been done on two families of food-storing birds. Kamil & Balda have studied members of the Corvidae (Kamil & Balda 1988, 1989; Olson 1989) while the Paridae have

Table 1. *A summary of experiments on behavioural comparisons of memory involving food-storing species*

author	task	species
Hilton (in Krebs <i>et al.</i> 1990 <i>b</i>)	spatial discrimination	great, blue, coal, marsh tit
Hilton (in Krebs <i>et al.</i> 1990 <i>b</i>)	colour discrimination	great, blue, coal, marsh tit
Hilton & Krebs (in press)	radial maze	great, blue, coal, marsh tit
Krebs <i>et al.</i> (1990 <i>a</i>)	window shopping	great and coal tit
Krebs <i>et al.</i> (1990 <i>b</i>)	window shopping	great and coal tit
Healy & Krebs (in prep.)	encountering	blue and marsh tit
Healy & Krebs (in prep.)	spatial DMTS	great and marsh tit
Balda & Kamil (1989)	retrieval of stored food	nutcracker and scrubjay
Balda & Kamil (1988)	radial maze	nutcracker
Olson (1989)	spatial DNMTS	nutcracker, scrubjay, pigeon

been studied by Krebs and co-workers (Krebs *et al.* 1990*a, b*; Healy & Krebs in prep.; Hilton & Krebs in press). The three Corvid species studied by Kamil & Balda (scrub jay *Aphelocoma coerulescens*, pinyon jay *Gymnorhinus cyanocephalus* and Clark's nutcracker *Nucifraga columbiana*) all store food, but range in the extent to which they rely on stored food. The Clark's nutcracker stores very large numbers of seeds and relies heavily on its stored food throughout the winter and spring, while the scrub jay relies on stored food to a much lesser extent. Among the tit species studied by Krebs and co-workers, two store food regularly (the marsh tit *Parus palustris* and coal tit *P. ater*), while two others (blue tit *P. caeruleus* and great tit *P. major*) do not.

Obviously, one cannot compare the memory capabilities of storing and non-storing species in a task that requires them to store food, therefore it has been necessary to study differences in memory in other kinds of task. It is a crucial assumption in this approach that the hypothesized special memory capacity of food-storing birds is also revealed in non-storing tasks. As Shettleworth (this symposium) shows, for one food-storing species and for one task that has been studied in some detail, there appear to be no clear differences in performance between retrieving stored food and remembering where food has been seen.

The memory tasks that have been studied in comparisons between species fall into two classes: those that have been devised because they seem to resemble and perhaps capture the essence of food-storing and those that have been chosen because they are standard laboratory procedures for studying spatial memory. The former category includes two procedures (described below as 'window shopping' and 'encountering') in which the bird has to return to a site where it has seen food once, as it does in retrieving stored food. The latter category includes both single-trial memory tasks (the radial maze, spatial delayed matching to sample, both described below) and multiple trial tasks in which the animal learns over a series of training trials (spatial and colour discrimination). Table 1 summarizes the experiments carried out to date.

(a) *Corvidae*

There have been three studies of corvids. Kamil & Balda (1989) measured the accuracy of retrieval of

