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Hippocampus and Memory in a Food-Storing and in a Nonstoring Bird Species

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Food-storing birds maintain in memory a large and constantly changing catalog of the locations of stored food. The hippocampus of food-storing black-capped chickadees (*Parus atricapillus*) is proportionally larger than that of nonstoring dark-eyed juncos (*Junco hyemalis*). Chickadees perform better than do juncos in an operant test of spatial non-matching-to-sample (SNMTS), and chickadees are more resistant to interference in this paradigm. Hippocampal lesions attenuate performance in SNMTS and increase interference. In tests of continuous spatial alternation (CSA), juncos perform better than chickadees. CSA performance also declines following hippocampal lesions. By itself, sensitivity of a given task to hippocampal damage does not predict the direction of memory differences between storing and nonstoring species.

Dependence on cached food requires that food-storing birds maintain in memory a large and constantly changing catalog of the locations of stored food. These birds may make hundreds of scattered caches in a single day and recover their stored food hours, days, or months later (Balda, Bunch, Kamil, Sherry, & Tomback, 1987; Sherry, 1985; Shettleworth, 1990). Comparisons conducted across a large number of bird families indicate that the hippocampal complex (hippocampus and area parahippocampalis, hereafter called hippocampus) is proportionally larger in food-storing birds than in nonstoring birds (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989). Black-capped chickadees require an intact hippocampus to accurately retrieve previously stored food (Sherry & Vaccarino, 1989). The survival value of hippocampus-dependent memories for the location of caches has probably resulted in enlargement of this structure in birds that store food (Krebs et al., 1989; Sherry et al., 1989). Enlargement of the hippocampus occurs in other animals subjected to exceptional demands for spatial cognition, either to find mates (Gaulin, 1995) or to find suitable sites in which to lay parasitic eggs (Reboreda, Clayton, & Kacelnik, 1996; Sherry, Forbes, Khurgel, & Ivy, 1993).

Although the characterization of hippocampal function continues to be debated (Eichenbaum, Otto, & Cohen, 1992; Macphail, 1993; Olton, Becker, & Handelmann, 1979; Squire, 1992; Sutherland & Rudy, 1989), it is clear that the hippocampus is involved in tasks that require spatial memory (Nadel, 1991). Evidence also exists indicating a role for the mammalian hippocampus in memory for nonspatial information (Sutherland & Rudy, 1989; Wan, Pang, & Olton, 1994; Winocur, 1990; Winocur & Olds, 1978). Although the avian and mammalian hippocampi differ in details of structure, the avian hippocampus also appears to play a role in spatial memory (Bingman, 1992; Hampton & Shettleworth, 1996; Sherry & Vaccarino, 1989). The avian hippocampus develops from the same pallial cells as does the mammalian homologue (Källén, 1962) and shares patterns of connectivity to the rest of the brain (Casini, Bingman, & Bagnoli, 1986). Additionally, the distributions of neuropeptides and neurotransmitters in the avian and mammalian hippocampi show similarities (Erichsen, Bingman, & Krebs, 1991; Krebs, Erichsen, & Bingman, 1991). The extent of documented similarities should not be exaggerated, however. It is not known whether or not a trisynaptic path exists in the avian hippocampus, nor are there clearly delineated subfields like those found in the mammalian hippocampus (Macphail, 1993, p. 386), and efforts to identify a mossy fiber system like that found in mammals have failed (Erichsen et al., 1991). Although theories of mammalian hippocampal function provide guidance for the formulation of theories of avian hippocampal function, it should not be assumed that the hippocampus serves identical functions in these two groups. Comparisons of structure and function between the mammalian and avian hippocampi may provide a productive route to insights about the physical basis of memory.

Studies comparing memory in scatter-hoarding birds with that of nonstoring species test the hypothesis that food-storing species have an adaptively specialized memory that facilitates the recovery of stored food (Shettleworth, 1995). Such studies

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can provide insight into the evolution and function of the hippocampus, and may also provide an opportunity for unique insights into the relationship between hippocampal structure and function. A relationship between food storing and memory cannot be established on the basis of a single comparison between two species. It is only after a relationship between food-storing and memory has been observed in a number of different comparisons, between many species and using different tasks, that a causal relationship between food-storing and memory can gain credibility (Kamil, 1988).

A relationship between food-storing and relative hippocampal volume is well established (Basil, Kamil, Balda, & Fite, 1996; Hampton, Sherry, Shettleworth, Khurgel, & Ivy, 1995; Healy & Krebs, 1992a; Krebs et al., 1989, Sherry et al., 1989). The existence of this relationship raises a question about what effect enlargement of the hippocampus has on memory. This question could have a number of different answers:

1. Enlargement of the hippocampus might benefit only memory for sites where food has been cached. This is unlikely to be correct. Comparisons among corvid species, using spatial tasks other than retrieval of stored food, have shown that memory performance is better in species with larger hippocampal volumes (Kamil, Balda, & Olson, 1994; Olson, Kamil, Balda, & Nims, 1995). Tests comparing both parid and corvid species indicate that storing species are more likely than are nonstoring species to use spatial information in both a food-finding task and an operant analogue of this task (Brodbeck, 1994; Brodbeck & Shettleworth, 1995; Clayton & Krebs, 1994). These tasks were designed to capture some of the features of food-caching, but do not require the subject to actually cache food.

2. Increased hippocampal volume may improve memory in a broad class of memory tasks. This answer also is unlikely given that Olson et al. (1995) showed in corvids that a larger hippocampus predicted better performance in spatial nonmatching-to-sample (NMTS), but not in color NMTS. Furthermore, in the food-finding task, differences were found in the way in which species solved the task, but not in their ability to perform correctly. Given the available evidence two other possible answers remain viable.

3. A larger hippocampus may improve performance in any task in which the hippocampus plays a role. The simplest hypothesis then is that food-storing birds should perform better than nonstoring species on any task that depends on hippocampal function. The hippocampus is certainly used for other tasks than the recovery of caches, and is therefore important for nonstoring species too. However, selection for good cache memory, and a large hippocampus, may also be reflected in the performance of other tasks that depend on hippocampal function. Food-storing birds might be better at all spatial-memory tasks, for instance.

4. Increased hippocampal volume may have a more subtle impact, reflecting enhancement of only some aspects of hippocampal function. It is possible that some currently unspecified aspect of spatial memory is enhanced in food-storing species.

One way to distinguish between Hypotheses 3 and 4 is to compare performance of food-storing and nonstoring species on a variety of tests of memory and to examine the effects of hippocampal lesions on the performance of these same tasks. Hypothesis 3 states that food-storing birds will perform better than nonstoring birds on any task that depends on hippocampal function. Hypothesis 4 states that storing species will perform better than nonstoring birds on only a subset of tasks shown to be hippocampus dependent.

Previous studies have documented the relationship between food storing and hippocampal volume (e.g., Krebs et al., 1989), tested whether food storing birds have a specialized memory (see Shettleworth, 1995), and examined the role of the avian hippocampus in some memory tasks (Bingman, 1992; Good & Macphail, 1994a, 1994b; Hampton & Shettleworth, 1996; Sherry & Vaccarino, 1989). This is the first attempt, to our knowledge, to bring these three approaches together in a single set of studies. Here we compare food-storing black-capped chickadees (*Parus atricapillus*) with nonstoring dark-eyed juncos (*Junco hyemalis*). We begin with a brief summary of the natural histories of the two species. We then present a neuroanatomical comparison, and the results of two tests of memory: continuous spatial alternation (CSA) and spatial non-matching-to-sample (SNMTS). Finally, we use lesions to investigate the role played by the avian hippocampus in the same two tests of memory.

Natural History of Chickadees and Juncos

Chickadees and juncos are small perching birds of the order Passeriformes. Both species are widely distributed in North America, and are often found in mixed and coniferous forests (Bent, 1968; Peterson, 1980; Smith, 1991). Chickadees forage primarily in trees, for insects and seeds, and do so in flocks during the winter (Smith, 1991). Juncos forage in flocks year round, searching for grains and seeds on the ground (Bent, 1968; Caraco et al., 1989).

Chickadees, like all North American members of the family Paridae, store food (Hampton & Sherry, 1992a; Sherry, 1989). Storing peaks in the fall (Odum, 1942), but has been observed to occur in midwinter (Brewer, 1963) and during breeding (Heinrich & Collins, 1983). Chickadees may store many items, each in a separate location, on a single day. In the laboratory chickadees can remember the location of caches for up to 28 days (Hitchcock & Sherry, 1990). After a single, brief visit to each cache site, chickadees in the laboratory remember both where they have stored food, and what type of food is at each site (Sherry, 1984). Once they have retrieved caches in the laboratory, chickadees avoid revisiting the now depleted cache sites (Sherry, 1984). This ability to remember the location and contents of a large number of caches, and to update memory rapidly as caches are depleted, suggests that chickadees' memory may be specialized in some way as a result of their dependence on stored food (Shettleworth, 1995). Juncos have been studied extensively and have never been observed to store food. Chickadees are therefore subject to an unusual demand for good memory that juncos do not face.

Experiment 1

Because juncos are a nonstoring species, the available evidence indicates that they should have a relatively small hippocampus compared to black-capped chickadees. How-

ever, prior to the present study, only one junco brain had been measured and compared with that of food-storing birds (Sherry et al., 1989). Furthermore, published anatomical comparisons used freshly caught birds, whereas the behavioral experiments reported in this article use birds that have lived in cages in the laboratory for as long as 2 years. Living in cages limits spatial behavior and food-storing opportunities. The purpose of this study was to determine whether for birds kept in the laboratory for extended periods, black-capped chickadees have relatively larger hippocampi than do dark-eyed juncos.

Method

Three black-capped chickadees and three dark-eyed juncos were captured near Toronto, Ontario, Canada, and housed individually in cages 61 × 37 × 38 cm on a 10:14-hr light–dark cycle. All birds were fed a mixture of soft-billed bird food (Rolf C. Hagen, Toronto, Ontario, Canada), boiled egg, and shredded carrots, supplemented with peanuts and mealworms (*Tenebrio molitor*). The juncos were also provided with a mixture of niger seed and millet. Grit was provided, and water with vitamin supplement was continuously available. The birds lived in the laboratory between 1 and 2 years while participating in various experiments in both aviary and operant settings. Subjects were deeply anesthetized with a combination of xylazine (100 mg/kg) and ketamine (50 mg/kg) injected into the pectoral muscle. Depth of anesthesia was confirmed by sharply pinching the animal's foot. The birds were perfused transcardially with 0.8% saline followed by 10% formalin. The brains were then removed from the cranium, placed in the fixative solution, and refrigerated.

