

## BEHAVIOURAL AND NEURAL BASES OF ORIENTATION IN FOOD-STORING BIRDS

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### Summary

Food-storing birds retrieve hoarded food by remembering the locations of large numbers of spatially dispersed caches. The basic patterns of spatial orientation in these animals have been established in research on two major groups of food-storing birds, chickadees and tits (Paridae), and jays and nutcrackers (Corvidae). Experiments using displacement of landmark arrays show that food-storing birds rely on visual information from nearby landmarks to locate concealed caches. The appearance of the cache sites themselves seems to be relatively unimportant in cache retrieval, perhaps because local features are subject to change during the lifetime of a cache. Under some conditions, food-storing birds use sun-compass information to orient their search for caches, but appear to integrate sun-compass information with

landmark information. Lesions of the avian hippocampus disrupt cache retrieval and other spatial tasks in food-storing birds without disrupting the formation of simple associations. Comparative studies show that food-storing birds possess a hippocampus larger than that of non-food-storing birds, probably as an evolutionary consequence of their dependence on spatial orientation for cache retrieval. Experience with cache retrieval plays a role in the development of increased hippocampal size, and there are indications of seasonal variation in hippocampal size in food-storing species.

Key words: food storing, birds, memory, landmarks, sun compass, hippocampus.

### Introduction

The problem is easily stated. A black-capped chickadee (*Parus atricapillus*) searches for food in the forest and, instead of eating all that it finds, carries some off and hides it. It disperses thousands of such caches over a wide area, and the problem is to find them again. There is now a large body of research showing that birds in two passerine families, chickadees and tits (Paridae) and jays and nutcrackers (Corvidae) remember the locations of their caches and return to them accurately to retrieve their stored food (Shettleworth, 1990; Sherry, 1992). Considered as a problem in animal navigation, the central questions are, what do these birds remember and how do they use what they have remembered to retrieve their stored food?

#### Dispersion of food caches in space and time

Food storing is seasonal in most species, occurring principally in autumn and winter and declining or ceasing in spring and summer. There are various estimates of how many food items may be stored in a year by a chickadee, tit, nutcracker or jay, ranging from tens of thousands to hundreds of thousands (Vander Wall, 1990).

Chickadees and tits store insect prey and seeds in scattered sites that typically include furrows in tree bark, conifer needle clusters, conifer cones, leaf buds, moss, lichen, hollow stems and other natural sites. A small number of food items, often

only one, are stored at each site, and cache sites are not re-used in the wild. Caches can be made anywhere in the winter home range, which ranges in size from approximately 10 to 30 ha (Smith, 1991; Brodin, 1992; Ekman, 1979). Food may be cached near the site where it was found, or as much as 40 m away (Cowie *et al.* 1981; Barnea and Nottebohm, 1995). Neighbouring caches are usually placed at least several meters apart (Cowie *et al.* 1981).

Jays and nutcrackers store larger food items such as acorns and pine nuts in caches they make in the ground with their bill. They store one or more food items in each cache and, like chickadees and tits, do not re-use caches. Jays and nutcrackers tend to transport food some distance from the place where it was found, sometimes travelling many kilometres to cache food (Vander Wall and Balda, 1981).

Chickadees and tits leave their stored food untouched for periods ranging from a few hours to many weeks, before returning to collect it (Cowie *et al.* 1981; Stevens and Krebs, 1986; Brodin and Ekman, 1994). The time that a cache is left in place probably depends on energy requirements, food availability and the kind of food stored. Black-capped chickadees have been shown to remember the locations of food caches in captivity for at least 4 weeks (Hitchcock and Sherry, 1990). In the wild, Clark's nutcrackers (*Nucifraga columbiana*) can return to their caches as much as 7–11 months after making them (Tomback, 1980; Vander Wall and

Hutchins, 1983) and have been shown to remember cache locations in captivity for at least 9 months (Balda and Kamil, 1992).

