

The role of the avian hippocampus in spatial memory

Euan M. Macphail*

University of York

Avian hippocampal function is surveyed, using data drawn from three areas: conventional laboratory paradigms, pigeon navigation, and food-storing. Damage to the avian hippocampus disrupts performance in laboratory tasks that tap spatial learning and memory, and also disrupts both pigeon homing and cache recovery by food-storing birds. Further evidence of hippocampal involvement in food-storing is provided by the fact that the hippocampus of food-storing birds is selectively enlarged. These findings lend support to the notion that the hippocampus plays a critical role in spatial learning and memory. However, avian hippocampal lesions (like mammalian hippocampal lesions) also disrupt certain laboratory tasks that do not have an overt spatial component. Moreover, analysis of the effects of hippocampal lesions on navigation find, first, that basic navigational processes are left intact, and second, that at least some of the disruption of homing may be caused by disruption of the associability of information derived from the sun compass - a non-spatial deficit. Finally, attempts to demonstrate that the enlarged hippocampus of food-storing birds is associated with enhanced spatial memory have failed to deliver conclusive support. The extensive parallels between effects of hippocampal lesions in birds and mammals suggest that both the spatial and the non-spatial deficits form part of a single syndrome, one that cannot readily be explained in terms of disruption of specifically spatial processes.

The notion that the mammalian hippocampus plays a central role in spatial processing has dominated theorising since the publication of '*The hippocampus as a cognitive map*' (O'Keefe & Nadel, 1978). There remain, however, serious difficulties opposing universal acceptance of the O'Keefe and Nadel account. Although there are indeed, as would be predicted by the theory, widespread disruptive effects of hippocampal damage on a wide variety of tasks that involve spatial learning and memory, there are effects of hippocampal lesions on a range of tasks that do not involve an overt spatial component (Macphail, 1993). One very real possibility is that although the mammalian hippocampus does, as O'Keefe and Nadel propose, play a spatial role, it has in addition other functions, independent of spatial processing. One way of exploring this issue is to explore the role of the hippocampus (or its

* Department of Psychology, University of York, Heslington, York, U. K. YO10 5DD
emml@york.ac.uk

homologue) in non-mammalian animals. If, for example, the constellation of deficits induced by hippocampal damage in mammals is due to disruption of a number of relatively independent processes, then it is possible that some, but not all, of lesion-induced deficits observed in mammals would be observed also in a non-mammalian species. In particular, it is possible that the same spatial deficits might be seen, but associated with different (or no) non-spatial deficits. If, on the other hand, the spatial deficits seen in mammals are properly to be explained in terms of disruption of a single process that disrupts certain non-spatial tasks also, then if spatial deficits are seen in some non-mammalian species, a similar range of deficits in non-spatial tasks should be observed also. In general, to the extent that similar syndromes of lesion-induced spatial and non-spatial deficits are seen in mammals and non-mammals, the likelihood is that the syndrome is the consequence of the disruption of a single process.

This paper will survey experimental work on the avian hippocampus and will explore not only evidence on spatial processing, but evidence also on its potential role in non-spatial tasks. One objective of the survey will be to see to what extent there is what might be termed a 'core' deficit common to all hippocampal-lesioned vertebrates, a syndrome that would surely indicate disruption of a single process (or a set of strongly interdependent processes).

ARE THE AVIAN AND THE MAMMALIAN HIPPOCAMPUS HOMOLOGOUS?

A preliminary issue concerns the question whether the area labelled 'hippocampus' in the avian forebrain is indeed homologous with the mammalian structure. The avian hippocampus, after all, differs considerably in gross appearance from the mammalian structure: in contrast to the familiar 3-layered mammalian structure with its interlocking dentate gyrus and hippocampus proper (Ammon's horn), the avian hippocampus consists of a V-shaped band of cells containing a relatively undifferentiated area. There seems, however, by now to be good general agreement that there is a true homology between these areas (e.g. Butler & Hodos, 1996; Colombo & Broadbent, 2000). There is, for example, evidence that the avian hippocampal region develops from a region of the embryonic forebrain that corresponds to that from which the mammalian hippocampal complex derives (Källén, 1962); that there are many parallels between the projection patterns, both afferent and efferent, of the avian and the mammalian hippocampus (e.g. Casini, Bingman, & Bagnoli, 1986); and that there are similarities in the neurotransmitters found in the region (e.g. Krebs, Erichsen, & Bingman, 1991). Finally, there are at least some parallels in electrophysiology. First, long-term potentiation, a phenomenon that may provide a basis for some kinds of memory formation (Macphail, 1993), is found in the avian hippocampus: both NMDA-receptor dependent and non-NMDA dependent long-term potentiation have been obtained in the avian hippocampus (Shapiro & Wieraszko, 1996) (as in the mammalian hippocampus, Zalutsky & Nicoll, 1990). Second, the theta rhythm has been recorded in the pigeon hippocampus (Siegel, Nitz, & Bingman,