After soaking in 30% sucrose 10% formalin for several days (until they sank), the brains were embedded in gelatin–sucrose and sectioned at 40-μm intervals. Robert R. Hampton was provided with sets of slides from birds of the two species, coded to conceal species identity, in an unpredictable order. Areas of hippocampus and telencephalon were measured bilaterally in every fourth cresyl violet-stained section with NIH Image 1.49 (National Institutes of Health) software. Volumes of these areas were estimated by multiplying the sum of the areas by the sectioning interval. The avian hippocampus is bounded dorsally by the surface of the brain, ventrally by the lateral ventricles, and medially by the midline. The lateral boundary of hippocampus is indicated by an abrupt increase in cell density. Observer error in the determination of hippocampal volume has been estimated as less than 4% (Krebs et al., 1989).

Results and Discussion

There is no overlap between the two species in the proportion of telencephalon occupied by hippocampus (Table 1). Chickadees have a relatively larger hippocampus ($t_2 = 4.02$, $p < .05$). The hippocampal complex of chickadees is also absolutely larger, on average, than is that of juncos, despite the fact that juncos on average have larger brains. Other studies examining the relationship between food-storing and hippocampal volume have applied multiple regression to data from many species to estimate the relative effects of body weight, brain size, and food storing on hippocampal volume (e.g., Healy & Krebs, 1992a; Krebs et al., 1989; Sherry et al., 1989). In a comparison of only two species this type of analysis is not appropriate. Instead, we correct for differences in brain size between the species by analyzing hippocampal volume as a proportion of telencephalic volume. These results are consistent with previous findings indicating that food-storing birds have relatively larger hippocampi than do nonstoring birds (Sherry et al., 1989; Krebs et al., 1989) and confirm that the same difference is found between juncos and chickadees kept for extended periods of time in the laboratory.

Table 1
Volume of Hippocampal Complex (HP-APH), Telencephalon (TEL), and the Ratio of These Volumes in Black-Capped Chickadees (BC) and Dark-Eyed Juncos (J)

Bird	Time in lab (months)	HP-APH (mm^3)	TEL (mm^3)	HP/TEL
BC91-13	24	14.66	321.71	0.046
BC91-24	18	13.57	315.69	0.043
BC91-19	18	14.43	293.79	0.049
M	20	14.22	310.40	0.046
J92-6	13	11.52	384.20	0.030
J91-6	17	12.44	356.50	0.035
J91-1	25	14.48	379.29	0.038
M	18	12.81	373.33	0.034

Three recent studies have investigated the possibility of seasonal variation in the chickadee hippocampus. In free-ranging birds, the hippocampus is relatively larger in October than at other times of year (Smulders, Sasson, & DeVoogd, 1995), and a peak of neuronal recruitment in hippocampus also occurs at this time of year (Barnea & Nottebohm, 1994). In contrast, Krebs, Clayton, Hampton, and Shettleworth (1995) found no variation in hippocampal volume in caged animals subjected to photoperiodic regimes capable of producing changes in food-hoarding (Shettleworth, Hampton, & Westwood, 1995). As the animals used in this study were housed under constant conditions for extended periods of time, it was not possible to determine seasonal state.

Experiment 2

The differences between chickadees and juncos in ecology and neuroanatomy suggest that the two species may also differ in memory. Three sources of information are available from which to make predictions about differences in memory between juncos and chickadees: the natural history of these two species, differences in hippocampal complex volume, and results of previous comparisons between storing and nonstoring species. Predictions made on the basis of convergence of these sources of information are most likely to be correct.

Natural History

Both chickadees and juncos must be able to navigate successfully in similar environments, be able to locate mates and nests, and be able to memorize the location of other resources that occur in stable locations. But black-capped chickadees face an additional demand on memory: the need to remember the locations of cached food. The existence of this selection pressure suggests that chickadees may manifest an adaptation of memory, absent in juncos, that makes successful return to cache sites likely (Krebs, 1990; Shettleworth, 1995). Chickadees depend on spatial memory to recover caches (Shettleworth, 1990), so whatever specialization is proposed, it

should come into play in the operation of spatial memory, although not necessarily exclusively so.

Unlike memory for unchanging characteristics of food items, memory for the location of stored food must be formed in a single brief visit to a storage site (Shettleworth, 1990). Memory for cache locations also differs from memory for foraging strategies in the relationship between reinforcement and the information to be learned. Learning to discriminate between the appearance of ripe and immature seeds, for example, can occur by trial and error. In the case of memorizing the location of stored food, however, there exists no stable relationship between the location of stored food and later reinforcement. Reinforcement will be attained in a new location every time. Chickadees recover food hours, days, or longer after it is stored. Reinforcement therefore occurs long after the behavior of storing the seed (Hampton & Sherry, 1992b) and at the time of storage, no explicit primary reinforcement occurs. Emphasizing this independence from reinforcement, chickadees avoid revisiting locations where they have already recovered stored food, and therefore been reinforced (Sherry, 1984). Finally, although chickadees do learn to avoid caching in an area where food is always stolen, choice of cache site is not affected by learning of a food-rewarded approach response to an area (Hampton & Sherry, 1992b).

These considerations suggest that chickadees face a memory problem on a day-to-day basis that does not confront juncos. They must rapidly encode the locations of many stored food items, without explicit reinforcement. On recovery of stored food, they should suppress the tendency to return to the same location, a tendency that would normally result from reinforcement.

Function of the Avian Hippocampal Complex

Spatial cognition is required for homing pigeons to return successfully to the home loft, and hippocampal lesions impair this ability (Bingman, 1992; Bingman, Ioale, Casini, & Bagnoli, 1988, 1990; Bingman & Mench, 1990). Hippocampal lesioned black-capped chickadees did not recall the location of food cached 3 hr previously, whereas intact and control lesioned birds accurately return to sites of cached food (Sherry & Vaccarino, 1989). Krushinskaya (1966) lesioned the hippocampus of nutcrackers (*Nucifraga caryocatactes*) and observed a deficit in cache retrieval accuracy in this species also. Lesioned chickadees performed poorly on a spatial memory task that required return to the same baited locations trial after trial, but performed as well as did controls on a task that required approaching color cues consistently associated with reward (Sherry & Vaccarino, 1989). Both chickadees and juncos were impaired in spatial matching-to-sample, but not color matching following hippocampal lesions (Hampton & Shettleworth, 1996). These results, combined with those showing that the hippocampus is relatively larger in food-storing birds than it is in other species (Krebs et al., 1989; Sherry et al., 1989), support the hypothesis that the hippocampus is essential for spatial cognition serving cache recovery.

Several experiments using pigeons as subjects also indicate a role for the avian hippocampus in memory and suggest that spatial memory is particularly dependent on this structure. Pigeons with hippocampal lesions were impaired at spatial delayed matching-to-sample (DMTS), but only at longer retention intervals (RIs; Good & Macphail, 1994a). In contrast, retention of nonspatial information was unaffected by the lesion. Hippocampal lesioned birds were impaired at SNMTS in a T-maze, but fully competent at CSA in an operant setting (Reilly & Good, 1987). Hippocampal lesioned birds were impaired in reversal of a position discrimination but performed as well as controls on reversal of a visual discrimination (Good, 1987). Although these results indicate a role for the avian hippocampus in spatial cognition, other results suggest that spatial cognition is not the only domain in which the avian hippocampus is important (Good & Macphail, 1994b; Reilly & Good, 1989; Sahgal, 1984).

Memory in Storing and Nonstoring Birds

Studies comparing storing and nonstoring species have tested whether differences exist in spatial memory, working memory, memory for nonspatial information, and resistance to interference. In a comparison of four corvid species, Olson et al. (1995) found that dependence on stored food predicted ability to retain spatial, but not color information in operant tests of non-matching-to-sample. Better performance in species that cache more in the wild was also observed in tests of the same species on a radial maze (Kamil et al., 1994). Neuroanatomical studies showed that food storing and hippocampal volume are correlated in corvids (Basil et al., 1996, Healy & Krebs, 1992a).

Results of other studies comparing storing and nonstoring species of the Paridae (chickadees and titmice) provide a more mixed picture. Two storing and two nonstoring species of titmice did not differ on an operant test of SNMTS, or matching-to-object (Healy, 1995; Healy & Krebs, 1992b). However, in aviary tests of matching-to-sample where birds have to relocate a partially eaten peanut after a retention interval, storers performed better than nonstorers when the location of the peanut had to be discovered by random searching during the "study" phase (Clayton & Krebs, 1994). When the peanut was visible during the initial search, no difference between storers and nonstorers was evident (Clayton & Krebs, 1994; Healy & Krebs, 1992c). The difference appears to be due to nonstorers' inability to discriminate sites visited and found empty during initial search from the site containing the peanut (Clayton & Krebs, 1994). This failure to discriminate indicates proactive interference, as information presented prior to the target (sites visited while looking for the peanut) interferes with retention of target information (the site containing the peanut).

It is possible that differences among corvids are larger than those that might exist in the family Paridae (see Shettleworth, 1995), or that procedural differences between the tests performed on corvids and those performed on parids account for the different pattern of results. Failure to observe differences between species can also be due to failure of the testing paradigm to tap into aspects of cognition relevant to food-storing memory. It might be argued that more naturalistic tasks are more likely to require ecologically relevant aspects of cognition, and that aviary tasks are more naturalistic than are

tests conducted in operant chambers. In the results reviewed above it is clear that the testing context does not predict the occurrence of species differences, as such differences are found in both operant and aviary contexts in corvids. Although no differences in accuracy have been reported between parid species in operant tests, neither do all aviary tests yield differences between the species (see Shettleworth, 1995).

Juncos and chickadees are less closely related than are the parid or corvid species discussed above. Differences between juncos and chickadees might be easier to detect than those among closely related parids. The junco is a nonstoring species, whereas "nonstoring" parid species do store food under at least some restricted conditions (Clayton, 1995). It might be expected that larger memory differences can be found between storers and nonstorers than would be evident among birds that all store, but that do so to differing degrees.

Some evidence of superior spatial processing in chickadees has been found in previous comparisons of juncos and chickadees. Following presentations of a compound sample consisting of a location and a color, chickadees' matching response is controlled primarily by spatial location, whereas the matching response of juncos is controlled equally by location and color (Brodbeck, 1994; Brodbeck & Shettleworth, 1995). In operant tests with these compound stimuli, there was a nonsignificant trend indicating that the juncos had begun to forget spatial location after 20 s, whereas the chickadees had not (Brodbeck & Shettleworth, 1995).

On the basis of the comparisons presented, we predict that chickadees should perform better than juncos on tasks requiring spatial memory in a context where interference is high. That the proposed specialization of memory in chickadees should come to play in spatial memory is suggested by the importance of spatial memory in cache recovery, the relatively larger hippocampus, and the indications that the avian hippocampus is important for spatial cognition. Clayton and Krebs' (1994) experiment suggests that storing birds may be especially resistant to interference, as might be expected in an animal required to maintain a large number of items in memory simultaneously.