stored food in the three corvid species referred to above. Scrub jays were less accurate (percentage of visits to correct sites) after a seven-day retention interval than were either Clark's nutcrackers or pinyon jays. The comparison between the pinyon jay and the other two species was confounded by the fact that pinyon jays tended to store seeds in clusters and hence changed the nature of the task from one of locating many individual sites to one of locating a single large cluster. However, the comparison of the scrub jay and nutcracker suggests that there is a difference in ability to remember the location of stored food under similar conditions between an intensive and a less intensive storing species (figure 1*a*). Olson (1989) also compared scrub jays and nutcrackers. She used a standard laboratory test for memory: spatial-delayed-non-matching-to-sample (DNMTS). The essence of this task is that the animal is presented with a 'sample' (an illuminated key that it pecks to initiate the choice phase of a trial) and then, after a delay, choice between the sample and an alternative illuminated key a few centimetres to one side of the sample. In the choice phase, the bird has to peck the alternative key to get a reward. In one experiment, Olson used a titration procedure to investigate the interval (retention interval) over which scrub jays, nutcrackers and pigeons could accurately remember the location of the sample. After each trial, the interval between presentation of the sample and the choice was incremented if the bird made a correct choice and decremented if its choice was incorrect. The experiment continued with each bird until the correct and incorrect choices balanced each other out and the retention interval stabilized at the point where the bird had reached its limit of performance. This titration showed that nutcrackers were able to remember the sample position for up to 60 s, which is significantly greater than either scrub jays (about 20 s) or pigeons (about 15 s). The latter two species did not differ significantly (figure 1*b*). In a second experiment, Olson compared scrub jays and nutcrackers. She varied the retention interval between 0 and 30 s, and the number of samples presented was varied between one and three. To vary sample number, she used four keys. If for example, three samples were presented, three out of four sample keys were illuminated in succession. In the choice phase the bird had to pick the one remaining key that had not been illuminated during the sample presentations. Nut-

crackers performed at higher levels of accuracy than scrub jays for all retention intervals and number of sample presentations, with the exception of a sample of one at a retention interval of zero.

Finally, Balda & Kamil (1988) studied the performance of nutcrackers in an open field analogue of the eight-arm radial maze (Olton & Samuelson 1976). In this task, to obtain maximum rewards, the animal has to visit each of eight reward sites ('arms of the maze') once. Each site holds one reward, so that by visiting each site once the bird can obtain eight rewards in eight visits, whereas any revisiting reduces the number of rewards obtained per visit. The standard procedure for investigating duration of memory in a radial maze is one in which each trial consists of two parts. In the first part, the animal is allowed to visit only four of the eight arms (the four being chosen randomly by the experimenter, by blocking access to the remaining sites) and in the second part the bird is allowed a free choice of all eight arms. If the bird can remember which places it went to in the first part it should avoid them in the second part. Kamil & Balda (1988) found that nutcrackers performed above chance with retention intervals between forced and free choice of less than six h. Although they did not compare species in their study, they pointed out that pigeons, when studied in a similar procedure, did not perform above chance with retention intervals longer than two hours (Spetch & Honig 1988). However, as will be discussed later, comparisons between experiments in which even slightly different procedures are used may be of dubious value.

(b) *Paridae*

Storing and non-storing tits have been compared in five different sets of experiments. In the first, Hilton (cited in Krebs *et al.* 1990*b*) studied the four species referred to above (two storers and two non-storers) in a spatial discrimination task. The birds were trained over a series of trials to search for food hidden in 6 out of 64 sites (the same 6 sites on each day). Both acquisition and asymptotic performance were measured. The asymptotic level of performance (measured over the last 10 out of a total of 20 trials) was significantly lower in food storers as a group than in non-storers. In a related experiment, Hilton trained birds of the same four species on a colour discrimination. In this experiment food was hidden in six different randomly chosen sites out of the total of 64 each day. The rewarded sites were shown by a coloured tag. No differences between species or between storers and non-storers as a group in either acquisition or asymptotic performance were observed.

In a second study, Hilton & Krebs (1990) studied the four tit species in a radial maze. A first experiment measured acquisition and asymptotic performance in an eight arm, open field analogue of the radial maze, allowing the animals to choose freely between all eight arms. There were no significant differences between species or between storers and non-storers as groups. By using the forced choice procedure described above with retention intervals of 30 s, 2 h and 24 h, they