### Landmarks, cues and features

Food-storing birds use the spatial relationships among objects in their environment to find hidden caches and seem more attuned to the spatial relationships among objects at a short distance from the cache site than to the features of the cache site itself. Although some food-storing birds can smell hidden food (Buitron and Nuechterlein, 1985), birds searching for their own caches overlook food concealed nearby (Bennett, 1993; Shettleworth and Krebs, 1982; Cowie *et al.* 1981). Further results show that experimentally removing stored food or changing the appearance of the cache site does not affect the accuracy of cache retrieval, provided that the landmark array at a short distance from the cache is not altered. This is what is generally meant by the claim that food-storing birds remember the 'spatial locations' of caches or use 'spatial memory' to retrieve caches.

One of the first demonstrations of the use of landmarks for cache retrieval was Vander Wall's (1982) experiment with Clark's nutcracker. An array of objects was dispersed in an open arena in an aviary in which nutcrackers could store pine seeds. After the birds had made caches, the object array on one side of the arena was displaced by 20 cm, leaving the array on the other side of the arena undisturbed. When birds returned to search for their caches they probed in the ground at sites that were correct with respect to the objects, missing their caches by 20 cm on the manipulated side of the aviary and retrieving them accurately on the undisturbed side. In the middle of the arena, birds missed their caches by approximately 10 cm, suggesting they were using both the displaced and the stationary objects to estimate cache locations.

Black-capped chickadees also use the spatial relationships between the cache site and nearby objects to retrieve stored food. Herz *et al.* (1994) observed chickadees storing food in a 2 m × 2 m × 2 m enclosure in which the walls, floor and ceiling were made as uniform and featureless as possible. Birds stored food in small holes on the branches of radially symmetrical artificial trees placed inside the enclosure. A large cue of a distinctive shape and colour could be added to or removed from each wall of the enclosure. The cues were a red circle, a purple rectangle, a yellow triangle and a multi-coloured poster, ranging in size from 40 to 80 cm. Small coloured cards in red, yellow, brown and grey could be added or removed at each cache site. The arrangement of cues at the cache sites was different on each tree, and different on each branch within a tree. The small coloured cards provided enough information, at least potentially, for the birds to distinguish among individual trees and branches. In practice, however, the birds were influenced more by the distal cues on the walls of the enclosure than by local cues at the cache sites. Removal of distal cues prior to cache retrieval reduced cache search accuracy, while removal of cues at the cache sites did not. In

a subsequent experiment, the birds stored food with only the large distal cues present. Rotation of these cues around the walls of the enclosure prior to cache recovery produced a rotation of the birds' search patterns.

Chickadees also learn spatial locations that predict the success of cache retrieval more readily than they learn common features that characterize good cache sites. In the field, tits and jays commonly lose caches to other birds and to rodents (Vander Wall, 1990). Hampton and Sherry (1994) investigated whether black-capped chickadees are able to learn that different categories of cache sites differ in the probability of cache loss. Birds stored food in an aviary in which one side was 'unsafe': caches placed there were gone when the bird returned to search for them. The other side of the aviary was 'safe': caches placed there were intact when the bird returned. Every potential cache site was also marked with a band of coloured Velcro tape, either blue or red, with equal frequency of red and blue tapes on the safe and unsafe sides of the aviary. Cache sites with tape of one colour were safe, and caches with tape of the other colour were always gone when the birds returned. Thus, for each bird, only caches placed in sites on the safe side and with the safe colour were still available when the bird returned to retrieve its stored food. Assignment of safe side and colour were counterbalanced across birds.

Chickadees learned to place more caches on the safe side of the aviary and to search for caches preferentially on this side. They did not learn to cache or search preferentially at sites marked with the safe colour. Control experiments showed that the birds could discriminate between the two colours of Velcro tape and between the two sides of the aviary. These results, like those described above, show that spatial information is retained in preference to cues common to cache sites or features that distinguish among caches.