The results of comparisons between species are always subject to the criticism that a difference observed between species may be due to a peripheral difference between the species, such as motivation, response to captivity, or differences in motor ability rather than to a central cognitive difference between the species. Two prominent approaches have been put forward to deal with this difficulty: systematic variation (Bitterman, 1965, 1975) and the synthetic approach (Kamil, 1988). Dissociation (Olton & Shapiro, 1992), a technique more familiar to cognitive neuroscientists, is a related solution to the difficulty of establishing species differences in cognition. A dissociation is established when a manipulation (such as a brain lesion) interacts with a second manipulation, such as task or memory load. The logic of dissociation can be applied to species comparisons by considering *species* as one experimental variable. This logic has been implicit in studies in which food-storers were predicted to perform better than nonstorers on one kind of task but not another (e.g., Clayton & Krebs, 1994; Olson et al., 1995). In the studies that follow, juncos and chickadees are tested on two similar tasks that differ in cognitive demand, CSA (Experiment 2), and SNMTS (Experiment 3). In CSA the subject is required to respond consistently at a location other than the location most recently used; the animal must respond in an ABAB pattern. In SNMTS the subject is exposed to a sample stimulus, and after a delay must choose the stimulus not previously seen. Then an intertrial interval (ITI) ensues and the same or a different sample appears. There is no pattern to the order of responses required in SNMTS, because the sample stimulus is chosen at random on each trial. CSA may permit memorization of a response strategy that can be performed by rote (Brito, Yamasaki, Paumgartten, & Brito, 1987; Green & Stanton, 1989; Olton et al., 1979; Olton, Shapiro, & Hulse, 1984), whereas SNMTS requires flexible use of a rapidly updated spatial memory, where the response reinforced on a previous trial often conflicts with the response required on the current trial.

CSA performance was not sensitive to hippocampal damage in pigeons, whereas discrete-trials SNMTS conducted in a T-maze was sensitive to hippocampal damage (Reilly & Good, 1987). This indicates that CSA task is not hippocampus dependent and that on the basis of hippocampal function, we should expect no difference between the two species. Here we test both chickadees and juncos on CSA and SNMTS. If the relatively large hippocampus of chickadees confers an enhanced ability to do "hippocampal tasks," then chickadees should do better than juncos at SNMTS, but not CSA, according to the results of Reilly and Good (1987).

Experiment 2A: Continuous Spatial Alternation

Method

Subjects. Four chickadees and four juncos were captured, housed, and fed as in Experiment 1, with the following changes. Food was removed from the birds' cages shortly before the lights went out in the evening, and the birds were without food until testing began approximately 3 hr (chickadees) or 4 hr (juncos) following light onset the next day. Subjects were transported in the home cage and then admitted to the testing chamber via a trap door. Birds were returned to their home cages between sessions where water, but not food was available. Testing was concluded, and food returned to all birds at least 2 hr before light offset. Subjects were typically tested 6 days a week, in three or four sessions per day.

Apparatus. The four testing cages measured 69 × 40 × 53 cm and contained a rear perch and photobeam 51 cm (detector and emitter separated by 10 cm) from the front of the chamber, a second perch 37 cm from the front panel and two standard pigeon pecking keys (1.9 cm in diameter) centered 41 cm apart, 13 cm above the floor of the cage (Figure 1). A feeder was centered in the floor 5 cm from the front panel with a photobeam projecting over the 1.2-cm diameter opening to detect pecks into the feeder. The feeder held a mixture of ground sunflower seed with 10% by volume soft-billed bird food (Rolf C. Hagen, Toronto, Ontario, Canada). A perch was located 7 cm below the pecking keys, 2.5 cm from the front wall. The cages were mounted one above the other along one wall of the room in which the birds lived. Events in the testing cages were controlled by a computer in an adjacent room.

Training. Birds were trained to eat from the feeder and to peck each key when it was illuminated; then subjects were required to break the rear photobeam to illuminate a pecking key. Pecking the illuminated key resulted in a period of food access, the duration of which was

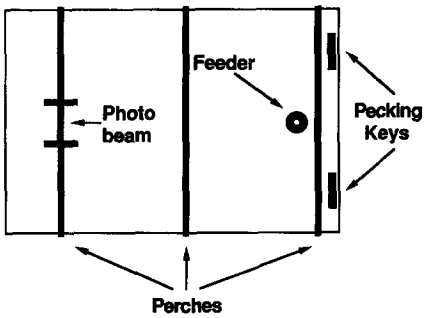

Figure 1. Sketch of the testing apparatus used in all behavioral studies described in this article, viewed from above (not drawn to scale). Note the photobeam on the rear perch, which animals had to break to start trials and to present tests after retention intervals. See text for measurements.

controlled by a timer that was triggered when the bird first broke the photobeam projecting across the feeder opening. Over the course of this training, feeder access time was reduced from 10 to 2 s. CSA training began at this point.

CSA training. Each session began with illumination of both pecking keys. The correct key on the first trial was determined by the last rewarded response from the previous session. Because each session consisted of an odd number of trials (31), the correct key alternated between sessions, as well as between trials. The first peck to either key extinguished the keylights. An incorrect response was followed by a 5-s time out and illumination of both keys again. No response was required to initiate these correction trials. This cycle repeated until the bird made a correct response. Data from correction trials are not reported. A correct response resulted in activation of the feeder, which remained activated for 2 s (first 70 sessions) or 1 s (all subsequent sessions) after the first break of the feeder photobeam. Following reinforcement, subjects had to break the photobeam in the rear of the box to illuminate the pecking keys and initiate the next trial. The correct key alternated following each reinforcement. Sessions were terminated after approximately 2 hr if birds did not complete the 31 trials. Each bird received 117 sessions of CSA training with a 0-s RI, followed by four sessions each with 10- and 20-s RIs, then 40 sessions with 30-s RI. The left panel of Figure 2 depicts the course of events in CSA.

Data analysis. Data were collapsed into blocks of 10 sessions of 30 trials each, excluding the first trial of each session. Because sessions were collapsed into blocks of 10 sessions, the last seven sessions of training with a 0-s RI were excluded from analyses. Training at 10- and 20-s RIs were not analyzed for the same reason. Finally, the first 10 sessions of training with a 30-s RI were not analyzed because they were considered warm-up sessions, during which subjects could adjust to the new RI and achieve stable levels of performance. Failure to complete all scheduled trials is mentioned only where a subject failed to complete more than 95% of all scheduled trials. Failure to complete trials meant that some blocks of 10 sessions contained less than the 300 scheduled trials for some birds. Hereafter, all percent correct scores were arcsine transformed prior to analysis to conform with the assumptions of analysis of variance (ANOVA). All RIs reported here are medians.

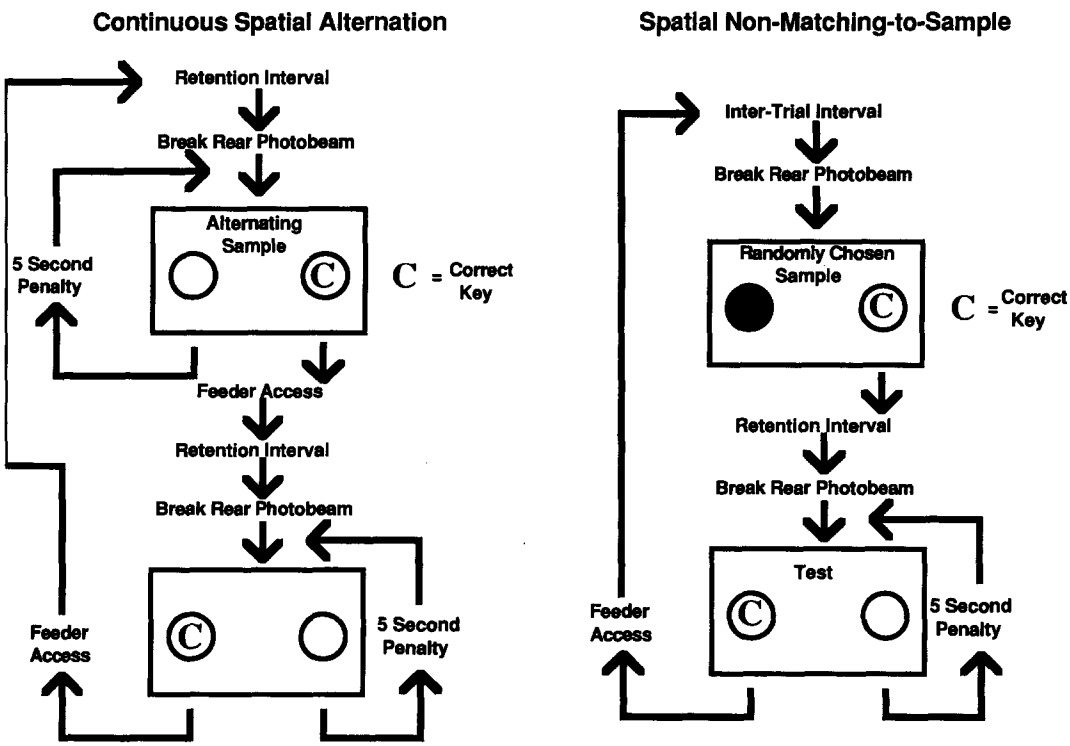

Figure 2. Flow chart of the events in continuous spatial alternation (CSA; left side) and spatial non-matching-to-sample (SNMTS; right side). The solid circle represents a dark key; open circles represent lit keys. Sample selection in CSA is patterned, whereas sample selection in SNMTS is random. The correction cycle ensures that every trial ends with a reinforced correct response.

Results and Discussion

Birds of both species improved with training and eventually performed well above the chance level of 50%, but the juncos consistently performed better than the chickadees (Figure 3). Repeated measures ANOVA (Species × Subject × Block) indicated a reliable effect of blocks of sessions, $F(10, 60) = 44.19, p < .01$, and species, $F(1, 6) = 7.08, p < .05$, but no interaction between species and blocks of sessions, $F(10, 60) = 1.42$.

Comparison to chance performance (50%) showed that both species matched reliably rather than alternating in the first 90 trials; chickadees: $t(3) = 6.33, p < .01$, juncos: $t(3) = 8.38, p < .01$. Chickadees alternated correctly on an average of 43.36% of trials, whereas juncos did so on 43.33% of trials. The species did not differ reliably from one another in this tendency to match, $t(6) = 0.02$.

Although the RI was programmed identically for all birds, the actual RI experienced depended on how quickly the birds sat on the rear perch after a reward. In the last block of training, chickadees selected significantly shorter RIs than did the juncos (M_{bcc} = 9.00 s; M_j = 20.75 s). This difference was evident throughout training as indicated by an effect of species, $F(1, 6) = 10.41, p < .05$. Both species took shorter RIs by the end of training, $F(10, 60) = 5.56, p < .01$, but species and block did not interact, $F(10, 60) = 1.05$. Chickadees' trials were therefore more closely packed in time than were those of the juncos, and the chickadees had to remember their previous response for a shorter period of time than did the juncos. Performance should decline as RI increases, so the difference between the two species in retention interval should have favored the chickadees.

