MEMORY FOR LOCATIONS OF STORED FOOD IN WILLOW TITS AND MARSH TITS

by

SUSAN D. HEALY[1,2] and JUKKA SUHONEN[3,4]

([1]Department of Psychology, University of Newcastle upon Tyne, Newcastle upon Tyne NE1 7 RU, UK; [3]Department of Biological and Environmental Sciences, PO Box 35, FIN-40351 Jyväsklyä, Finland)

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Summary

Some food-storing animals use spatial memory in food retrieval. There is variation amongst food-storing species in the duration over which food is stored and it is positively correlated with differences in the size of the part of the brain that is involved with memory for storage locations, the hippocampus. For example, British marsh tits (*Parus palustris*) are generally thought to retrieve their stores after a few hours or days whereas Scandinavian willow tits (*P. montanus*) have been shown to store their food for several weeks to months. Marsh tits also have a smaller hippocampus than do willow tits. This experiment tested the hypothesis that retrieval success (and thus memory capacity) of the two species differs depending on the usual length of time for which food is stored. Individuals of both species were tested on their ability to retrieve five stored food items after two differing delays: 2-3 h ('short') and 17 days ('long'). The prediction was that there would be no differences in retrieval performance between the species after the short delay but that willow tits would be more accurate at retrieving their stores than marsh tits after the long delay. The results did not provide support for this hypothesis as there were no differences between the species in retrieval performance following either delay: both species successfully retrieved food after both delays.

[2] e-mail address: s.d.healy@ncl.ac.uk

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Introduction

Food storing has been documented in a taxonomically wide range of species, from ants and bees to bears and monkeys (reviewed in Vander Wall, 1990). There is an accumulating body of evidence that animals use memory to retrieve their stores (Sherry, 1989; Vander Wall, 1990) and that this memory is multi-faceted and large. For example, food-storing birds in the families Paridae and Corvidae may store many food items, *e.g.* Clark's nutcrackers (*Nucifraga columbiana*) may store as many as 33 000 hoards in an autumn (Tomback, 1978; Vander Wall, 1983). They appear to remember the quality of the food they store in each site (Sherry, 1984a) and on retrieval seem to recognise that they have emptied the site and avoid it subsequently (Shettleworth & Krebs, 1982; Sherry, 1984b).

There is variation in storing strategy both within and among species. One of the most obvious ways in which the strategies vary is in the number of food items placed at each storage site. For example, scrub jays (*Aphelocoma coerulescens*) will often put several seeds into a storage site whereas another storing corvid, the magpie (*Pica pica*) usually stores items singly. The length of time over which food is stored also varies. Clark's nutcrackers, for example, relocate stored seeds after as long as 11 months (Vander Wall, 1983), whereas marsh tits (*P. palustris*) usually retrieve their stores within a few hours or days (Cowie *et al.*, 1981; Stevens & Krebs, 1986). This variation provides an opportunity to examine whether there is a specificity to the memory capacity involved in food retrieval. For example, do those species which store food for shorter periods of time forget storage sites more quickly than those species which retrieve their food after much longer intervals?

Available field data suggest that variation in storing strategy between the four storing species of north-western European Paridae is very much less than it is within the Corvidae. The different tit species tend to use the same kind of storage sites, store singly, similar insect and plant seed species (Haftorn, 1956a, b; Alatalo & Lundberg, 1983) and space storage sites at similar distances (Sherry *et al.*, 1982; Brodin, 1992). The most apparent differences between the species in storage are the length of time which elapses before food is retrieved and the number of items stored. Those species which store tens or hundreds of food items and retrieve their stores within a few days or a few weeks include coal tits (*P. ater*)

(Haftorn, 1956a), marsh tits (*P. palustris*) (Stevens & Krebs, 1986), and black-capped chickadees (*P. caeruleus*) (Sherry, 1989). Species which store thousands of seeds and do not retrieve their stores for several months include the willow tit (*P. montanus*). Observations document individuals of this species retrieving *Galeopsis* seed in December-March, seeds which must been stored some three to four months earlier (Haftorn, 1956b).