### *The ranking of cache retrieval cues*

Brodbeck has directly compared the relative importance of spatial and featural information for cache retrieval (Brodbeck, 1994; Brodbeck and Shettleworth, 1995). Chickadees were trained to store food in small distinctively coloured and patterned blocks of wood. Arrays of blocks were hung on the wall of an aviary and the position of the blocks could be varied following food storing. Brodbeck (1994) allowed chickadees to store food in one of four blocks, and then exchanged the block in which food had been stored with another block from the array. When birds returned to search for their stored food, they first searched at the block in the correct spatial location in the array and then at the block with the correct colour and pattern.

In another experiment, Brodbeck (1994) trained birds to find food hidden by the experimenter in one feeder among an array of four and then to return after 30 min to obtain another piece of food at the same feeder. On test trials with no food present in any feeder, the array was shifted laterally by 44 cm and the formerly baited feeder was exchanged with another one in the array (Fig. 1). Birds searched first at the feeder that was in the correct location in the aviary, that is the feeder nearest the place that the baited feeder had originally occupied. They then

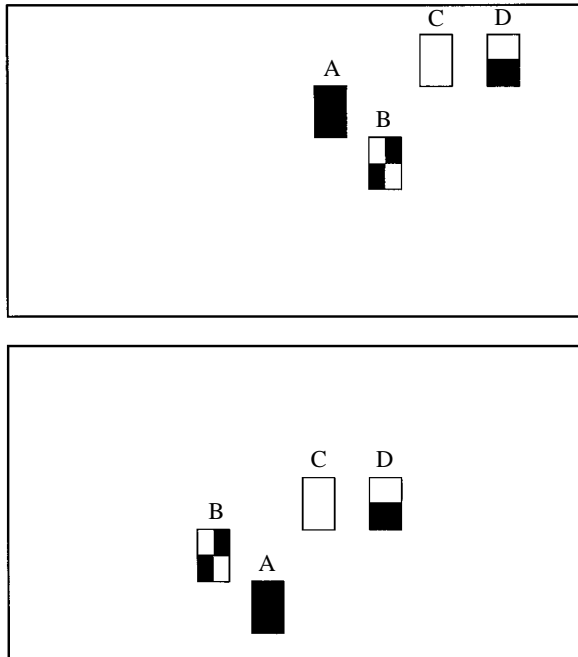


Fig. 1. Black-capped chickadees were trained to find food at one feeder in an array of four and to return after 30 min to take additional food from the same feeder. The placement and appearance of feeders was unique on each trial. In the upper panel of this illustration the baited feeder is B. On test trials, shown in the lower panel, the position of the feeders was changed. Feeder D occupies the same location in the aviary as had the baited feeder, feeder A occupies the same position in the array of feeders, and feeder B has the colour and pattern of the baited feeder. Redrawn from Brodbeck (1994).

searched at the feeder in the correct position within the array, and finally searched at the feeder that matched the baited one in colour and pattern (Fig. 2). This is a striking result. It shows that the birds retain a good deal of information about the food site (and by implication about cache sites, too), but have a clear preference ranking for using this information. They will search first at the place that is in the correct location with respect to global landmarks, despite conflicting information from the local spatial array and features of the cache site. They remember relative spatial location and features too, however, because if food is not found in the expected place, they will then search at the remaining sites according to the ranking: first local array, then features.

This preference ranking appears to be widespread in food-storing birds and absent in non-food-storing birds: it occurs in food-storing black-capped chickadees, marsh tits (*Parus palustris*) and European jays (*Garrulus glandarius*) and is absent in non-food-storing dark-eyed juncos (*Junco hyemalis*) bluetits (*Parus caeruleus*) and jackdaws (*Corvus monedula*; Brodbeck, 1994; Clayton and Krebs, 1994a).