During testing with 30-s RI, 1 chickadee missed 6% of scheduled trials in the last block, and 1 junco missed 13% of these trials. ANOVA was applied to the three blocks of testing with 30-s RI. Juncos continued to perform better than chickadees, $F(1, 6) = 9.32, p < .05$, and the performance of both species was stable across the three blocks of training: Block $F(2, 12) = .65$; Species × Block $F(2, 12) = 0.66$. Adding the enforced RI had the desired effect of both increasing RI and decreasing the difference between species in RI (M_{bcc} = 31.75 s; M_j = 35.50 s, in the last block of testing). The two species did not differ in RI experienced: species $F(1, 6) = 2.46$, block $F(2, 12) = 1.48$, Species × Block $F(2, 12) = 0.27$.

Juncos did better than chickadees in CSA, both during acquisition, and under testing at 30-s RI. It has been reported that CSA is not hippocampus dependent in pigeons (Reilly & Good, 1987). Chickadees with their large hippocampus would therefore not be predicted to perform better than juncos. However, juncos would not be predicted to perform better than chickadees either. The reliability of juncos' superior performance was therefore tested in Experiment 2B.

Experiment 2B

Method

We used 5 chickadees and 5 juncos captured and maintained as in Experiment 2A. In Experiment 2A, birds were initially trained to respond on the pecking keys by rewarding responses on only one of the two keys during a given session. This procedure may have encouraged matching to sample, rather than alternation. Here, each bird was given sessions on which the target key was chosen at random on each training trial, once they were reliably breaking the rear beam and pecking both keys. Feeder access was reduced more rapidly in this experiment and was at 1 s by the end of training. Birds were usually run 6 days a week, in two or three sessions per day. After completion of pretraining, subjects were given 70 sessions of CSA training identical to the trials conducted in Experiment 2A with the exception that feeder access was limited to 1 s. Birds were then tested at longer RIs, in blocks of 12 sessions of 10-s RI, 12 sessions of 20-s RI, and 32 sessions of 30-s RI.

Results and Discussion

The juncos performed slightly better than the chickadees during the first 70 sessions, but the difference was not so large as in Experiment 2A (Figure 4). Both species improved with training, $F(6, 48) = 29.88, p < .01$, whereas neither the difference between the species, $F(1, 8) = 1.98$, nor the interaction of species and training, was significant, $F(6, 48) =$

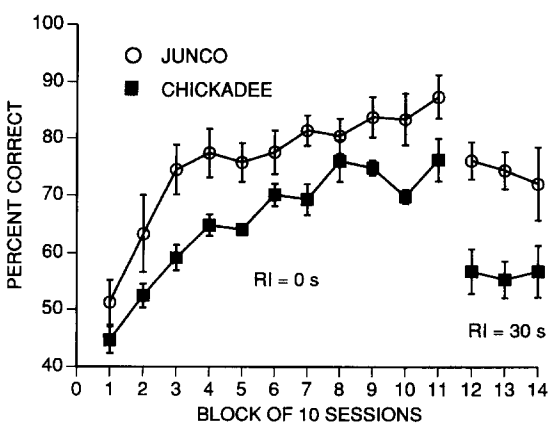

Figure 3. Acquisition of continuous spatial alternation by juncos and chickadees and performance at 30-s retention interval (RI), in blocks of 10 sessions (Experiment 2A). Error bars indicate standard errors.

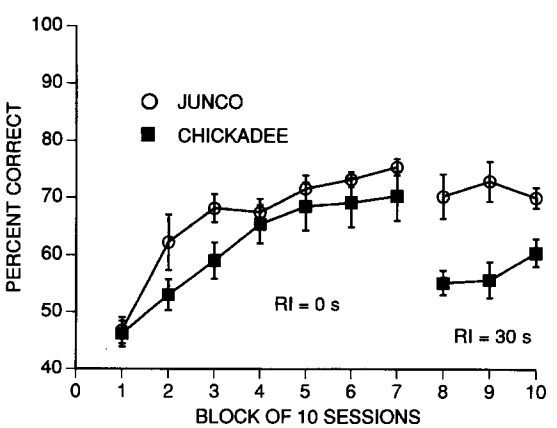

Figure 4. Acquisition of continuous spatial alternation by juncos and chickadees, and performance at 30-s retention interval (RI), in blocks of 10 sessions (Experiment 2B). Error bars indicate standard errors.

0.97. During the first block 1 chickadee missed 12% of scheduled trials, and 2 juncos missed 26% and 10%, respectively, of scheduled trials. During Block 7, 2 juncos missed 25% and 5% of scheduled trials, and chickadees took shorter RIs than did juncos (M_{bcc} = 7.60 s; M_j = 17.40 s). This difference in RI did not change during training: species $F(1, 8) = 6.54, p < .05$, block $F(6, 48) = 1.64$, Species × Block $F(6, 48) = 0.05$.

Juncos performed better than chickadees at the longer RIs. The first two sessions at each RI were considered warm-up sessions and were not included in the analysis. During the last block of testing with a 30-s RI, 2 chickadees missed 7% and 23% of scheduled trials, whereas juncos missed 7%, 7%, and 9% of these trials. The superiority of juncos during RI testing is indicated by a significant species effect, $F(1, 8) = 13.90, p < .01$, whereas no other effects were significant: block $F(2, 16) = 0.95$, Block × Species $F(2, 16) = 2.82$. Selection of RIs by the two species converged when the RI was increased (M_{bcc} = 32.60 s; M_j = 36.60 s, Block 10). Neither species, block, nor Species × Block had significant effects on RI, $F(1, 8) = 4.53$; $F(2, 16) = 2.44$; $F(2, 16) = 0.61$, respectively.

In Experiment 2B the juncos did not perform better than the chickadees during acquisition of CSA, as they did in Experiment 2A, although the difference between the species was in the same direction as it was in the previous experiment. This failure of replication may reflect the effects of the slight changes in training and in reward size, or the species difference in acquisition may be slight and not always detectable with the sample sizes used in these studies. There was almost no overlap between RIs taken by the two species during acquisition, as there was in Experiment 2A, and this may also have decreased the size of the difference between the species.

Despite the failure to replicate the difference between juncos and chickadees found during acquisition in Experiment 2A, the present results again demonstrate that juncos perform better on the CSA task, when the two species are equated for RI. Furthermore, juncos performed at least as well as chickadees during acquisition, even though they experienced longer RIs.

Previous results indicate the hippocampus is not critical in CSA. Reilly and Good (1987) tested pigeons with hippocampal lesions on CSA in an operant environment similar to that used in the work described here, with at least one possibly important difference. They did not require their subjects to move away from the pecking keys between trials. Under these conditions it may be easier for subjects to adopt postural or procedural solutions to the CSA task. This caveat aside, their result indicates that CSA is not sensitive to hippocampal damage. This result suggests that, at least on the basis of differences in hippocampal function hypothesized to result from the volumetric differences between juncos and chickadees, we should not expect to find that chickadees are superior at CSA.

Experiment 3A: Non-Matching to Sample

In corvids, dependence on stored food correlated with performance in an operant test of spatial non-matching-to-sample (Olson et al., 1995), as well as with nonmatching performance in a radial maze (Kamil et al., 1994). Although no difference was found between storing and nonstoring parids in an operant test of SNMTS (Healy, 1995), or in a radial maze analogue (Hilton & Krebs, 1990), there are no reports of superior performance by nonstoring parids on these tasks. Lesions of the pigeon hippocampus impaired SNMTS in an operant setting (Good & Macphail, 1994a), and in a T-maze (Reilly & Good, 1987). SNMTS performance is also sensitive to hippocampal damage in rats (e.g., McDonald & White, 1993; Wan et al., 1994). Taken together, these considerations suggest that chickadees should perform better than juncos in SNMTS.

Spatial NMTS can be conducted in the same environment used for CSA, using the same stimuli, manipulanda, and rewards. Many of the requirements of the two tasks are similar. The two tasks do differ in several ways, however (see Figure 2). In SNMTS, responding to the sample location is not rewarded, whereas in CSA the rewarded location from the previous trial serves as the sample stimulus for the current trial. In SNMTS there are discrete study and test portions to a trial. CSA lacks this separation of sample and test, because each test serves as a sample for the next test. In SNMTS the choice of sample is random, within some constraints. Therefore, the animal is sometimes rewarded for making the same response on consecutive tests, and other times is rewarded for making opposite responses on consecutive tests. In contrast, the sequence of correct responses is systematically patterned in CSA; each trial requires a response opposite the response previously used.

Method

Subjects and apparatus. The 5 chickadees and 5 juncos that had participated in Experiment 2B were used in this study. The birds started this experiment immediately after finishing their last session in the CSA study. They were maintained as described previously. The same apparatus was used.

Procedure. The procedure is diagrammed in the right panel of Figure 2. Each trial began with an ITI of either 35, 40, or 45 s chosen randomly without replacement such that each block of six trials had two ITIs of each type. A trial began immediately following the expiration of the ITI if the bird was breaking the photobeam. Otherwise the trial began the next time the bird broke the photobeam. The left and right keys were chosen to be the sample randomly without replacement, such that each block of six trials contained three samples of each type. The sample key was illuminated and the bird required to peck the sample three times (FR 3), at which point the keylight was extinguished. The bird was then required to break the rear photobeam to illuminate both pecking keys. Pecking (FR 3) the key not presented as the sample resulted in 1 s of feeder access. A single peck to the sample key prior to completion of the FR on the correct key resulted in a 5-s timeout period, and a correction cycle identical to that used in Experiments 2A and 2B. Data from correction cycles were not used. The trial cycle then began again with an ITI. Birds were given sessions with a maximum of 40 trials, not counting correction cycles, twice per day, 6 days a week until they had completed 1,000 trials. Sessions were terminated after about 1 hr if birds had not completed all 40 trials.

Results and Discussion

Both species performed well above chance from the beginning of training, although performance improved with blocks

of training, $F(3, 24) = 7.04, p < .01$ (Figure 5). Chickadees initially performed better than did the juncos, as is indicated statistically by a significant Species × Block of Trials interaction, $F(3, 24) = 3.21, p < .05$. The simple effect of species was not significant, $F(1, 8) = 4.63$. Juncos took significantly longer RIs, and this difference did not abate with training: species $F(1, 8) = 7.01, p < .05$, block $F(3, 24) = 1.40$, Species × Block $F(3, 24) = .65$. In Block 4 the group median RIs were 4.2 s and 8.0 s for chickadees and juncos, respectively.

Because only two response locations were used, each trial other than the first trial had either the same sample as the previous trial (Same trials), or the other sample (Different trials). The preceding trial can be a source of proactive interference (PI) on the current trial (Edhouse & White, 1988; Wilkie, 1986; Wright, Urcuioli, & Sands, 1986). Proactive interference is inferred from a comparison of performance on the Same and Different trials. The constraint on randomization of the sample ensuring that three instances of each sample occurred in each block of six trials resulted in there being 40% sample Same and 60% sample Different trials, on average. The right side of Figure 5 depicts trials broken down as Same and Different trials. Juncos performed least well on the Same trials initially, indicating that they were alternating from the last rewarded response, probably as a result of previous experience with CSA. Repeated measures ANOVA (Species × Block × Trial Type) showed that juncos improved more than chickadees on both types of trials: Block × Species $F(3, 24) = 3.24$, $p < .05$. Juncos showed the greatest improvement on Same trials: Species × Block × Trial Type $F(3, 24) = 3.97, p < .05$. The simple effects of block and trial type were significant, $F(3, 24) = 6.56, p < .01$; $F(1, 8) = 8.69, p < .05$. No other effects were significant.