2000); in mammals, theta ranges between 3 and 12 Herz, depending on the species, and in the Siegel et al. (2000) report, frequencies of 4-5 herz predominated. As in mammals, theta was observed more frequently during movement than while the pigeons were awake but not moving.

The parallels listed above should not obscure the many differences between the avian and the mammalian hippocampus. There is, for example, no direct input to the avian hippocampus from the medial septal nucleus (Krayniak & Siegel, 1978); since the mammalian theta rhythm is driven by pacemaker cells in the medial septal nucleus, this suggests that there may be significant differences between avian and mammalian theta. There is, moreover, no evidence in the avian hippocampus of a pathway corresponding to the mammalian trisynaptic pathway; and it is not clear that there are avian areas that correspond to the dentate gyrus and the hippocampus proper. Earlier authors (cited in Erichsen, Bingman, & Krebs, 1991) had suggested that the V-shaped band corresponds to the dentate gyrus but recent work (Erichsen et al., 1991) suggests that it may correspond to the hippocampus proper and that the region within and dorsal to the V-shaped band may correspond to the dentate gyrus. Butler and Hodos (1996), however, point out that if this is so, the flow of information seems to run in birds from Ammon's horn to the dentate gyrus to cortical regions rather than, as in mammals, from the dentate gyrus to Ammon's horn to cortical regions.

In the light of the correspondences between the avian and mammalian hippocampal regions, it is reasonable to expect that there might be at least some functional roles in common; the differences, of course, might lead us to anticipate functional differences also. The avian hippocampus therefore seems well-suited for the goal of exploring mammalian hippocampal function by seeking dissociations between hippocampal processes.

HIPPOCAMPAL FUNCTION IN BIRDS

The remainder of this article will concentrate on behavioural data from three sources: the first set of data is drawn from conventional laboratory studies of learning, and one object in considering these studies will be to see to what extent the results parallel those from corresponding studies on mammals; the second and third sets of data concern the role of the hippocampus in pigeon navigation, and in food storing and cache recovery by parids and corvids. These paradigms exploit the natural occurrence in birds of activities that clearly make special demands on spatial processing; if the hippocampus is critically involved in spatial learning and memory, it might be expected that it should play a pivotal role in navigation and in cache recovery.

One major source of information concerning the role of the hippocampus in mammals has been the analysis of the effects of hippocampal lesions, and this technique has been used extensively with birds in both conventional laboratory studies and investigations of pigeon navigation. A second source has been exploited particularly in birds, and concerns the role of hippocampal size in food storing; variation in hippocampal size is an area of interest that has to date been explored less vigorously in mammals. It should, however, be noted at the outset that one source of data that has been

important in the mammalian literature will, necessarily, be excluded. O'Keefe and Nadel (1978) provided good support for their mapping theory by pointing to the existence of single hippocampal cells (place units) whose firing correlated with the location of the animal. There are, unfortunately, no data yet available that could answer the question whether similar units occur in the avian hippocampus.

HIPPOCAMPAL FUNCTION EXPLORED IN CONVENTIONAL LABORATORY PARADIGMS

Effects on conventional spatial tasks

There have been a number of reports of disruption by lesions of the hippocampal and adjoining parahippocampal region of performance by pigeons (*Columba livia*) in conventional laboratory tasks that involve processing of spatial information. Such tasks include: acquisition of spatial discriminations (Broadbent & Colombo, 2000; Watanabe, 1999); reversals of spatial discriminations (Broadbent & Colombo, 2000; Good, 1987); spatial delayed-matching-to-sample (Good & Macphail, 1994a); spatial alternation in a T-maze (Reilly & Good, 1987). Finally, disruption has been observed of tasks that are analogues of the Morris water maze (Fremouw, JacksonSmith, & Kesner, 1997) and of the radial maze (Colombo, Cawley, & Broadbent, 1997a). It is clear that in pigeons, as in mammals, hippocampal damage leads to disruption of a wide range of conventional spatial tasks.