### Sun-compass orientation

It has recently been shown that some food-storing birds orient using the sun compass when searching for caches

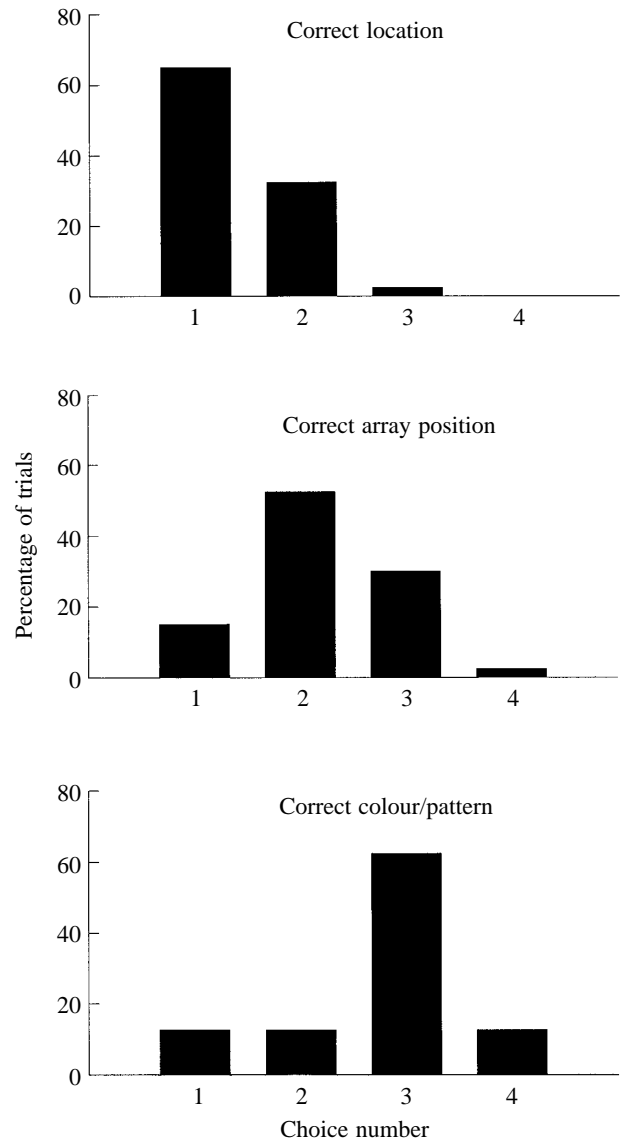


Fig. 2. Choice on test trials by black-capped chickadees. Birds tended to make their first choice to the correct location, their second choice to the correct array position and their third choice to the feeder of a matching colour and pattern. Birds would be expected to make these choices by chance on 25% of trials. Redrawn from Brodbeck (1994).

(Wiltschko and Balda, 1989; Balda and Wiltschko, 1991). The sun compass is generally regarded as most useful for navigation over long distances or in unfamiliar areas because it provides directional information in the absence of cues that identify particular locations. Food caches, in contrast, are particular locations in a familiar area, often with little systematic directional pattern in their placement (but see Barnea and Nottebohm, 1995). Sun-compass orientation during cache recovery thus seemed both intriguing and puzzling.

Because the use of the sun as a compass requires compensation for its daily change in azimuth, the critical test for sun-compass orientation is the clock-shift procedure, a

phase advance or phase delay of the circadian rhythm. A phase delay (or 'slow' clock-shift) of 6h, for example, causes a bird to treat the observed 15:00h position of the sun as if it were the 09:00h position, with a corresponding rotation of the cardinal points of the compass. Wiltschko and Balda (1989) found that following a 6h slow clock-shift, scrub jays that had previously stored food in one sector of an octagonal aviary searched for their caches in the sector 90° clockwise from the original sector, the result predicted if the birds were using a sun compass.