found that all four species performed above chance after 30 s and 2 h, and two of the species (the coal tit, a storer, and the blue tit, a non-storer) were above chance above 24 h. Storers as a group were above chance after 24 h, while non-storers were not (figure 1*c*). This suggests that the performance of non-storers may decline more steeply with increasing retention interval than that of non-storing species, although the interaction term in the analysis of variance was only marginally significant ($p = 0.06$). Krebs *et al.* (1990*a, b*) compared coal tits (storer) and great tits (non-storer) in a task referred to as 'window shopping', in which each trial is divided into two phases. In the first, the bird encounters a hidden seed behind a small window and in the second, after an experimentally determined retention interval, it has to return to the site of the seed to eat it (the window having been removed) (Shettleworth & Krebs 1986; Shettleworth *et al.* 1990). The results varied in different versions of the task. In the simplest version, with a 30 min retention interval, seven potential sites and one seed, coal tits were able to relocate the seed in the second phase of a trial after fewer encounters than required by great tits. At least in part, the superior performance of coal tits may have resulted from the fact that they were better at discriminating between the places where they had seen the seed in the first phase of a trial and the other places they had visited while searching for the seed. This trend was also apparent in a second experiment with a more complex environment (7 seeds in 64 sites) and a longer retention interval (2 h), although the overall performance of the two species (number of seeds found in the first 15 looks in phase 2) did not differ (Krebs *et al.* 1990*a*). In the simpler version of the task with a retention interval of 24 h the difference between the two species in discrimination between classes of site visited in phase one of a trial disappeared (Krebs *et al.* 1990*b*).

Window shopping was chosen as an experimental procedure because it represented some of the essential features of food-storing: the animal has a single experience of the location of a hidden food item to which it has to return at a later time. However, Shettleworth *et al.* (1990) found that the presence of the window in some way degrades performance in comparison with retrieval of stored food, but when the bird encounters a seed not hidden behind a window, performance is indistinguishable from that in retrieval of stored food (see Shettleworth 1990). Therefore, Healy & Krebs (unpublished data) compared a storer (marsh tit) and a non-storer (blue tit) by using a procedure in which the bird encounters and eats part of a seed in the first half of a trial and then has to return to the same site to locate the hidden seed in the second half of a trial. The two species were compared with three retention intervals, 1 min, 30 min and 24 h. Although some individuals were above chance at all retention intervals, there were no consistent differences between the two species in the number of places visited to find the seed in phase two of a trial.

Finally, Healy & Krebs (unpublished results) compared marsh tits (storer) and great tits (non-storer) in a spatial delayed matching to sample (DMTS) task. The