The behavioural variation in food storing is accompanied by differences in the part of the brain involved in processing memories for storage sites, the hippocampus (Krushinskaya, 1966; Sherry & Vaccarino, 1989): food-storing species have a larger hippocampus than non-storers (Krebs *et al.*, 1989; Sherry *et al.*, 1989). This difference is dependent on the degree of food storing: those species which store more and for longer have a larger hippocampus (Healy & Krebs, 1992a, 1995). In addition, developmental studies have shown that the enlargement of the hippocampus occurs at the time food storing begins (Healy & Krebs, 1993; Clayton & Krebs, 1994; Healy *et al.*, 1994).

One of the possible advantages of an enlarged hippocampus is a greater ability to retain spatial information. In the experiment presented here we tested the hypothesis that marsh tits, which store food for relatively short intervals (hours), will not be as able to remember multiple food storage sites as willow tits, which have a larger hippocampus than marsh tits and store food for weeks to months. The retrieval performance of wild-caught individuals of these two species was compared after a 'short' delay (2-3 h) and a 'long' delay (17 days). The short delay was chosen as representative of the time period over which marsh tits are known to retrieve. The longest time period over which marsh tits have been seen to retrieve stores is about three days, which is well short of the 17-day period. We did not want to test the birds over delays typical of willow tit storage time (30-90 days) as we could not be sure that the willow tits, in a laboratory setting, would perform well. We predicted, therefore, that both species would accurately retrieve stored seeds after the short interval, whereas the willow tits would perform better than the marsh tits after 17 days.

Subjects

The birds used in this study were seven wild-caught willow tits from coniferous woodland near Konneversi, Finland and nine wild-caught marsh tits from deciduous woodland near

Oxford, England. Both species were maintained on a diet of insectivorous bird mix, peanuts, and sunflower seeds, with fresh water provided daily. The birds were kept indoors in individual cages (0.44 m wide × 0.77 m long × 0.44 m high) that were connected to the experimental room by electronic doors. The experiment was run in February-March 1991 and November 1991-February 1992 at the Department of Zoology at Oxford and birds were maintained on an 8 : 16 light : dark cycle.

Experimental environment

The birds were tested in a room measuring 3.75 m × 3.9 m × 2.4 m high. Along the 3.9 m wall were twelve black electronic doors through which the birds flew into the room and the 3.75 m wall had a door with a one-way Plexiglas window through which the experimenter could view the birds. In the experimental room were six 'trees' which were tree branches set into white plastic umbrella stands, arranged in approximately circular fashion. On each of the trees were 10 potential storage sites: small holes (0.5 cm diameter, 1-cm deep) drilled into the trees no less than 15 cm apart (providing a total of 60 potential storage sites). The holes were placed irregularly on the tree's trunk and branches. Each hole was covered with a piece of black cloth (2.5 × 2.5 cm) stapled just above, and covering, the hole such that the bird was unable to see the contents of the hole without raising the cloth. This cloth was readily raised by all the birds, both when storing and retrieving.

At the centre of the ring of storage trees were two bowls of food in which were storable food items: one contained pieces of peanut and husked sunflower seeds, the other wax moth larvae. Wax moth larvae were only ever available to the birds in this experimental room.

Experimental procedure

Throughout the experiment the birds' food bowls were removed at dark (16:30 GMT). The birds were tested between 09:00 and 14:00 and were subsequently fed a fresh portion of the maintenance diet.

The birds were trained to enter the room when the door connecting their cage to the experimental room was opened and then to fly to the food bowls. They were then allowed to eat from either bowl and storing usually ensued. Over the course of five to seven days the birds were trained to store only in the storage sites on the experimental trees. This is done by consistently removing all items stored in 'illegal' sites. During the experiment the bird was allowed to store only five items. When this had occurred the bird's electronic door was opened and the lights in the experimental room turned off.

In the retrieval phase of the experiment the bird was allowed to return to the experimental room after a retention interval in order to retrieve its stored food. The food bowls had been removed and the contents of each hole were covered by the cloth flaps. For each bird food was replaced in the five holes in which it had stored previously. The bird was observed until it had visited a maximum of 10 sites. The retrieval phase typically lasted for about five minutes. In this experiment there were two delays at which each bird's retrieval performance was tested. There was a 'short' delay of 2-3 h and a 'long' delay of 17 days. On short-delay

days the birds were not fed during the retention interval. Birds were not deprived of food nor did they go in to the experimental room during the seventeen day interval.