We have recently conducted similar experiments with black-capped chickadees and found that their search patterns, too, were influenced by the clock-shift procedure. Birds were trained in the morning to find food in small holes along one edge of an octagonal cage. In several experiments conducted outdoors under sunny conditions, birds exhibited clockwise rotations of their search patterns ranging from 22.5 to 47.9°. Tests conducted in the afternoon prior to clock-shifting showed that birds were oriented in the training direction and, thus, they were not simply using the sun as a fixed landmark. In these experiments, as in Wiltschko and Balda's, a variety of fixed landmarks were visible through the wire mesh of the octagonal cage, including buildings, fences, brightly coloured doors and children's playground equipment (our experiments were conducted at the university preschool during summer recess). Thus, although food-storing birds do locate caches and food sites by their spatial relationships to landmark arrays, they will search in sites that are clearly in conflict with the landmark array under clock-shift conditions. Clock-shift effects were often smaller than those predicted by the use of sun-compass information alone, an effect also observed in homing studies (Wiltschko *et al.* 1994). For chickadees, the locations visited may have been a compromise between conflicting sun-compass and landmark array information.

To examine the relationship between sun compass and landmark use further, we performed an experiment in which birds were tested following a clock-shift either at the site where they had been trained or at a site 20m away. The new site was on the opposite side of a barrier that blocked the view of objects that had been visible at the training site and presented views of novel objects that could not be seen from the training site. Birds tested at this novel site showed no significant pattern of orientation in any direction, while birds tested at the familiar site showed a moderate clock-shift of 41.7° (Fig. 3). This result shows that sun-compass information alone is not sufficient for black-capped chickadees to orient in a completely novel landmark array. Sun-compass information is used for orientation when the birds can view a familiar landmark array, however, even though when clock-shifted, the use of sun-compass information causes the birds to search at sites that are in conflict with the landmark array.

This result seems to present a paradox. If sun-compass information is used at all, why is there no indication of its use in novel surroundings? Wiltschko and Balda's experiment, our experiment and similar experiments by Chappell and Guilford (1995) and others have used radially symmetrical enclosures in which direction alone was adequate to specify the locations

of caches or food sites: birds were observed under conditions in which directional information alone was sufficient for orientation. Nevertheless, in our experiments with chickadees, a clock-shift did not produce the 90° rotation predicted by exclusive use of the sun compass. Birds evidently continued to use landmark information, with the result that searching occurred at sites that were compromises between sun-compass and fixed landmark information. In novel surroundings, in the absence of a familiar landmark array, direction derived from the sun compass was not sufficient for the birds to search in any systematic way. It appears that, for small-scale orientation, direction derived from the sun compass must be combined with information from a familiar landmark array.

Chappell and Guilford (1995) trained pigeons in the presence of a set of landmarks and found that rotation of these landmarks had no effect on the birds' orientation. That is, the pigeons did not use the landmark information provided. The clock-shift procedure in Chappell and Guilford's study resulted in birds