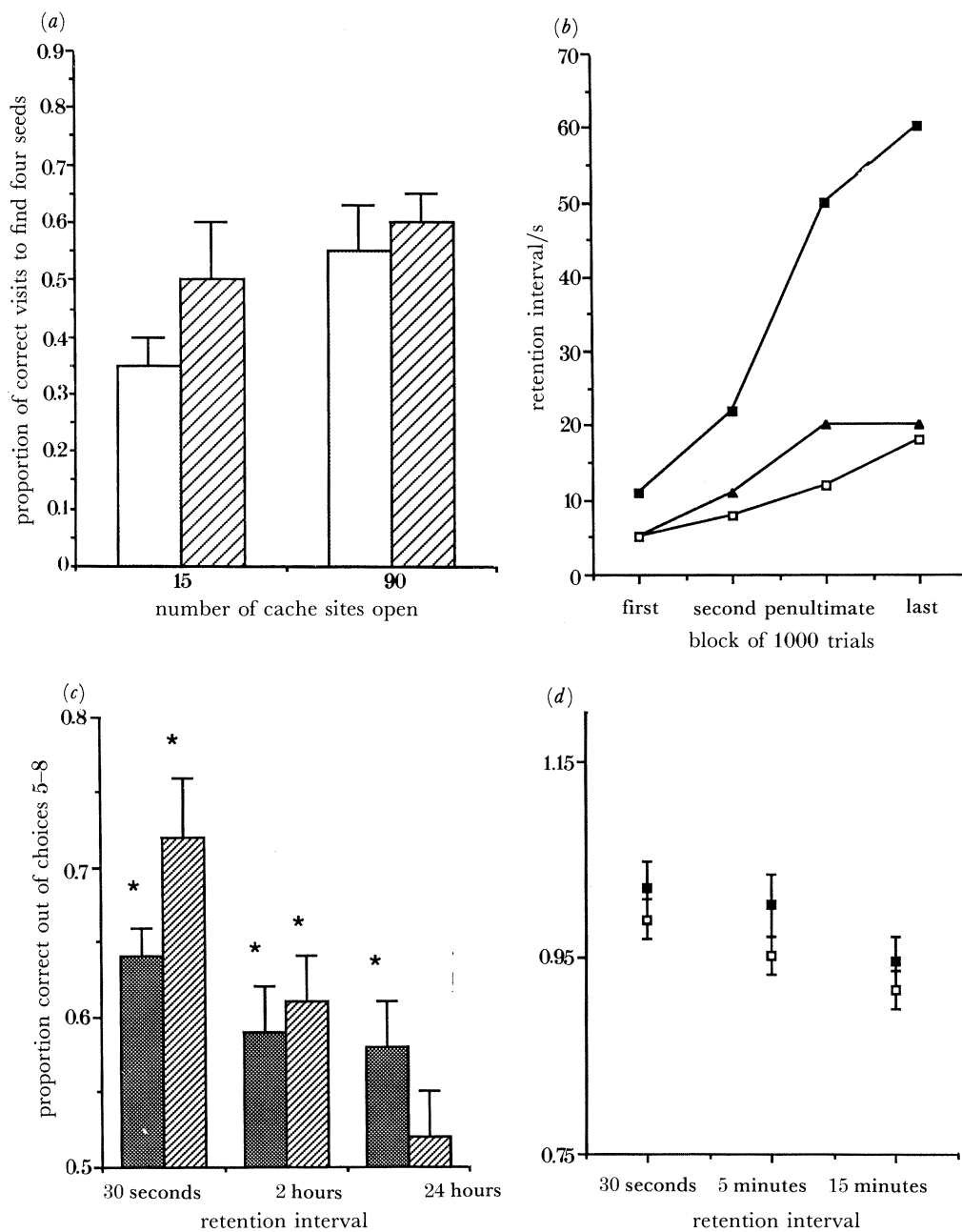


Figure 1. (a) Cache recovery by two food-storing corvids, Clarks nutcracker and scrub jay. The measure of performance was the percent correct visits (visits to cache sites) in retrieving the first four seeds of a cache. In one treatment the birds were allowed to cache in only 15 out of 180 potential sites, in the other they could cache in 90 sites. The purpose of restricting access in this way is to eliminate the role of site preference (after Balda & Kamil 1989), ($\bar{x} \pm \text{s.e.}$). \square , scrubjays; \square , nutcracker. (b) The results of a spatial DMTS titration experiment in which the retention interval was incremented by 0.1 s following a correct choice and decremented by 0.3 s following an incorrect choice (after Olson 1989). \blacksquare , nutcracker; \square , pigeon; \blacktriangle , scrubjays. (c) Comparison of two species of storing and two species of non-storing tits ($n = 4$ of each species) in an open field analogue of the radial maze at three retention intervals. Asterisk indicates performance above chance (after Hilton & Krebs 1990). The measure shown is the proportion ($\bar{x} \pm \text{s.e.}$) of correct choices (choices to previously unvisited sites) in the first four choices of the second phase of a trial (see text). \blacksquare , storer; \square , non-storer. (d) Comparison of great tit (non-storer) and marsh tit (storer) in a spatial DMTS experiment at three retention intervals. The difference between species is significant ($p < 0.01$) at 300 s but not at 30 s or 900 s. The measure shown is transformed ($\arcsin \sqrt{\cdot}$) proportion of correct choices per ten trials. \blacksquare , marsh tits; \square , great tits.

sample consisted of a small object (e.g. a coloured bead) glued onto a plastic counter, which covered a food well containing a piece of food. In the choice phase the bird was presented with the same sample covering the same well (rewarded) and an alternative object covering a neighbouring well (non-rewarded).