One difficulty facing confident assessment of the results outlined above is that all these studies used electrolytic or aspiration lesions. This raises the possibility that the effects seen are due, not to hippocampal damage, but to damage of fibres of passage running through the hippocampal formation. This problem can be tackled - as it has in many mammalian studies - by using neurotoxic lesions, which selectively destroy cell bodies while leaving fibres intact. In the absence of neurotoxic studies, we can note the effects reported and their parallels with effects seen in mammals: but we cannot yet be certain that the effects obtained are in fact due to hippocampal damage.

In this context it should be noted that there is one study in birds that explored the effect of neurotoxic (ibotenic acid) hippocampal lesions on spatial learning (Patel, Clayton, & Krebs, 1997), and these authors did find disruption of a spatial associative task (a simple version of one of the 'window-shopping' procedures to be described in the section concerned with spatial memory in storing birds); they also found that the disruption was subsequently attenuated by transplanted hippocampal tissue.

Effects on conventional non-spatial tasks

Tasks that show no disruption. There is evidence for birds, as for mammals, that the general disruption of spatial tasks by hippocampal damage does not reflect a universal learning deficit: there are a number of similar but non-spatial tasks that do not show disruption following hippocampal lesions. These include, for pigeons: visual discrimination and reversal learning;

(Broadbent & Colombo, 2000; Good, 1987; Good & Macphail, 1994b); visual delayed-matching-to-sample (and non-matching-to sample) (Colombo, Swain, Harper, & Alsop, 1997b; Good & Macphail, 1994a); negative patterning (Broadbent, Gallagher, & Colombo, 1999); concurrent discrimination learning (using 6 pairs of visual discriminanda) (Colombo et al., 1997a); overshadowing and blocking in visual discriminations (Good & Macphail, 1994b). For all of these tasks, there is corresponding evidence from work on mammals showing absence of disruption by hippocampal damage.

Tasks that show disruption. There are in mammals reports of non-spatial tasks that are susceptible to hippocampal damage (and these non-spatial deficits do, as noted previously, cause difficulty for the spatial mapping account of hippocampal function). The evidence currently available on this issue from experiments on birds is sparse, and, as has been seen, difficult to assess in the light of the fact that electrolytic lesions were used.

Reilly and Good (1989) reported that autoshaping is disrupted by hippocampal lesions in pigeons. This report is of particular interest in that it provides a nice example of work on birds leading to novel paradigms with mammals, since, as a consequence of this report, the effect of hippocampal damage on autoshaping in rats was explored (Good & Honey, 1991). Good and Honey in fact found that hippocampal-lesioned rats did, like pigeons, show slower acquisition of autoshaping (although this finding was not replicated in a subsequent study: Hall, Purves, & Bonardi, 1996). Good and Macphail (1994b) found that hippocampal lesions attenuate the disruptive effects of rewarded pre-exposure of visual discriminanda on subsequent discrimination. They pointed to the parallel between this procedure and latent inhibition, and to the fact that latent inhibition was disrupted by hippocampal damage in mammals (e.g. Kaye & Pearce, 1987).

There are, then, data that suggest interesting parallels between avian and hippocampal function in non-spatial tasks, but those parallels, in the absence of neurotoxic studies, cannot yet be interpreted unambiguously.

ROLE OF THE HIPPOCAMPUS IN NAVIGATION IN PIGEONS

The remarkable capacity of pigeons to fly home rapidly from both familiar and unfamiliar release points makes these birds ideal subjects in which to explore the spatial role of the hippocampus, and an elegant series of experiments by Bingman and his colleagues has exploited this talent. It is generally agreed that pigeons' homing requires a navigational system that enables them to establish the direction in which their home loft lies, and a compass that enables them to fly in a constant direction. We can, then, ask whether the pigeon hippocampus plays a critical role in either the navigational system or the compass.