It is striking that birds of both species performed well above chance in the first block of training. From the outset, chickadees performed better in SNMTS than they had ever done in CSA (Figure 5). Performance on the first 25 trials of SNMTS indicates how rapidly the birds learned the new task. Two chickadees performed perfectly on these first 25 trials, 2 were 96% correct (1 error), and 1 was correct on 68% of the trials. Although no junco performed at 100% on the first 25 trials, all but 1 got more than 80% of the trials correct. The 5th bird was correct on 60% of trials.

Block 7 of CSA (Experiment 2B) was the last block in which RI was 0, and is therefore the best comparison to make with the SNMTS performance. We compared the birds' performance during these trials of CSA (the culmination of about 2,000 trials of training), with performance on the first 100 trials of SNMTS (Figure 6). Chickadees improved more than juncos when SNMTS began, as indicated by a Species × Task interaction, $F(1, 8) = 12.82, p < .01$. The simple effect of species was not significant, $F(1, 8) = .54$, but the simple effect of task was significant, $F(1, 8) = 16.10, p < .01$. While juncos performed better than chickadees on CSA, the species difference abruptly changed direction when the birds began testing in SNMTS procedure. Both species took shorter RIs when they began SNMTS, $F(1, 8) = 14.28, p < .01$, probably because no time was taken consuming a reward following the sample in SNMTS, whereas samples were rewarded in CSA. Juncos took longer RIs in both tasks, $F(1, 8) = 6.49, p < .05$. Chickadees' mean median RI decreased from 7.60 s to 4.80 s, juncos' from 17.40 s to 11.60 s. The interaction of species and task was not significant for RI, $F(1, 8) = 1.74$. Although the juncos took longer RIs than did the chickadees during SNMTS, this is an unlikely cause of the species difference, because the juncos also took longer RIs during CSA, at which they did better than the chickadees. The near absence of acquisition of SNMTS in Experiment 3A and the comparison between performances on CSA and SNMTS indicate that SNMTS is easier for birds of both species. Transfer of training from CSA to SNMTS probably resulted from the correction cycle the birds were exposed to in CSA. When birds made errors in CSA, responding was not reinforced, but nonmatching to the erroneously chosen key was reinforced after a 5-s penalty period.

Experiment 3B: SNMTS at Longer RIs

Experiment 3A demonstrated that SNMTS is an easier task for both species than is CSA, and suggested that a reversal of the species difference favoring juncos observed in CSA might

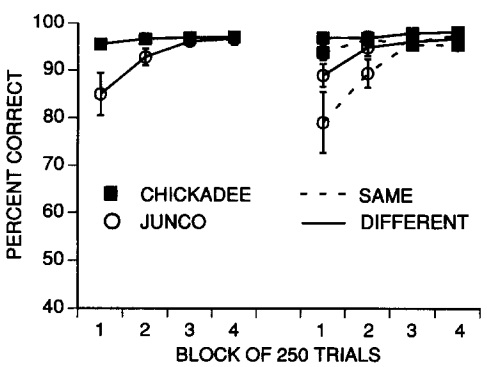

Figure 5. Acquisition of spatial non-matching-to-sample after training on continuous spatial alternation (Experiment 3A). The left side of the figure depicts overall percentage correct in blocks of 250 trials; on the right, trials are broken down into those in which the sample was the Same and those in which it was Different.

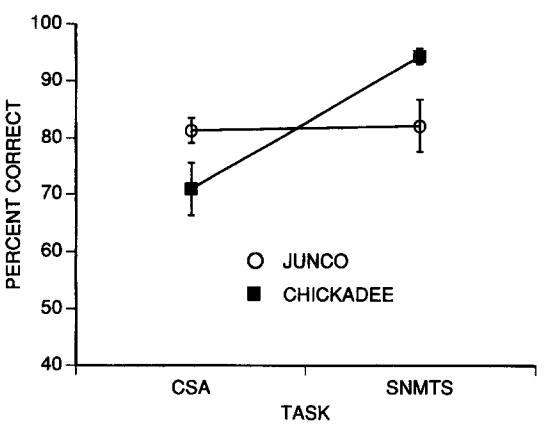

Figure 6. Performance of birds in the last block of continuous spatial alternation (CSA) during which retention interval equaled 0 s (Experiment 2B), and in the first 100 trials of spatial non-matching-to-sample (SNMTS) training (Experiment 3A).

occur in the case of SNMTS. We were unable to equate RI between the species in Experiment 3A, however, and the species difference was no longer evident by the end of training at RI of 0 s. The current experiment was therefore conducted to equate RI between the species, and to examine performance under more challenging conditions, where differences in memory are most likely to be revealed. Three birds of each species that had participated in a previous study of matching-to-sample (Hampton, 1995) were trained on SNMTS to achieve samples of 8 birds of each species.

Method

The 5 birds that had participated in Experiment 3A and had received 1,000 trials of SNMTS acquisition began testing with random RIs of 5, 15, 30, 60 s immediately. On each trial one of the four RIs was drawn without replacement from a pool containing two RIs of each duration at the beginning of sampling. When the pool of RIs was exhausted, the sampling process began anew. ITI was determined as before. The 3 birds of each species from the DMTS study were first given a minimum of 340 trials of SNMTS with 0-s RI and were not moved to random retention-interval testing until they had achieved at least 90% correct over the last four sessions. All birds received 1,200 trials of random retention-interval testing.

Results and Discussion

The first 400 trials of random retention-interval testing were discarded as training trials. Trials 401 to 1,200 were collapsed and analyzed. Chickadees performed better than juncos on overall percent correct as revealed by a significant species effect, $F(1, 14) = 4.77$, $p < .05$ (Figure 7, left side). Programmed RI had a significant effect on the performance of both species, $F(3, 42) = 238.05$, $p < .01$, but there was no interaction between species and programmed RI, $F(3, 42) = 2.14$. There was no significant species difference in median RI, $F(1, 14) = 3.46$, nor was there an interaction between programmed RI and species, $F(3, 42) = 0.55$. Programmed RI did, of course, have a significant effect on the actual RI taken, $F(3, 42) = 50759.67$, $p < .01$.

Chickadees did equally well on Same and Different trials, whereas juncos did less well on Different trials than on Same trials (Figure 7, right side). Analysis of performance as a function of trial type indicated no simple effect of species, $F(1, 14) = 2.84$, but an interaction of trial type with species, $F(1, 14) = 9.02$, $p < .01$. The simple effect of trial type approached significance, $F(1, 14) = 4.44$, $p < .10$. Programmed retention interval significantly affected performance on both trial types, $F(3, 42) = 266.64$, $p < .01$, but the interaction of this variable with species was not significant, $F(3, 42) = 1.90$. Trial type interacted with programmed RI, $F(3, 42) = 4.99$, $p < .01$, but the three-way interaction was not significant, $F(3, 42) = 0.76$.

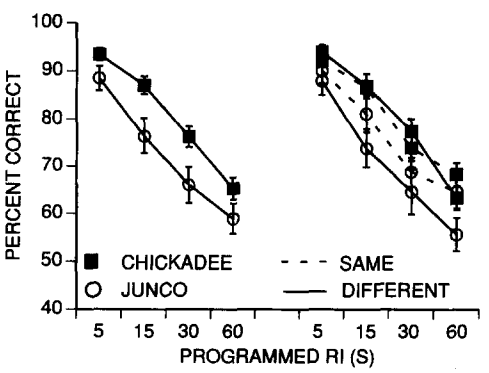

Figure 7. Spatial non-matching-to-sample performance during testing at four randomly presented retention intervals (RIs; Experiment 3B). The left side of the figure depicts overall percentage correct; on the right, trials are broken down into sample Same and sample Different trials.

Performance declines with increasing RI, as seen in the current experiment, and therefore the species difference obtained in Experiment 3A could be due to differences in RI alone. In the present experiment the two species experienced similar RIs at each programmed retention interval, thereby removing RI as a confounding variable. That the difference in overall accuracy is due at least in part to a difference in the ability to perform correctly on sample different trials may be diagnostic of differences in information processing between the two species. The juncos seem to be more vulnerable to proactive interference, where information from the previous trial intrudes into the current trial, than are chickadees.

Juncos perform better than chickadees on CSA, particularly at 30-s RI; upon transfer to SNMTS, chickadees immediately perform better than juncos. When tested on SNMTS with RIs from 5-60 s, chickadees do better than juncos at all RIs and juncos are more vulnerable to proactive interference than are chickadees. Non-matching-to-sample is a good test of working memory because the correct response varies randomly from trial to trial. Subjects have to update memory rapidly and repeatedly. In contrast, the correct response in CSA is determined systematically. It is possible that the systematic structure of CSA permits a solution that depends less on working memory, and more on reference memory (see Brito et al., 1987; Olton et al., 1979). However, it is difficult to imagine how a subject could solve the CSA task without using working memory at all, given that the appropriate response on the current trial always depends on the response made on the last trial.

Although CSA and SNMTS are often lumped together as delayed-response tasks, differences between them have been documented previously. Olton et al. (1979) summarized hippocampal lesion studies using delayed response tasks, and characterized the tasks used in those studies as being either continuous or discrete. CSA is a continuous task, because the correct response on each trial depends on the response made on the previous trial, in a patterned manner. During SNMTS, in contrast, the studied sample is chosen randomly on each trial, making this a discrete trials task. Olton et al. (1979) concluded that hippocampal deficits are always observed when the sample is randomly chosen on each trial as in SNMTS, but often not observed in the case of continuous tasks, like CSA. In support of their argument, Olton et al. (1984) showed that intact hippocampal function is not required for successful serial pattern performance. Brito et al. (1987) tested rats on both CSA and SNMTS in a T-maze. CSA performance was less sensitive to changes in retention interval than was SNMTS performance. On the basis of this difference in sensitivity to

delay interval, Brito et al. (1987) argued that performance of SNMTS depends more on working memory than does CSA.

During development, rats can learn both CSA and a position habit before they are able to learn SNMTS (Green & Stanton, 1989). This developmental dissociation suggests that the position habit and CSA share a common process, possibly reference memory, and that these tasks differ from SNMTS in cognitive requirements. The effects of hippocampal lesions in pigeons lead to the same conclusion. In pigeons, a hippocampal deficit is found only in SNMTS, not in CSA (Reilly & Good, 1987).

The preceding considerations suggest that chickadees, with their larger hippocampus, should not perform better than juncos in CSA. The superiority of juncos in CSA, however, remains to be explained. In the experiment of Reilly and Good (1987), hippocampus-lesioned birds performed better, but not significantly so, than did either control lesioned or unoperated subjects. Jackson and Strong (1969) reported that hippocampal lesions enhanced the ability of rats to learn to alternate responding on two operant levers (CSA), indicating that hippocampal function can interfere with successful CSA performance. It is possible that in the present studies hippocampal memory interfered with the execution of an alternative strategy that birds use in CSA.