Thus the bird could solve the problem either by choosing the same object as the sample or by choosing the same location. (Pilot studies suggested that the birds primarily rely on spatial cues rather than recognition of the object.) A large pool of objects was used so that each one was presented only three or four

times to each individual. The birds were tested at three retention intervals, 30 s, 5 min and 15 min. Preliminary results suggest that there was no significant difference in percentage correct choices between the two species at the longest and shortest intervals, but marsh tits were significantly better than great tits at 5 min (figure 1*d*).

INTERPRETATION OF BEHAVIOURAL DIFFERENCES

(a) *Are there differences between storers and non-storers?*

The tasks summarized in table 1 do not present a consistent picture. In the results obtained with tits, no differences in relation to food-storing behaviour were observed in the colour discrimination and encountering the tasks and food storers were worse than non-storers in the spatial discrimination task. Food-storers were slightly better than non-storers in some versions of window shopping and in the radial maze at long retention intervals. The clearest differences in the tits and corvids were seen in the matching-to-sample tasks DNMTS (corvids) and DMTS (tits). In the tits the difference between storer and non-storer was apparent only at the 300 s retention interval; one interpretation of this is that at 30 s both species found the task easy, whereas at 900 s both species found the task difficult. In the corvids, although there was also an effect of retention interval (Olson's second experiment referred to above): the difference between nutcracker and scrub jay was greater at longer intervals. Similarly, the difference between two species at a retention interval of 0 s increased with the number of samples presented. The results of Olson's titration experiment only partially support the hypothesis that food-storers have a specialized memory capacity, because although nutcrackers did better than scrub jays, the jays were indistinguishable from pigeons. Finally, nutcrackers do better than jays in retrieving stored food after a seven-day retention interval.

At the moment, three tentative conclusions can be drawn. First, to the extent that food storers (or in the corvids more intensive storers) do better, they do so in situations in which the bird has to remember a location on the basis of a single experience. Secondly, it is important to compare species across a range of values of 'task difficulty'. Task difficulty can be varied, for example, by varying the retention interval or the number of to be remembered items. Four studies that have shown differences between species that are correlated with food storing (radial maze, DNMTS, DMTS, window shopping) have shown the effects most clearly at some values of task difficulty and either not at all, or less clearly, at others. Finally, the differences in performance between storers and non-storers (tits) or intensive and less intensive storers (corvids) are very small. Thus the results of each individual experiment are not as convincing as the accumulated evidence of several different studies.

(b) *Are the differences between storers and non-storers confounded with other variables?*

Macphail (1982, 1988) has pointed out that many supposed differences between species in learning and memory abilities may in fact be due to differences in motivation and/or motor skill. Three factors reduce the likelihood that these arguments apply to the present results. First, the species of tits and corvids within each comparison are similar in their ecology and morphology. Second, as discussed in the previous section, differences between species within each comparison were not apparent at all levels of task difficulty. If the differences were not due to memory, it would be unlikely that one would observe an interaction between task difficulty and difference. Finally, in one of the studies (Krebs *et al.* 1990*a*) it was shown that reward size and deprivation, two major motivational variables, did not affect performance of one of the two species, the great tit. This control has not been done in other studies and at this stage it is not possible to rule out the possibility that differences other than those attributable to memory affect performance.