Basic findings

Bingman's early experiments established two striking facts. First, pigeons with hippocampal lesions when released from unfamiliar sites show an initial orientation towards home that is no less accurate than that of control pigeons (Bingman, Bagnoli, Ioalè, & Casini, 1984): the hippocampus is not, then, necessary for the efficient operation of the navigational system. Second, although hippocampal birds successfully return to the general region of their home lofts (indicating that their use of a compass was intact), they do not enter their home lofts even when they are in sight of them (Bingman et al., 1984). It appeared from these results that hippocampal birds were capable of homing successfully, but failed to recognise their home lofts. Subsequent studies found that if hippocampal pigeons were given sufficient postoperative experience of their home lofts (seven days or more), then they did successfully re-enter their home lofts (Bingman, Ioalè, Casini, & Bagnoli, 1985; Bingman, Ioalè, Casini, & Bagnoli, 1987). This finding in turn suggested that hippocampal pigeons suffer from retrograde amnesia for cues, presumably visual, associated with their home lofts.

A similar conclusion was supported by some work on anosmic pigeons. One of the processes used by pigeons in establishing the direction of home relies on smell, and anosmic pigeons do not orient successfully towards home from unfamiliar release sites. But anosmic pigeons do orient successfully if released from familiar sites, which suggests that the birds learn visual landmarks associated with the direction of home, and can use those landmarks to orient themselves if olfactory cues are unavailable. Unlike intact anosmic pigeons, anosmic pigeons with hippocampal lesions do not orient successfully from familiar sites (Bingman et al., 1987; Bingman, Ioalè, Casini, & Bagnoli, 1988b), suggesting that the lesions induce retrograde amnesia for the landmarks round the release site. However, if hippocampal pigeons are given sufficient postoperative experience of a release site before being made anosmic, they do then orient successfully at the release site (Bingman et al., 1988b). These early findings suggested, then, that the hippocampus was not involved in either the navigational map or the compass used by pigeons; the deficits found seemed rather to relate to a retrograde - but not anterograde - amnesia for both release-site and home-loft cues.

There is, however, some recent evidence that when hippocampal pigeons learn about locations, they may use different cues from those relied upon by intact birds. Specifically, when in a laboratory task pigeons could use either the colour of a bowl or its location in the room to identify which (of four) bowls contained food, hippocampal pigeons were more likely than controls to rely upon the colour cue (Strasser & Bingman, 1997; Strasser & Bingman, 1999). Since intact pigeons rely upon location cues as opposed to colour cues in returning to their home lofts (Strasser & Bingman, 1996), the implication is that hippocampal birds may re-learn their home loft location by relying upon local visual cues to a greater extent than intact birds. It is therefore possible that hippocampal pigeons show both retrograde and anterograde amnesia for more global cues used (in association with specific local cues) by intact birds. This in turn could explain why, although hippocampal pigeons do show efficient initial orienting, and do home

successfully if given postoperative home-loft experience, they nevertheless consistently take somewhat longer than control birds to complete the flight home (Bingman, Ioalè, Casini, & Bagnoli, 1988a).

Acquisition of the navigational map

Although hippocampal pigeons continue to have access to their navigational map, Bingman's more recent work has revealed hippocampal involvement in the establishment of the map.

The basic evidence derives from a study (Bingman, Ioalè, Casini, & Bagnoli, 1990) that showed that, in contrast to experienced hippocampal pigeons with hippocampal lesions, pigeons that were young (4 weeks old) when their hippocampus was damaged did not orient efficiently when released from unfamiliar sites. The three release sites in this study were from 23 to 42 kilometres distant from home, and releases took place 10 weeks after the operations were carried out; during those ten weeks, the birds were confined to an outside aviary in which their lofts were located. The hippocampal birds in fact showed a significant tendency to fly westward from all three release sites, a tendency that was (unlike that of the control birds) stronger than the tendency to orient homeward.. The significant westward tendency of these birds shows that the compass mechanism was intact: these birds were capable of following a particular compass bearing - their problem lay in establishing the direction in which home lay.