Experiment 4A

Experiment 3B showed that black-capped chickadees are better at operant SNMTS than are juncos. This result, combined with those from Experiment 1 showing that chickadees have a relatively larger hippocampus than do juncos, suggests that the species ordering of performance in SNMTS reflects differences in spatial cognition caused by differences in hippocampal volume between the species. In Experiments 2A and 2B juncos performed better than chickadees on CSA. Continuous spatial alternation is not dependent on the hippocampus in pigeons (Reilly and Good, 1987). Therefore, in contrast to the impairment expected in SNMTS following lesions, no impairment is expected in the CSA task following lesions.

The current experiment was designed to test the hypothesis that subjects were using their hippocampus to solve the SNMTS task. If damage to the hippocampus does not affect SNMTS performance in the experimental setting used in Experiment 3B, the argument relating performance to relative hippocampal volume would clearly be false. Experiment 2B also showed that juncos were more prone to intrusions of information from the previous trial into the current trial. It is possible that resistance to such intrusions is also a product of hippocampal function (Shapiro & Olton, 1994). The effect of hippocampal lesions on intrusion of information from the previous trial was therefore also examined in the current experiment.

Method

Subjects. Birds used in this study had participated in Experiment 3B. They were housed and fed as described previously. Subsequent to completing 1,200 trials of retention interval testing (5, 15, 30, and 60 s) in Experiment 3B, each bird was operated on. Four juncos and 4 chickadees were assigned to the hippocampal lesion group (HP), and 3 juncos and 4 chickadees to the control group (CTRL). One HP junco failed to respond following the lesion and was therefore dropped from the experiment. One HP chickadee and 2 CTRL chickadees did not survive the course of the experiment, and are therefore not included. Complete data on 3 HP juncos, 3 HP chickadees, 3 CTRL juncos, and 2 CTRL chickadees are therefore presented below.

Surgery. Subjects were deprived of food for about 1 hr to empty the stomach, weighed, and anesthetized by injection of a combination of 25 mg/kg ketamine and 50 mg/kg xylazine into the pectoral muscle. Once anesthesia was confirmed, the bird was placed in a rodent stereotaxic instrument modified according to Vaccarino (1986) in an aseptic area. The feathers were removed from the middle of the head and an incision was made. A pointed scalpel was then used to cut a rectangular window in the skull, which was removed. Bilateral hippocampal lesions were produced by aspirating tissue through a squared-off 18-gauge syringe needle. No tissue was aspirated from control subjects, but because the central sinus was inevitably severed when lesions were made, this blood vessel was also severed in control subjects. Dissolvable sponge was placed over the wound up to the level of the upper surface of the skull. The skin was then pulled over the opening and sealed with cyano-adhesive. The injured area was treated with antibiotic, and the bird was permitted to recover in a warm environment. Subjects had free access to food for 5 days before resuming participation in the experiment.

Testing. Birds resumed testing with the four retention intervals. Each bird completed 1,000 test trials before it was killed for histology.

Histology. Birds were deeply anesthetized and perfused transcardially with 0.8% saline followed by 10% formalin in saline. The fixed brain was removed from the cranium and stored for several days in the refrigerator in fixative. Brains were then transferred to 30% sucrose, 10% formalin and kept refrigerated until they sank. Sections were made with a freezing microtome at 40-μm intervals. Every eighth section (320-μm intervals) was mounted and stained with cresyl violet. Sections were then examined using a microscope and an enlarger. Lesions were drawn onto images previously made using brain sections prepared for Experiment 1.

Results and Discussion

Histology. The hippocampus was damaged in every HP subject, while caudal area parahippocampalis was substantially spared (Figure 8). Lesions intruded into the lateral ventricles, and sometimes into the underlying neostriatum (N). Lesions also typically extended further anterior than does the hippocampus, at the level of the surface of the brain. This resulted in damage to the anterior hyperstriatum accessorium (HA). This area receives projections from the thalamofugal visual pathway, one of two visual pathways in birds (Horn, 1985). It is therefore of some concern that most birds had damage to this region. However, lesions of hyperstriatum accessorium, used in the operated control group of Sherry and Vaccarino (1989), had no effect relative to unoperated controls on either spatial on nonspatial tasks. Effects of lesions to this region are generally subtle or nonexistent (Ebbesson, 1980). In contrast, manipulation of the other of the two avian visual pathways, the tectofugal pathway, results in severe memory impairments. Unlike the thalamofugal pathway, the tectofugal pathway is completely crossed. By covering one of a marsh tit's (*Parus palustris*) eyes temporarily, Sherry, Krebs, and Cowie (1981) showed that memories for the location of caches were stored in only one half of the brain, and this must have taken place by way of the tectofugal visual pathways (see also Clayton, 1993).

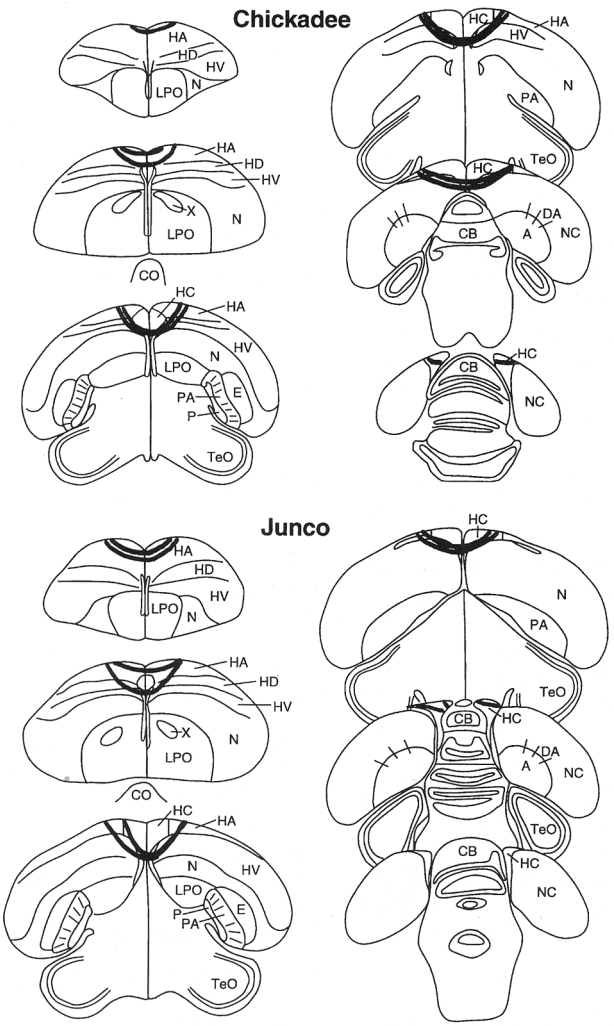

Figure 8. Hippocampal lesions in chickadees (top) and juncos (bottom; Experiment 4A). Lesions were drawn with the aid of an enlarger after inspecting sections under a microscope. HA = hyperstriatum accessorium; HD = hyperstriatum dorsale; HV = hyperstriatum ventrale; N = neostriatum; LPO = lobus parolfactorius; CO = chiasma opticum; X = area X; HC = hippocampal complex; E = ectostriatum; PA = paleostriatum augmentatum; P = paleostriatum primitivum; TeO = optic tectum; A = archistriatum; DA = tractus archistriatalis dorsalis; CB = cerebellum; NC = neostriatum caudale.

Taken together, the foregoing evidence indicates that damage to the hyperstriatum accessorium in conjunction with damage to the hippocampus should not substantially complicate interpretation of any memory deficits observed following the lesions.

Behavior. For the first few days after recovery from surgery, the birds typically completed fewer trials than normal, and accuracy was generally lower than normal. For this reason, the first 200 trials of SNMTS following the lesions were discarded as recovery trials. The remaining 800 trials were collapsed and analyzed as in the previous studies, providing about 200 trials at each retention interval for each bird. Before the lesions juncos performed slightly less well than did the chickadees, and lesion groups performed similarly to the control groups (Figure 9, left side). ANOVA (Group × Species × Subject × RI) applied to the data from this phase of the experiment revealed a significant effect of programmed RI only, $F(3, 21) = 183.76$, $p < .01$. No other effects were significant.

Following lesions, performance by both species in the HP lesion groups was impaired (Figure 9, right side). The effect of group, programmed RI and their interaction were all significant, $F(1, 7) = 18.89$, $p < .01$; $F(3, 21) = 70.98$, $p < .01$; $F(3, 21) = 8.90$, $p < .01$. No other effects attained significance.

Just as potential differences between species in actual RI experienced can complicate interpretation of species differences, differences in RI between the lesion groups would complicate interpretation of the effects of the lesions. However, there was no difference between species or lesion groups. Before the lesion the only significant effect on RI was that of programmed RI, $F(3, 21) = 35254.26$, $p < .01$. The pattern of statistical results was the same after surgery; only programmed RI affected RI, $F(3, 21) = 26754.66$, $p < .01$. The absence of a difference in RIs between lesioned and control animals suggests that the lesions did not impair perception or coordination. All subjects were able to perch promptly between the rear photobeams and to perceive, approach, and respond on the pecking keys.

The lesion affected the performance of chickadees on both sample same and sample different trials (Figure 10, top panel). During the prelesion phase of the experiment, no effects were significant other than that of programmed RI, $F(3, 9) = 177.49$, $p < .01$. Following the lesions, there was a significant effect of group, $F(1, 3) = 58.88$, $p < .01$, as well as of programmed RI, $F(3, 9) = 16.58$, $p < .01$, although the interaction was not significant, $F(3, 9) = 1.89$. A substantial difference between sample Same and sample Different trials, not evident in the control group, occurred in the HP group. Hippocampal lesions impaired performance on Different trials more than it affected SAME trials, shown by a significant interaction of Group × Trial Type, $F(1, 3) = 25.30$, $p < .05$. This pattern of results is reminiscent of the pattern of differences found between chickadees and juncos in Experi-

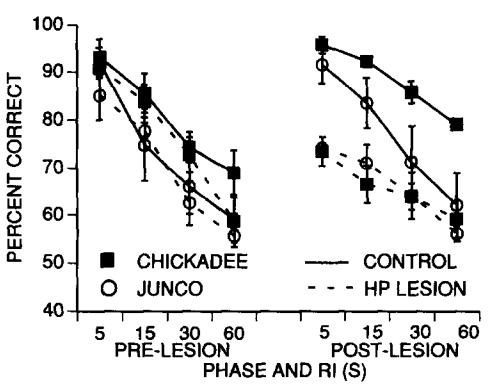

Figure 9. Spatial non-matching-to-sample performance by juncos and chickadees in the hippocampal (HP) lesion group and the control lesion group, before (left side) and after (right side) surgery (Experiment 4A). RI = retention interval.