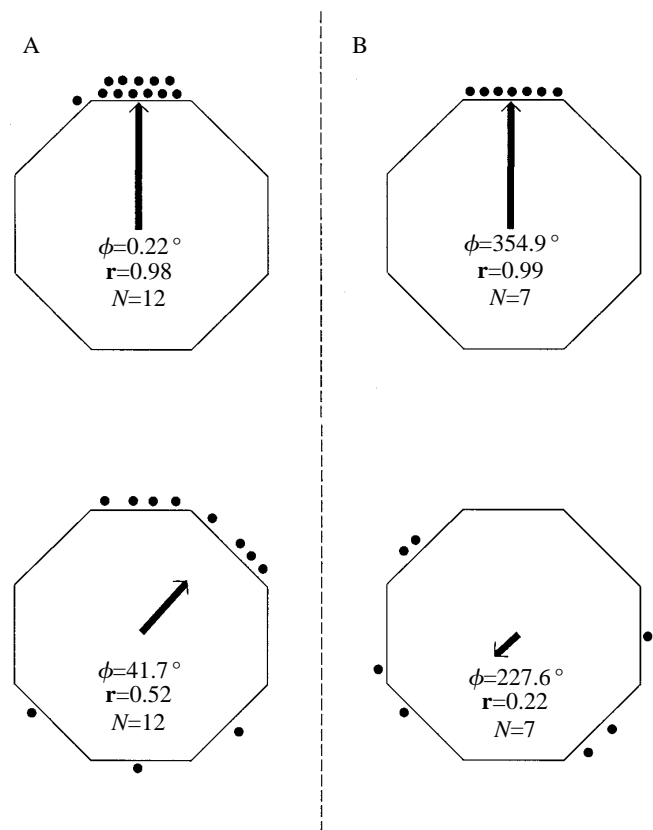


Fig. 3. The effect of clock-shift on black-capped chickadees in familiar and unfamiliar surroundings. Two groups of birds were trained in familiar surroundings to take food from one side of an octagonal cage (upper octagons A and B). The topmost side of each octagon represents the training direction. Following a 6h slow clock-shift (lower octagons), the mean direction of choice ( $\phi$ ) by birds tested in the same familiar surroundings was 41.7° clockwise of the training direction (A). Birds tested in unfamiliar surroundings were not significantly oriented in any direction (B). Each dot represents one subject and shows the mean direction of the first five choices.  $\phi$  is the mean direction for all birds (also shown by the arrow),  $r$  is the length of the mean vector and  $N$  is the number of subjects.

with no significant pattern of orientation, a result similar to the one we obtained with chickadees in novel surroundings. This result, too, suggests that, when birds use sun-compass information for small-scale orientation, compass direction must be combined with information from a familiar landmark array.

### The avian hippocampus

The avian hippocampus is a wedge of neural tissue in the dorso-medial telencephalon, extending rostro-caudally for about half the length of the brain (Fig. 4). Krushinskaya (1966) discovered that Eurasian nutcrackers (*Nucifraga caryocatactes*) with lesions of the dorso-medial telencephalon that included the hippocampus were unable to relocate their food caches. The birds continued to cache and search for stored food but failed to find it. Since that time there has been a considerable amount of research on the avian hippocampus, much of it conducted with food-storing birds. Recent research on the hippocampus of homing pigeons is reviewed by Bingman (1993).

Bilateral lesions of the hippocampus of black-capped chickadees disrupt cache recovery without disrupting caching itself or searching for caches (Sherry and Vaccarino, 1989). These lesions also disrupted performance on a task that required chickadees to remember a small number of highly familiar spatial locations where food could be obtained. Following hippocampal lesions, birds could not recall these locations and showed no indication of re-learning them. Hippocampally lesioned chickadees showed no disruption in another task that required them to remember a simple association for cues that marked the location of food. In both tasks, however, birds made large numbers of errors by repeatedly revisiting sites they had already inspected, an error

that control birds rarely made. The deficits produced by lesions of the avian hippocampus resemble those produced in rats by such lesions (Jarrard, 1993). There is an obvious parallel between the use of landmarks rather than features to recall cache locations, described earlier, and the dissociation between spatial and associative memory that occurs following hippocampal lesions in food-storing birds.

### Comparative studies of the hippocampus

Comparative studies provide further evidence that the hippocampus plays an important role in cache retrieval. Most members of the chickadee, jay and nuthatch families store food, and these families, considered as groups, have hippocampuses that are considerably larger than those of non-food-storing passerines of comparable body size (Fig. 5; Sherry *et al.* 1989; Krebs *et al.* 1989). Comparisons within taxonomic groups also show that species that store more food have a larger hippocampus, relative to the size of the brain, than species that store less food (Hampton *et al.* 1995; Healy and Krebs, 1992).

In a rather different ecological context, differences in hippocampal size occur between the sexes. Female brood-parasitic brown-headed cowbirds search for host nests in which to lay their eggs and probably retain in memory the spatial locations of several, perhaps many, potential host nests. Males do not participate in searching for host nests. The hippocampus of females is larger than that of males, an effect not observed in closely related non-parasitic icterine blackbirds (Sherry *et al.* 1993).