A subsequent experiment (Bingman & Yates, 1992) found a similar deficit in adult (4-year old) pigeons. In this experiment, experienced birds were moved to a new loft after hippocampal lesions had been carried out. They were confined in the novel loft area for 4 months prior to release at an unfamiliar site 16 km from home. Control birds oriented efficiently in a homeward direction, but the distribution of vanishing bearings of the hippocampal birds was not significantly non-random. We have seen that if pigeons are kept throughout in the same loft, adult birds with hippocampal lesions show normal orientation when released from unfamiliar sites: the compass of adult birds is not, then disrupted by hippocampal damage, and we can conclude that acquisition (but not the retention) of the navigational map, by both young and adult birds, is dependent on the hippocampus. A recent study, however, suggests that the dependence is not absolute: young hippocampal pigeons *can* acquire a map if, instead of being held in an outdoor aviary, they are allowed to fly around freely before being subjected to test releases (Ioalè, Gagliardo, & Bingman, 2000). The hippocampus is involved in, but not necessary for, the establishment of the navigational map.

The sensory bases of the navigational map and the compass used by pigeons are not yet fully understood. It seems clear, however, that for at least some locations, the map relies on olfactory cues, and that the location of the sun may be used for establishing a compass bearing toward home. More recent evidence suggests that the hippocampus is involved in processing sun-compass information, and that disruption of this process may be the source of the disruption of map acquisition.

Role of the sun compass

Use of the sun to provide a compass requires an internal clock that allows calculation of the current location of the sun at home. When pigeons' internal clocks are 'shifted' by maintaining them in artificial light-dark schedules, their initial orientation on release at unfamiliar sites changes accordingly so that they now fly on a bearing shifted from home that reflects their clock-shift. Hippocampal pigeons, like controls, show a shift away from the homeward orientation following clock-shifts (Bingman, Gagliardo, & Ioalè, 1996). This result confirms, then, that hippocampal pigeons do use the sun compass for orientation.

Despite their possession and successful use of the sun compass for orientation, hippocampal pigeons show a surprising inability to use the sun compass in another paradigm. Bingman and Jones (1994) trained pigeons in an outdoor circular arena with a clear plexiglas top and opaque walls that prevented the birds from seeing any landmarks; only the sky was visible outside the arena. Each of the eight identical walls of the arena contained an opening that gave access to a cup that might contain food. The food was located in the same compass direction each day (the actual direction varied between birds), and pigeons were given one (20-trial) session each day, at different times on different days. The only way to obtain the food consistently was, then, to use the position of the sun and the current time of day to determine compass bearings. Control birds rapidly learned the task (in about eight sessions); hippocampal pigeons, however, showed little sign of learning across the maximum (20) sessions allowed. Subsequent experiments found: first, that the same hippocampal pigeons acquired as rapidly as controls a similar discrimination in the same apparatus, in which a colour cue indicated the location of the food; second, that following a clock shift the control pigeons systematically misdirected their responses from the previously learned compass direction, thus indicating that they had indeed used the sun compass to solve the problem. This striking result indicates, then, that hippocampal pigeons, unlike controls, cannot use the sun compass in an associative paradigm.

Bingman and his colleagues (e.g. Bingman, Jones, Strasser, Gagliardo, & Ioalè, 1995) have suggested that the deficit in associability of sun-compass derived directional information may in turn account for the impairment of hippocampal pigeons in establishing the navigational map. A map based, for example, on the differing odour patterns of different parts of the environment could not develop if those odours could not be associated with different directions. An interesting feature of this proposal is, of course, that it supposes that the primary hippocampal deficit in navigation lies in the associability of the output of the sun compass, the spatial deficits being secondary to this deficit. Further evidence of a hippocampal deficit specific to the sun compass comes from the observation that in fact hippocampal pigeons overcompensate following clock shifts: their orientation when released deviates further from the original home direction than that of clock-shifted controls (Bingman et al., 1996).

More recent work once again points to the conclusion that, although involved in some way, the hippocampus is not always necessary for the

association of sun-compass information with visual input. When anosmic but otherwise intact pigeons are released in a distant but familiar location, they use landmarks to find their way home. This ability could reflect their association of local landmarks with a specific compass direction, or could reflect their following a series of landmarks on the route home. These alternatives can be tested by clock-shifting the birds so that the learned compass direction clashes with the route indicated by landmarks. Gagliardo, Ioalè, & Bingman (1999), using this technique, established that control anosmic clock-shifted pigeons flew home efficiently, indicating that they relied on landmarks in preference to a learned compass direction; perhaps surprisingly, hippocampal pigeons flew in the now-inappropriate compass direction. This result indicates, first, that hippocampal pigeons do associate visual landmarks with specific compass directions, but, secondly, that they use landmarks less efficiently than intact birds.