(c) *Do corvids and parids differ from standard laboratory animals?*

Regardless of the differences between storers and non-storers, it appears at first sight that the corvids and parids perform extremely well in comparison with rats and pigeons that are usually used in studies of spatial memory. For example, the food-storing tits performed at above chance level in a radial maze after a retention interval of 24 h (Hilton & Krebs 1990), while the maximum for pigeons is 2 h (Spetch & Honig 1988) and for rats 6–8 h (Beatty & Shavalia 1980). In a version of spatial DMTS, black-capped chickadees reached asymptotic performance after less than 10 trials (Brodbeck 1989) while rats in a similar task required 300 trials to reach an asymptote (Roitblat & Harley 1988). In the encountering tasks studied by Healy & Krebs (unpublished data), both marsh tits and blue tits performed at above chance after a retention interval of 24 h, whereas pigeons have been reported to be able to return to a rewarded location on the basis of a single trial for only about 30 s (Wilkie *et al.* 1981). However, these comparisons are confounded by the fact that the different studies have used different experimental procedures. The importance of details of procedure are emphasized by comparisons within a species. For example, Macphail & Reilly (1989) showed that the capacity of pigeons to recognize novel slides is much higher when the pool of slides is extremely large than when a relatively small number of stimuli are used (Macphail 1980). By using large numbers of novel slides, Bhatt & Wasserman (1988) report that pigeons can discriminate between novel and previously presented slides after an interval of 24 h with one presentation, a feat comparable to that seen in the studies of tits reported here. A further caution against concluding that parids and corvids have much better memories than rats or pigeons is the observation that in two tasks studied in both corvids and parids

there were large differences in performance between members of these two families. While nutcrackers performed above chance in the DNMTS task up to retention intervals of 60 s, marsh tits were still above chance after retention intervals of 900 s in DMTS. Similarly, nutcrackers in the radial maze had dropped to chance level by a retention interval of 6 h while two species of tits were above chance after 24 h. This could mean that food-storing tits have a longer lasting memory than nutcrackers, but it seems more likely that the differences are related to procedural differences. In the matching to sample task, Healy & Krebs (unpublished data) used a large pool of objects whereas Olson used only a single stimulus type. As reported above, in studies of pigeons, using a large number of objects improves performance, presumably because it reduces memory interference. In Hilton & Krebs' radial maze study, the birds were forced to return to a central start perch between each choice, whereas in the nutcracker study, the birds were free to wander all over the room, which might well have encouraged the birds to develop fixed search strategies rather than remembering individual visited sites.

BEHAVIOURAL COMPARISONS: SUMMARY

The experiments summarized in table 1 show differences in memory related to food-storing behaviour in both parids and corvids, but the differences are small and do not appear in all experiments. The fact that differences are seen in these two independent groups greatly strengthens the interpretation that the differences are to do with food-storing and not some other variable. However, the scale of both absolute performance and differences between species is small in relation to the scale of food-storing. The memory tasks described above require birds to remember one or a small number of locations for times ranging from a few seconds to 24 h. In contrast, by using memory to retrieve stored food in the field would seem to require accurate performance in a task that is several orders of magnitude greater in difficulty both with respect to number of items and duration of retention interval. This raises the question of how relevant the observed differences are to food-storing memory. Two views can be put forward. One could either argue that the observed differences reflect only part (for example the initial processing) of memory used in retrieving stored food or that the design of the laboratory memory tasks (such as separation of spatial locations, richness of cues provided) degrade performance so that only part of the memory capacity is revealed. Finally, it is worth noting two methodological difficulties with the comparative work. One is that it is simply not possible to do the experiments blind, so that observer bias cannot be totally ruled out. Second, if one treated each comparison between a storer and non-storer (or between an intensive and less intensive storer) as one observation, then a minimum of five pairs, all showing the same direction of difference, would be needed to obtain statistical significance. This may, however be a simplistic view of the comparisons reported here. They are made with a strong *a priori* hypothesis, so that even

two independent comparisons provides a strong indication of a link between food storing and memory performance.