In general, comparative studies indicate that differences between species or between the sexes in relative hippocampal size are correlated with differences in the use of space. Food storing, brood parasitism and polygyny can all produce an evolutionary increase in hippocampal size because they have

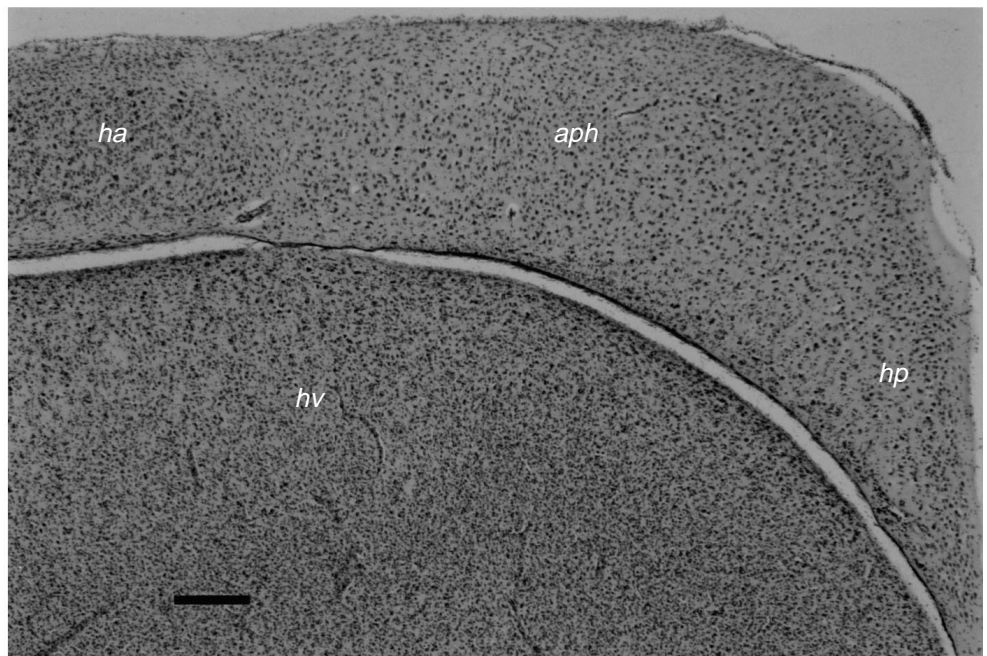


Fig. 4. The hippocampus of a food-storing bird, the white-breasted nuthatch (*Sitta carolinensis*). *aph*, area parahippocampalis; *ha*, hyperstriatum accessorium; *hp*, hippocampus; *hv*, hyperstriatum ventrale. Scale bar, 200  $\mu$ m.