CONCLUSIONS

The work of Bingman and his colleagues leads to the following conclusions: first, the navigational map of homing pigeons is not located in the hippocampal formation; second, hippocampal pigeons show an impairment in the associability of sun-compass information, an impairment that may be the cause of the impaired acquisition of the navigational map seen in them; third, hippocampal pigeons rely more than intact birds upon specific local cues as opposed to more global distal 'location' cues.

More generally, the conclusion is that the impairments seen in navigation are not limited to 'spatial' impairments: although the hippocampal birds may show a shift in reliance from global to local cues, the impairment in associability of sun-compass information does not seem specifically spatial. And if the navigational map is seen as perhaps the clearest natural example of a cognitive map (Bingman et al., 1995), then in pigeons, at least, that map is not stored in the hippocampus.

ROLE OF THE HIPPOCAMPUS IN FOOD STORING AND CACHE RECOVERY

A number of avian species, principally of the corvid and parid families, store food in caches that they recover some time – ranging from days to months – later. The most spectacular food-storing performance is that of Clark's nutcracker, *Nucifraga columbiana*, which stores some 30,000 or so pinyon seeds in about 7,000 caches in the autumn, and recovers them over the course of the winter (Balda & Kamil, 1992). Since there is evidence from both field and laboratory studies (e.g. Vanderwall, 1982) to show that the birds use memory to locate the caches, this is an activity that clearly places a heavy demand on spatial memory.

Hippocampal enlargement in food storing birds

The notion that the hippocampus might play a role in food storing has received strong support from neuroanatomical studies that have shown that food storing birds have, relative to telencephalon size, a larger hippocampus than non-food storers (Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989). A striking example of this phenomenon is provided by two parid species, the marsh tit, *Parus palustris*, and the great tit, *P. major*. The marsh tit, at 11 gm, is a much smaller bird than the great tit (20 gm), and possesses a telencephalon that is about 20 percent smaller than the great tit telencephalon. But the hippocampus of the marsh tit is some 30 percent larger than that of the great tit. Further support for a hippocampal role in food storing is provided by studies that find disruption of cache recovery by hippocampal lesions (Sherry & Vaccarino, 1989). It is important to note that hippocampal damage does not disrupt the tendency to cache food: it is the memory for the locations of the caches that appears to be disrupted.

Enhanced spatial memory in food storing birds?

A reasonable interpretation of the hippocampal enlargement seen in storing birds is that it is an adaptive specialisation that enhances the spatial memory that is served, in storers and non-storers alike, by the hippocampus. This in turn leads to the expectation that food-storing birds should show, relative to non-storers, superior spatial memory in all tasks – not cache recovery alone – that tap spatial memory. This expectation has been intensively explored in both parids and corvids, and the experimental data have recently been reviewed by Macphail and Bolhuis (2001), who concluded, perhaps surprisingly, that the data do not support the notion that spatial memory is superior in food-storers. Two of the best-explored paradigms will be described here, to give some flavour of the data that led to their conclusion.

'Window-shopping' studies

The first set of experiments used parids in a design (sometimes described as 'window-shopping') consisting of two phases: in Phase 1, food, previously placed by the experimenter in a number of locations in an experimental room, is located (but cannot be eaten) by birds allowed to fly freely in the room; in Phase 2, which occurs after a retention interval, the birds are released once more and their ability to return selectively to those locations in which they had previously seen food is assessed. Macphail and Bolhuis (2001) found 11 studies that used this basic design, but Phase 1 of those studies varied in one important respect. In 4 studies, the birds had actively to search for the food, which was hidden behind, for example, a piece of cloth; in the other 7 studies, the food was clearly visible, so that the birds flew directly to the food sites without active searching. None of the latter 7 studies found a significant difference in Phase 2 between storing and non-storing species (in 4 of these studies the storers' mean performance was better than that of the nonstorers, in 2, the nonstorers were superior; in the remaining study, identical performance was obtained). But all the 4 studies in which the birds had

actively to search for food sites in Phase 1 found significantly superior performance by storing species in Phase 2. Why should the nature of the Phase 1 task (active search versus readily visible sites) affect the relative performance of storers and nonstorers?