HIPPOCAMPAL SPECIALIZATION OF FOOD-STORERS

Two studies have shown that damage to the hippocampal region of birds impairs ability to retrieve stored food (Krushinskaya (1966) on European nutcrackers; Sherry & Vaccarino (1989) on black-capped chickadees). The latter authors showed that removal of the hippocampal region did not impair either storing behaviour or searching for stored food, but did impair accuracy of retrieval of stored food. They also showed that the performance of lesioned birds on a colour discrimination task similar to the one studied by Hilton (see above) was not impaired while performance on a spatial discrimination task like the one studied by Hilton was impaired. Furthermore, lesioned birds were more likely to make working memory errors (revisits) within a trial. Thus Sherry & Vaccarino conclude that the hippocampal region plays a role in processing food-storing memory and perhaps in other kinds of spatial and/or working memory as well. Hippocampal lesions also appear to affect spatial behaviour in homing pigeons. Lesioned birds are less able than controls to fly directly towards home when released from a novel site within the area close to the home loft where landmarks are used for navigation (Bingman 1990). Long-distance homing, which depends on another mechanism (perhaps olfaction) is unimpaired by hippocampal lesion. However, the experiments of Good (1988) show that hippocampal damage in pigeons does not exclusively affect spatial memory. He studied the effects of hippocampal damage in a variety of learning tasks and concluded that the most parsimonious explanation of his results was that the hippocampus plays a role in classical conditioning. The avian hippocampus, therefore, has at least some functional equivalence to that of mammals in that it is involved in memory processing, although its precise function, as in mammals, still remains to be ascertained. Furthermore, although not directly relevant to the current functional considerations, studies of the cytoarchitecture (Ariens Kappers *et al.* 1936; Craigie 1935; Showers 1982), connectivity (Cassini *et al.* 1986), neurochemistry (Krebs *et al.* unpublished data; Erichson *et al.* unpublished data) and cell types (Pisana 1986; Smith 1988) all support the view that the avian hippocampus is homologous with that of mammals.

Two parallel studies (Krebs *et al.* (1989) and Sherry *et al.* (1989)) have shown that food-storing birds have a specialized hippocampus. These authors measured the hippocampal volume of storing and non-storing passerine birds. Krebs *et al.* studied 35 species or subspecies belonging to nine different families, while Sherry *et al.* studied 23 species and did their analysis at the level of sub-families of which 13 were represented in their data set. (Families or subfamilies were used in the analyses to ensure taxonomic independence.) Both studies used stepwise multiple regression to partial out the effects of body size, telencephalon volume and

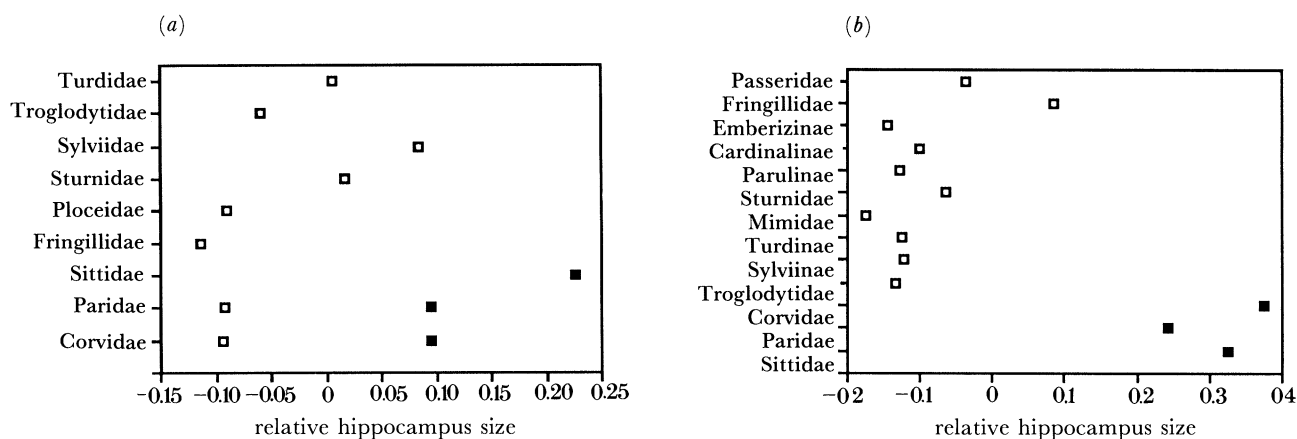


Figure 2. Residual variation in hippocampal volume after removing (by multiple regression) effects of body size and telencephalon volume (see text). ■, food storers; □, non-storers. (a) Data from Krebs *et al.* (1989). (b) Data from Sherry *et al.* (1989).