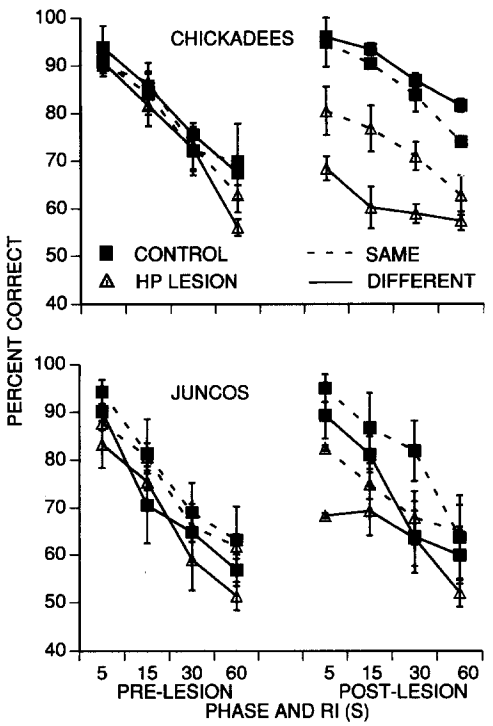

Figure 10. Spatial non-matching-to-sample performance by chickadees (top) and juncos (bottom) in control and hippocampal (HP) lesion groups, before and after surgery (Experiment 4A). Data are broken down into sample Same and sample Different trials. RI = retention interval.

ment 3B. Hippocampal lesioned chickadees behave like intact juncos, compared with control chickadees; however, the difference is larger between lesioned and control birds than it is between the two species. The simple effect of trial type was also significant, $F(1, 3) = 15.69, p < .05$, but no other effects were significant.

The pattern of results for the juncos is similar to that observed in the chickadees, but the differences are less dramatic (Figure 10, lower panel). Performance drops on both types of trials following the lesions, particularly at shorter RIs, where the performance of controls is well above the floor of 50% correct. Two effects were significant for juncos prior to surgery: programmed RI, $F(3, 12) = 73.74, p < .01$, and trial type $F(1, 4) = 35.54, p < .01$. The occurrence of an effect of trial type in the juncos prior to the lesion again supports the argument that intact juncos behave similarly to hippocampal lesioned chickadees. No other effects were significant prior to surgery.

Following surgery juncos demonstrated a significant effect of programmed RI, $F(3, 12) = 70.32, p < .01$, and programmed RI and group interacted significantly, $F(3, 12) = 9.90, p < .01$. The simple effect of group, however, was not significant, $F(1, 4) = 2.63$, indicating that the lesion affected performance more at short retention intervals than it did at long ones. The effect of trial type was also significant after the lesion, $F(1, 4) = 33.55, p < .01$. No other effects were significant.

The effects of hippocampal lesions on performance in the SNMTS task clearly indicate that the hippocampus is important for successful performance in this task. This result supports the argument that the superiority of chickadees in the SNMTS task results from differences in hippocampal function between the two species. This argument gains further support from examination of the effects of hippocampal lesions on the pattern of interference effects. Intact juncos show more interference from the previous trial than do intact chickadees; lesions of the hippocampus have the effect of depressing overall performance in both species, and these lesions result in intrusions of information from the previous trial in normally resistant chickadees.

The results of this experiment are consistent with theories specifying a role for the hippocampus in spatial memory (Nadel, 1991), working memory (Olton et al., 1979), and in resistance to interference (Mayes, Pickering, & Fairbairn, 1987; Shapiro & Olton, 1994; Winocur, 1979). These theories are primarily based on work with mammals, and the similarity of hippocampal lesion effects in birds to those found in mammals therefore suggests similarity in the function of the avian hippocampus with that of mammals (Bingman, 1992; Good & Macphail, 1994a; Macphail, 1993; Reilly & Good, 1987, 1989).

Experiment 4B

The results of the previous experiment are consistent with the simple hypothesis that chickadees perform better than juncos on tasks that require an intact hippocampus. The present experiment further tests this hypothesis, using a second task, CSA. In the previous experiment we predicted and found an impairment in SNMTS resulting from hippocampal lesions. Here we predict that hippocampal lesions will not affect CSA, in accord with the results of a lesion study in pigeons (Reilly & Good, 1987), and because juncos do better in CSA than do chickadees.

Method

Eight chickadees and 8 juncos were captured and housed as in previous experiments. The birds were trained as in Experiment 2B, with the following changes. Each subject was given 60 sessions of CSA training with a 0-s RI, followed by 5 sessions with a 10-s RI, 4 sessions with a 20-s RI, and 34 sessions with a 30-s RI. Four birds of each species were then given hippocampal lesions, and the remaining birds received control surgery, as in Experiment 3B. Following recovery from surgery as in Experiment 3B, birds received 34 sessions of CSA with a 30-s RI, 30 sessions with a 0-s RI, and finally 14 sessions where the RI was again 30 s. At the conclusion of testing subjects were killed, and histology was conducted as in Experiment 2B. One chickadee in the control group died after completing three blocks of testing after surgery. This bird was included in all analyses for which complete data were available, but not for the analysis of performance in the last 4 blocks of testing following surgery.

Results and Discussion

Histology. The lesions (Figure 11) were similar to those obtained in Experiment 4A, with the following exceptions. In 1 chickadee and 1 junco there was slight damage to the dorsal surface of the cerebellum. There was also slightly more

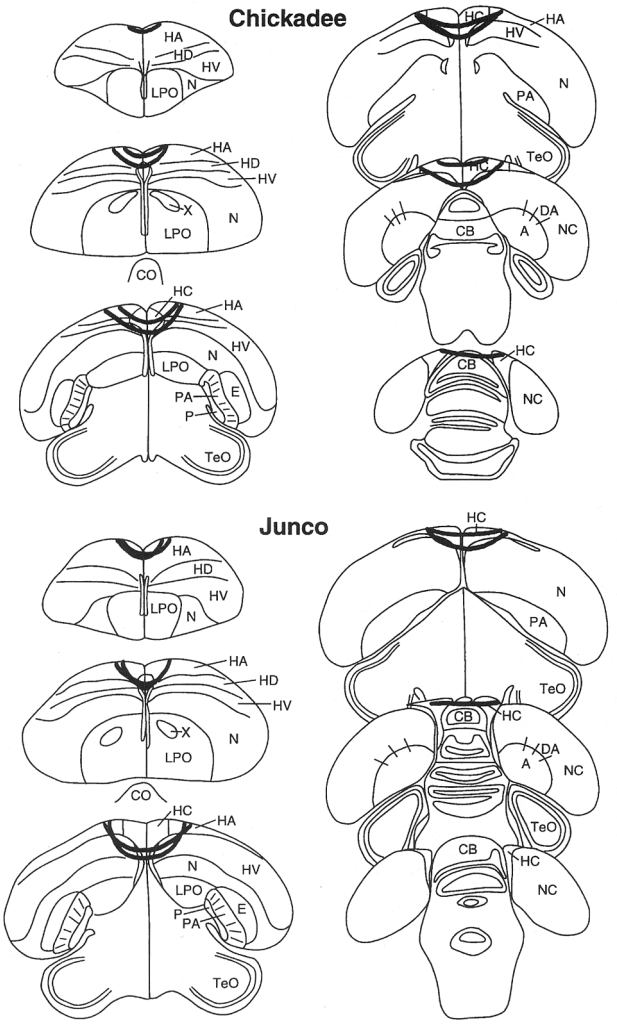

Figure 11. Hippocampal complex lesions in chickadees (top) and juncos (bottom; Experiment 4B). HA = hyperstriatum accessorium; HD = hyperstriatum dorsale; HV = hyperstriatum ventrale; N = neostriatum; LPO = lobus parolfactorius; CO = chiasma opticum; X = area X; HC = hippocampal complex; E = ectostriatum; PA = paleostriatum augmentatum; P = paleostriatum primitivum; TeO = optic tectum; A = archistriatum; DA = tractus archistriatalis dorsalis; CB = cerebellum; NC = neostriatum caudale.

damage to the medial portion of hyperstriatum ventrale in the present study.

Behavior. To make even blocks of 10 sessions, we discarded the data from the first four sessions on each 34 or 14 sessions of 30-s RI. Performance of animals prior to surgery was similar to that of the birds in Experiment 2B (Figure 12). During acquisition (RI = 0 s), the only significant effect was that of blocks of training, $F(5, 60) = 46.55, p < .01$. Because some chickadees took atypically long RIs during the beginning of training, the only significant determinant of actual RI was the interaction of Species × Blocks, $F(5, 60) = 3.20, p < .05$. During testing at RI 30 s, a species difference was revealed, $F(1, 12) = 15.74, p < .01$, while no other results were significant. Once again, juncos performed more accurately than chickadees at this RI. No factor had a significant effect on actual RI during these blocks of testing at RI 30 s.

Hippocampal lesions reduced accuracy in both species relative to their controls. Lesion group had a clear effect on performance during testing at RI 30 s after surgery, $F(1, 12) = 21.23, p < .01$, and the species effect was still evident, $F(1, 12) = 5.31, p < .05$. No other main effects or interactions were significant. There were no significant differences in RI. The effect of lesion group persisted in both species tested at RI 0 s, $F(1, 12) = 32.77, p < .01$, but there was no longer a significant effect of species, or any other factor. During these blocks of trials, juncos took significantly longer RIs than chickadees, $F(1, 12) = 9.04, p < .05$, but there was no other significant determinant of RI.

In the final block of testing, the same effects on performance were evident as observed during previous testing at RI 30 s following the lesions. There was a significant effect of both species and group, $F(1, 11) = 10.10, p < .01$; $F(1, 11) = 16.35$, $p < .01$. The interaction of these factors approached significance, $F(1, 11) = 4.30, p < .10$. During this block of testing, juncos took longer RIs than did chickadees $F(1, 11) = 5.04$, $p < .05$, but there was no other significant determinant of RI.

The impairment of CSA performance by hippocampal lesions was unexpected on the basis of the results of Reilly and Good (1987), which showed that CSA was not hippocampal dependent in pigeons. It is probable that the inclusion of the rear perching requirement in the current experiment can explain the difference between the present results and those from pigeons. Forcing subjects to the back of the operant chamber between responses makes adoption of a postural mediation strategy more difficult. Most similar tests conducted in mammals do reveal impairments following hippocampal damage (Gray & McNaughton, 1983), with some exceptions including cases of enhanced performance following hippocampal lesions (Jackson & Strong, 1969). The present results therefore agree with the bulk of the mammalian literature, but contradict the only other study of this type conducted in birds. Whatever the reason for the discrepancy between these results

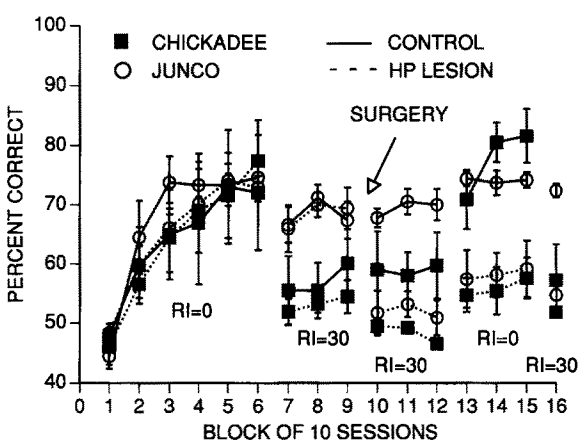

Figure 12. Continuous spatial alternation performance by juncos and chickadees in the hippocampal (HP) lesion and control groups, before and after surgery and at 0-s and 30-s retention intervals (RIs; Experiment 4B).

and those from pigeons, the fact that juncos have a relatively small hippocampus and yet perform better than chickadees on a hippocampus-dependent task is puzzling.