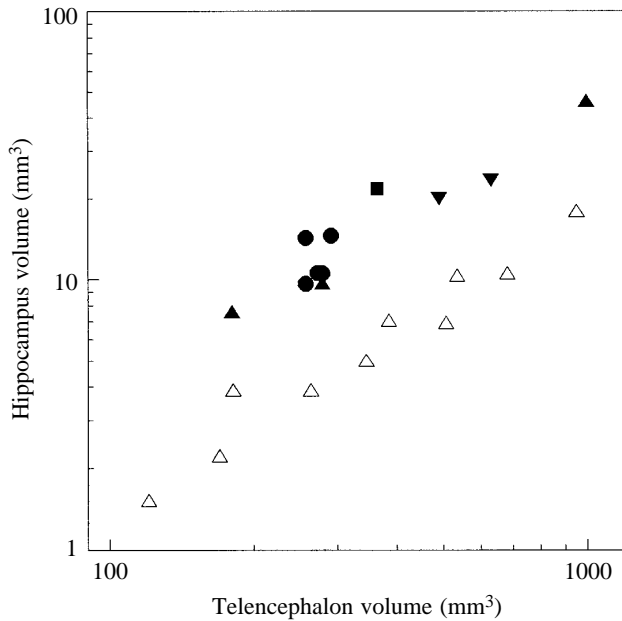


Fig. 5. Size of the hippocampus, relative to the telencephalon, in families and subfamilies of food-storing (filled symbols) and non-food-storing (open symbols) passerines. Redrawn from Sherry *et al.* (1989) with additional data for *Parus atricapillus*, *P. sclateri*, *P. wollweberi* and *P. palustris* (filled circles) from Hampton *et al.* (1995), Krebs *et al.* (1989) and K. Petersen and D. F. Sherry (in preparation). *P. lugubris* (filled square) courtesy of Frank Gill and Fred Sheldon and *Sitta carolinensis* (filled inverted triangles) courtesy of Karin Petersen.

a common feature: they can all increase the demands on spatial orientation and spatial memory (Sherry *et al.* 1992).

#### *Developmental and seasonal change in the hippocampus*

In a remarkable series of studies, it has been found that food-storing experience plays a role in the development of the hippocampus (Clayton, 1995; Clayton and Krebs, 1994b). If food-storing marsh tits (*Parus palustris*) are prevented from storing food early in development, the relative size of their hippocampus lags behind that of age-matched controls. Unravelling the link between food-storing experience and hippocampal development may provide important insights into the relationship between cognitive activity and brain development.

A further indication of the role the hippocampus plays in cache recovery is the identification in black-capped chickadees of a seasonal pattern in hippocampal neurogenesis and hippocampal size that is correlated with the seasonal pattern of food storing (Barnea and Nottebohm, 1994; Smulders *et al.* 1995). Food storing by chickadees reaches its maximum in autumn, persists through the winter and declines in spring and summer. Both hippocampal neurogenesis and relative hippocampal size reach their maximum in October. Barnea and Nottebohm (1994) are cautious in their interpretation of this correlation and point out that autumn is a time when the chickadee social system is changing from breeding pairs to

winter flocks and the deciduous forest is undergoing a dramatic change in appearance. Nevertheless, the correlation between the onset of food storing and hippocampal enlargement and neurogenesis suggests that the changes observed in the hippocampus may be related to the increased memory demands of food storing in autumn and winter.

The proximate cause of seasonal change in the hippocampus is not clear. J. R. Krebs, N. S. Clayton, R. R. Hampton and S. J. Shettleworth (in preparation) found that changes in daylength that were sufficient to induce autumn-like food-storing behaviour in captive birds had no effect on the relative size of the hippocampus. The hippocampus may be more refractory to daylength manipulations than is behaviour. It is also possible that seasonal change in the hippocampus is experience-dependent and that no effect of daylength on the hippocampus was observed because it is not easy to induce adequate levels of food-storing behaviour in the laboratory.

#### **Conclusions**

Food-storing birds use the remembered relationships between landmarks and caches in order to return accurately to cache sites. In the wild, they can, in all likelihood, remember the locations of thousands of caches for periods of several weeks to many months. Local features of cache sites seem to be relatively unimportant in cache retrieval, probably for two functional reasons. Local features of cache sites are more subject to change, caused by rain, snowfall and other natural processes, than are prominent nearby landmarks. In addition, memory for only local features would require exhaustive searching of the habitat, in essence the needle-in-a-haystack problem. A preference ranking for the use of global, local and featural information, of the kind described by Brodbeck (1994), permits efficient searching at successively finer scales of resolution until the cache is located.

Research on sun-compass orientation has identified a previously unsuspected use of compass information by food-storing birds. How sun-compass and other kinds of spatial information are integrated during searching for food caches remains to be determined.

The avian hippocampus clearly plays an important role in cache retrieval and spatial orientation in food-storing birds, as shown by lesion experiments and comparative neuroanatomical studies. Natural selection for spatial abilities has caused an increase in size of the hippocampus in food-storing birds, brood-parasites and other species of animal (Sherry *et al.* 1992). Recent results show that, in addition to these evolutionary influences, food-storing experience and seasonal factors can cause changes in hippocampal size over the lifetime of a food-storing bird.

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