storing behaviour. In both cases, it was found that food-storers have a larger hippocampus relative to forebrain volume and body size than do non-storers (figure 2). The study of Sherry *et al.* was based entirely on between sub-family comparisons, but Krebs *et al.* were also able to make two comparisons within a subfamily: in both Paridae and Corvidae, storers had a relatively larger hippocampus than did non-storers. Thus the behavioural specialization of food-storing birds is associated with an anatomical specialization of the brain that has evolved at least twice in the passerines. It seems plausible to hypothesize that the enlargement of the hippocampal region of food-storers is related to the fact that the hippocampus is involved in processing spatial memory and that food-storers required a greater processing capacity. In both studies, confounding ecological and behavioural variables (such as migration distance and mating system) were examined and found not to be important.

Is the difference between storing and non-storing simply one of volume? Krebs *et al.* (1990*b*) compared the cell density of four species of storer and four non-storers in the dorso-lateral part of the hippocampal region and found no significant differences. These same authors reported that the volume of the septo-hippocampal junction, through which major afferent and efferent pathways pass (Cassini *et al.* 1986, Erichsen *et al.* 1990), is significantly larger relative to brain and body size in food-storing birds than in non-storers. Smith (1988) found that the major cell types, as revealed by Golgi staining, were similar in the marsh tit and the great tit. So far, the only differences that have been identified are in volume of the hippocampal region and in the size of one of the major projection pathways. However, further work is in progress to examine differences at the cellular level.

CONCLUSIONS

The main conclusions of the studies reported here lead to the following working hypothesis. Food-storing birds have a specialized memory capability used for retrieving stored food, which is revealed in interspecific comparisons of performance in various memory tasks.

This specialized memory is reflected in a specialization of brain anatomy: food-storers have an enlarged hippocampus relative to telencephalon volume and body size. To test this hypothesis it will be necessary, in future work, to do three things: (a) characterize more fully the differences in memory between storers and non-storers and show that these differences are robust between species and between families; (b) characterize in more detail the anatomical differences between storing and non-storing species; (c) show by appropriate lesions that the anatomical differences between storers and non-storers are causally related to behavioural differences in memory.

What are the broader implications of this work? The most obvious general message is an evolutionary one. This study of food-storing birds provides the first documented example of an evolutionary specialization of the brain associated with memory processing. Indeed it is one of very few studies to have shown an association between development of a particular brain region and a particular behavioural or ecological variable across a wide range of species. (For another example, see Healy & Guilford 1990).

The second general point to be drawn from the study of food-storing memory is that it may provide a useful model system for investigating how memories are processed and stored in the brain. If, for example, it were possible to identify precise anatomical differences between species and precise behavioural differences reflected in memory performance, this would lead some way towards understanding where and perhaps how those memories are presented in the brain. The work may also lead to some interesting comparisons with the literature on the mammalian hippocampus. In broad terms, there is some functional similarity between the avian and mammalian hippocampus. However, the detailed anatomical organization of these two structures is rather different (Pisana 1986; Smith 1988; Erichsen *et al.* in prep.). Thus a question for future research is whether or not the avian hippocampus does a similar job to the mammalian hippocampus.

Finally, these studies raise a question about the overall organization of the avian telencephalon. Although food-storers have an enlarged hippocampus,

they do not have an enlarged telencephalon as a whole. This implies that there may be compensation elsewhere in the forebrain for the enlargement of the hippocampus. Does this mean that there is an overall constraint on telencephalon size in passerine birds and that there is therefore a trade-off involved in evolutionary enlargement of one region? Do food-storing birds pay a price for their remarkable spatial memory (Harvey & Krebs 1990)?

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