General Discussion

This work is part of a broader program of research examining the relationship between food storing and hippocampal function. This work can be characterized as testing, in part, the hypothesis that food-storing birds should perform better than nonstoring species on memory tasks that depend on the hippocampus (Krebs, 1990; Sherry, Jacobs, & Gaulin, 1992; Shettleworth, 1995). Here we have examined the relationship between food storing, hippocampal volume, hippocampal lesions, and performance in two tests of memory in a single series of studies. In Experiment 1 we confirmed the result expected from previous comparisons of food storing and nonstoring bird species: Black-capped chickadees have a relatively larger hippocampus than dark-eyed juncos. This result contributes to a growing body of literature demonstrating a relationship between the spatial memory challenges faced by animals, investment in neurons making up the hippocampus, and spatial cognition (Gaulin, 1995; Sherry et al., 1992). This difference in relative hippocampal volume between black-capped chickadees and dark-eyed juncos found in laboratory-kept subjects suggests that comparisons of spatial cognition between these two species in the laboratory should reflect differences in hippocampal function. Enhancement of some feature of hippocampal function is predicted both on the grounds that chickadees have been exposed to selection for good spatial memory over many generations, and on the observation in extant individuals of a relatively larger hippocampus.

Further consideration of the demands placed on food-storing birds by the need to remember the location of many cached items suggests more detailed predictions about the possible specialization of chickadees' spatial memory. Food-storing birds have to maintain a constantly changing catalogue of active cache sites. They should be able to recall accurately the location of caches that have not yet been recovered, while avoiding revisits to cache sites they have already depleted or found empty. Return to an active cache site results in reinforcement. The normal effect of reinforcement is to increase the probability of repetition of the reinforced behavior, but this is exactly the effect that would be detrimental to the food-storing bird, because returning to a depleted cache site is a waste of time and energy. This suggests, then, that food-storing birds should show an unusually developed immunity to the interfering effects of reinforcement in working-memory tasks. The pattern of results in SNMTS is consistent with this suggestion (Experiments 3A, 3B). Chickadees performed better than did juncos on this spatial working-memory task during acquisition, and during testing over many trials at four retention intervals. Chickadees were also less likely to base their choices on the location that had been rewarded on the previous trial. The effects of hippocampal lesions in Experiment 4A were consistent with the differences between chickadees and juncos on SNMTS. Lesions attenuated performance in the task overall, but also resulted in a specific increase in the intrusion of information from the previous trial in chickadees. These results support the argument that the difference in performance observed between juncos and chickadees in SNMTS results from a difference between the species in hippocampal function.

CSA shares many features with SNMTS, but juncos perform better than chickadees in this task (Experiments 2A and 2B). This dissociation shows that the difference in cognitive ability between the two species is circumscribed. The reversal of the direction of the species difference on the two tasks also suggests that a trade-off occurs; being particularly adept at one task may exclude superior performance at the other. Successful CSA performance is hippocampal dependent in juncos and chickadees, however (Experiment 4B). The species differences reported here cannot, therefore, reflect hippocampal function generally. It is likely that the hippocampus is involved in many cognitive functions, and only a subset of these functions is closely related to food storing. Lesions generated by the same method used in the present studies impair spatial working memory in chickadees and juncos while leaving intact memory for color in an otherwise identical delayed matching task (Hampton & Shettleworth, 1996). It is therefore not the case that these lesions affect memory generally. The unexpected dependence of CSA on hippocampal function in birds indicates that the relationship between food storing, hippocampal volume, and performance in tests of memory is not a simple one. It is possible that the hippocampus is necessary, in a permissive sense, for successful CSA performance, but that it does not drive the difference in performance between chickadees and juncos in this task.

At present it is not clear why CSA is so difficult, or why juncos do better than chickadees on this hippocampus-dependent task. Some possibilities are worthy of consideration, however. The repetition of stimuli without ITIs in CSA may produce high levels of intertrial interference compared with SNMTS where trials are separated from one another by an ITI. High interference can potentially account for the relative difficulty of CSA, but not for the pattern of species differences. The results of Experiment 3 indicated that chickadees are more resistant to interference than are juncos. Chickadees should therefore do better than juncos in CSA due to the high levels of interference; the opposite result is obtained.

In SNMTS the sample stimulus the animal is required to remember is not reinforced, whereas in CSA the animal always has to avoid the most recently rewarded location. It is possible that this is a crucial difference between the two tasks, although we do not see how to use this difference to account for the complete set of results. In Experiment 2A, both species tended to repeat responses to a recently rewarded location early in training, indicating that both species initially use a win-stay strategy during training in the operant chamber. Furthermore, the two species did not differ in the extent to which they used this strategy. After training in CSA, a win-shift strategy dominates, demonstrating flexibility in the choice of strategy in both species. In SNMTS (Experiment 3), chickadees were able to ignore information from previous trials, whereas juncos tended to respond to the location rewarded on the previous trial. This tendency to choose a recently rewarded stimulus is

exactly opposite the win-shift strategy that juncos use effectively in CSA.

At present, the critical differences between CSA and SNMTS remain undetermined. Previous workers have suggested that CSA performance depends more on habit, or reference memory, whereas SNMTS depends more on working memory (Brito et al., 1987; Olton et al., 1979; Olton et al., 1984). Although the application of this distinction is not without difficulties, we offer some suggestive evidence that may be compatible with this view. Observation of juncos and chickadees during shaping for operant tasks suggests that juncos are relatively strict rote learners, whereas chickadees make more flexible use of information acquired in training. Juncos' responses appear more stereotyped. Because successful CSA performance can result from relatively stereotyped responding compared with SNMTS, this putative difference in how the birds learn may in part explain the differences in performance between the two tasks. Future research should explore this notion directly.

CSA and SNMTS may depend to different extents on working memory, and likely also differ in their relationship to the function of particular brain regions. In mammals frontal cortex appears to be involved in fine motor control, discrimination reversal, the production of sequential behavior, and performance on learning tasks (Kesner, 1985; Kolb, 1984). The frontal cortex is involved in the organization of behavior—the development of response rules, skill learning, and the use of memory. In contrast, the hippocampus is important for memory of specific events. The two neural systems interact in a working-memory task where specific rules have to be applied to recently acquired information (Winocur, 1991; Winocur & Moscovitch, 1990).

The posterodorsolateral neostriatum (PDLNS) of the bird brain may be comparable to the frontal cortex of rats, based on strong dopaminergic innervation (Divac, Mogensen, & Bjorklund, 1985). Lesions of the PDLNS impair performance of CSA, while sparing performance of a color discrimination and a brightness discrimination (Mogensen & Divac, 1982, 1993). No data are available regarding the role of the PDLNS in SNMTS. Because the frontal cortex and hippocampus appear to serve different cognitive functions (Winocur, 1991; Winocur & Moscovitch, 1990), and both structures may exist in the bird brain, comparisons of PDLNS function and the function of the avian hippocampus may shed light on the differences observed between juncos and chickadees in CSA and SNMTS. Performance of CSA may involve the execution of a serial pattern stored in reference memory, and this serial pattern may function independently of of working memory, as argued by Olton et al. (1979) and Olton et al. (1984). According to this argument, CSA depends on the cognitive processes permitting sequentially structured behavior that are ascribed to frontal cortex (Kesner, 1985; Kolb, 1984). If the above arguments are sound, it might be predicted that while chickadees show greater investment in hippocampal tissue, compared with juncos, the reverse pattern might be true regarding the PDLNS. Alternatively, as suggested by the results of Jackson and Strong (1969) showing improved CSA performance following hippocampal lesions, hippocampus-based response strategies may interfere with strategies supported by the frontal cortex and appropriate to solution of the CSA task. The dependence of chickadees on hippocampal function may impair their ability to adopt the appropriate frontal-type strategy suitable for CSA. Our results show that CSA is not independent of hippocampal function, however, even if CSA and SNMTS depend on the hippocampus to different degrees or in different ways.

Volume is a crude measure of the capabilities of the hippocampus, just as aspiration of hippocampal tissue is a crude method of interfering with these capabilities. Stimulated by the many observations of species and sex differences in relative hippocampal volume associated with ecological demand on spatial memory, investigators have been trying to define these differences more narrowly. Food-storing birds in two separate families have cells containing the calcium-binding protein calbindin in the dorsal and medial hippocampus, where such cells are not found in nonstoring species (Montagnese, Krebs, Székely, & Csillag, 1993). Food-storing birds also have higher levels of nitric oxide synthase than do nonstoring birds (Székely & Krebs, 1993). More neurons are recruited into the rostral portion of the hippocampus of adult chickadees than are found in other parts of this structure (Barnea & Nottebohm, 1994), suggesting a possible distinct role for this part of the hippocampus in memory for the location of caches. Our results indicate that there is no simple relationship between the effects of enlargement of the hippocampus as a whole and the effects of damage to the hippocampus. Of the four hypotheses presented to describe the relationship between hippocampal volume and memory, only the fourth remains viable. Enlargement of the hippocampus in food-storing birds does not result in enhancement of all hippocampal function, but rather in enhancement of a yet to be described subset of hippocampal functions. Identification of the relevant set of hippocampal functions affected in food-storing birds remains a major goal of researchers in this area. Similarly, neuroanatomical comparisons of food-storing and nonstoring species need to refine our picture of how the hippocampi of these groups of species differ (see Clayton, 1995, and Clayton & Krebs, 1995, for a review of the current status of this work).

Natural selection, acting over hundreds of generations, likely brings a sophistication to brain "surgery" unattainable by the most diligent neurosurgeon working over a single lifetime. By capitalizing on differences between related species in the cognitive demands required for survival in their unique ecological niches, it may be possible to gain a view of the results of this sophisticated form of natural surgery. Exploitation of the natural variation in both the structural and functional properties of the nervous systems of similar species facing divergent cognitive demands promises to provide unique insights, complementary to those gleaned from more traditional approaches.

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The Publications and Communications Board has opened nominations for the editorship of *Developmental Psychology* for the years 1999–2004. Carolyn Zahn-Waxler, PhD, is the incumbent editor.

Candidates should be members of APA and should be available to start receiving manuscripts in early 1998 to prepare for issues published in 1999. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self nominations are also encouraged.

To nominate candidates, prepare a statement of one page or less in support of each candidate and send to

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