When the birds had learned to store and retrieve in the experimental room they were given five short-delay tests followed by a long-delay test. The data recorded in the retrieval phase were the ten sites which birds inspected. Revisits within a retrieval phase were very uncommon and were not recorded.

Results

The retrieval ability of the birds was assessed by determining how many stored items they found in the retrieval phase. For the short delay the mean number of successful retrievals (seeds found within the 10 visits allowed during the retrieval phase) made over the five days was taken as the bird's score. For the long delay the bird's score was taken as the number of successful retrievals made in the first 10 visits of the retrieval phase.

Marsh tits took significantly longer than willow tits to store five items (marsh tits: 13.04 ± 0.98 min; willow tits: 9.87 ± 0.73 min (mean $\pm$ SE); Mann-Whitney U-test: $U = 10.5$, $U' = 52.7$, $N_1 = 7$, $N_2 = 9$, $p = 0.026$). There was no difference between the species in time taken to retrieve stores (marsh tits: 5.63 ± 0.46 min; willow tits: 4.29 ± 0.45 min (mean $\pm$ SE); Mann-Whitney U-test: $U = 14$, $U' = 49$, $N_1 = 7$, $N_2 = 9$, $p = 0.064$).

Performance with respect to random

In order to determine how the birds were performing on retrieval with respect to random it is first necessary to show whether the birds were using storage sites at random. If the distribution of storage sites is no different from that of a random site usage then the calculation of retrieval performance can be based on all 60 potential storage sites in the room. If the birds were using sites for storage differently from that of a random expectation then analysis of retrieval cannot include sites birds would not visit. The binomial distribution was used to calculate, for five successive days, the probabilites that the birds used unique sites on each day. These probabilities were then used to generate the expected number of unique storage sites used over 5 days. A Z-test showed no significant difference between the distribution of the number of unique storage sites used by the birds over the 5 days of the short delay (average no. of sites used = 19.68 ± 0.68 SE, $N = 16$) and the expected number of unique sites used

over 5 days (expected number = 19.84; $z = -0.66$, $p = 0.51$, two-tailed test). This result suggests that the birds did not have marked preferences for particular sites and therefore we assumed that the birds were effectively choosing storage sites at random.

Z-tests were used to test whether the birds' retrieval success was better than that expected by chance. A hypergeometric distribution was used to calculate the expected number of successes (0.83). The retrieval performance of both species was better than random after the short delay of 2-3 h (willow tits: $z = 7.47$, $p < 0.0001$, $N = 7$; marsh tits: $z = 8.26$, $p < 0.0001$, $N = 9$). Both species also performed better than at random after 17 days (willow tits: $z = 7.70$, $p < 0.0001$, $N = 7$; marsh tits: $z = 7.5$, $p < 0.0001$, $N = 9$).

There was no difference between the species at either delay (2-3 h: Mann-Whitney $U = 30$, $U' = 33$, $N_1 = 7$, $N_2 = 9$, $p = 0.87$; 17 days: $U = 27.5$, $U' = 35.5$, $N_1 = 7$, $N_2 = 9$, $p = 0.64$) (see Fig. 1).

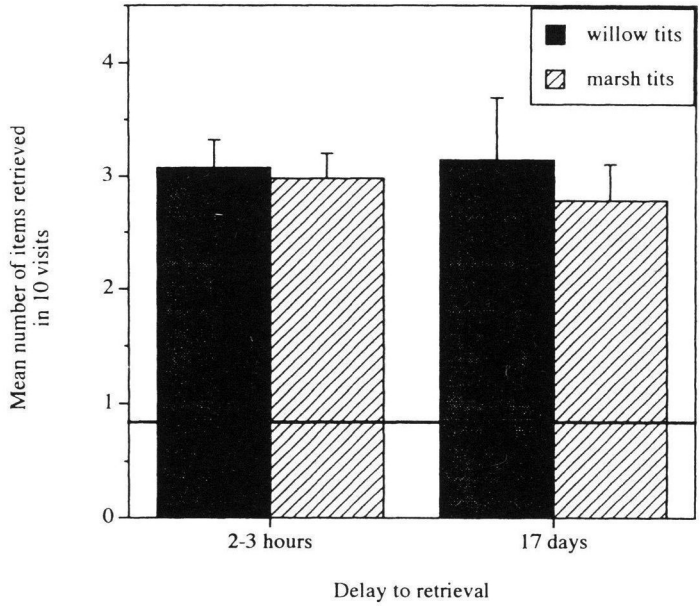

Fig. 1. The mean number (± SE) of food items found by marsh tits ($N = 9$) and willow tits ($N = 7$) after retention intervals of 2-3 h and 17 days. The solid line indicates how many seeds would be retrieved if the bird retrieved its stored food at random.

For neither species was there a difference in performance between the delays (Wilcoxon paired sign tests: willow tits: $p = 1.0$, $N = 7$; marsh tits: $p = 0.40$, $N = 9$). This result could be due to an effect of training as all birds were tested with short delays before the long delay.

Discussion

The main results from this experiment are (i) marsh tits and willow tits did not differ in their ability to retrieve their stored food; (ii) both species performed better than at random after both short and long delays; (iii) after 17 days neither species' retrieval performance was significantly worse than it was after 2-3 h (Fig. 1).

This experiment was designed to test the hypothesis that a bird's ability (as measured by retrieval performance) to remember the locations of stored food is correlated with the length of time the information needs to be retained for. It was proposed that willow tits, which store their food for several weeks to a few months, would show high retrieval accuracy after a long delay. As marsh tits store food for only a few hours or days it would seem unnecessary for them to remember storage locations for long periods and they were not expected to perform well after a long delay. The data from this experiment show that the marsh tits are as capable of successful retrieval for at least 17 days, even though this is considerably longer than the time period over which they have been observed to store (Cowie *et al.*, 1981; Stevens & Krebs, 1986).

There are several possible explanations for the failure to find a close coupling between retrieval success and memory demand in this experiment. The first possibility is that the general belief that willow tits store food for longer than do marsh tits may be inaccurate. Thus it may be that marsh tits store food for longer than has been observed so far. It is possible that even though the birds may recover most of their stores within a few hours or days, some part of their store is left for retrieval at some much later date.

A second possibility is that storage locations are remembered until food is retrieved from them, independent of time. Whilst the passage of time alone does not explain forgetting (see Baddeley, 1990) most theories would predict that storage locations would over lengthening periods of time be

remembered less well, due in part to the effects of interference (*e.g.* Underwood, 1957; Squire, 1987). For the marsh tit in the field storing and retrieving on a daily basis, there must be competition, to some extent at least, between memories for different storage locations. Interference is presumably even higher because the birds appear to remember emptied storage sites (in order to avoid them) in addition to baited sites. However, in this experiment the lack of food storing in the experimental room during the retention period may have decreased interference, and thus memory loss, especially given the small number of storage sites to be remembered. Good performance by the marsh tits, then, after 17 days may have been achieved by low levels of interference and therefore their performance in this experiment may not be fully indicative of memory abilities in the field.

The ability of these birds to retrieve stored food after 17 days as well as after 2-3 h is impressive when considered in the context of the results from other laboratory studies of animal memory. Rats and pigeons, for example, both show a marked decline in memory performance within a few hours (*e.g.* Roitblat & Harley, 1988; Spetch & Honig, 1988). However, the nature of the tasks these species are tested on is undoubtedly the single largest factor in explaining such apparently poor performance. Food-storing species tested on delayed-non-matching-to-sample tasks show memory deficits after a few minutes (Olson, 1991; Healy & Krebs, 1992b; Brodbeck & Shettleworth, 1995) whereas when tested on retrieval of food stores, these birds may perform better than expected by chance up to at least 28 days (Balda & Kamil, 1989; Hitchcock & Sherry, 1990).

The lack of difference in performance between the two species may contribute to the current speculation as to the role of the hippocampus in birds. As in this comparison of two storing species, those testing memory retention over differing periods of time (30 min-24 h) between non-storing and closely related storing parids have not shown substantial differences between the species (great tits and marsh tits: Healy & Krebs, 1992b; blue tits and marsh tits: Healy & Krebs, 1992c), even though there are considerable differences in hippocampus size. Those results led to the suggestion that the differences in hippocampus size may be more closely correlated with the amount of information stored rather than the duration over which memories are kept and the results from this experiment lend support to this hypothesis.

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