One critical effect of requiring active search is that in Phase 1 birds visit potential cache sites that do not contain food, and analysis of the birds' Phase 2 performance showed that the nonstorers erred by re-visiting sites that they had visited in Phase 1 whether or not they contained food; they did not, however, show any increased tendency to visit sites that they had not visited in Phase 1. In other words, it seems that the nonstorers did recall all the locations that they had visited, but, unlike the storers, were not efficient in Phase 2 at avoiding those that had not contained food in Phase 1. The other 7 studies, in which the only sites visited were those containing food, thus found no systematic difference between the storers and the nonstorers. The most economical account of these data is, then, that nonstorers recall locations as efficiently as storers – that, in other words, their spatial memory is as efficient as that of storers.

Radial maze analogue studies

A second paradigm involves the use of radial-maze analogues, in which both corvids and parids have been tested. In these experiments, a number of potential food sites are available, and some or all of these sites contain food at the beginning of each test. The birds find and consume the food, and have then to avoid returning to those sites, now empty, that originally contained food. One study (Hilton & Krebs, 1990) used parids, and found no difference between 2 food-storing and 2 non-storing species. Three studies used corvids, almost all of which tend to store food to a greater or a lesser extent. We shall concentrate here on 3 species that were used in all three studies. One is Clark's nutcracker, which stores more food than any of the others; the second is the pinyon jay (*Gymnorhinus cyanocephalus*), which stores less food than Clark's nutcracker, but more than the third species, the scrub jay (*Aphelocoma coerulescens*); if degree of dependence on stored food is associated with an enhanced spatial memory, then on spatial tasks the more dependent species should outperform the less dependent. In the first of these studies (Kamil, Balda, & Olson, 1994), Clark's nutcrackers did outperform (significantly) pinyon jays and scrubjays; in the second (Balda, Kamil, Bednekoff, & Hile, 1997), however, pinyon jays outperformed Clark's nutcrackers (significantly, in the final stage of the experiment), and both those species outperformed scrubjays; in the final experiment (Gould-Beierle, 2000), pinyon jays significantly outperformed both Clark's nutcrackers and scrubjays – but in this study, scrubjays significantly outperformed Clark's nutcrackers. It can be seen that no consistent ranking of the three species emerges: Clark's nutcracker, the species that shows the most dependence on stored food showed significantly poorer radial maze performance than the less-dependent pinyon jay in 2 out of 3 reports, and significantly poorer performance than the least-dependent species, the scrub jay, in one of those reports.

CONCLUSIONS

Overall, Macphail and Bolhuis' (2001) review found no consistent superiority (or inferiority) of storing to nonstoring parids across a range of spatial tasks, and no consistent ranking of storing corvid species according to degree of dependence on stored food. Macphail and Bolhuis concede that they cannot give a satisfactory alternative explanation for the relatively large hippocampal size of storing species, but this does not affect the finding that the tendency to store food does not appear to correlate with spatial memory capacity in other contexts. Until a satisfactory explanation of hippocampal enlargement is developed, it may be premature to dismiss the notion that the enlargement is in some way associated with enhanced spatial memory capacity. But it is clear that the data currently available from food-storing species do not allow any confident assertion to be made about the interpretation of hippocampal enlargement in food-storing birds.

More generally, the conclusion that emerges here is that although it seems clear that the hippocampus is in some way involved in food-storing and/or recovery, it is not clear that this association strengthens the case for supposing a role for the avian hippocampus in spatial learning and memory.

SUMMARY AND CONCLUSIONS

The work surveyed here indicates, first, that damage to the avian hippocampus does disrupt performance in a number of laboratory spatial tasks; second, that damage to the hippocampus disrupts homing in pigeons; third, that the hippocampus is involved with food-storing and/or recovery. Evidence was found, however, in both laboratory tasks and studies of pigeon navigation, that avian hippocampal damage also disrupts performance in tasks that are not overtly spatial in nature (as is the case with mammals). Moreover, although the hippocampal enlargement seen in food-storing birds provides striking evidence of an association between the hippocampus and food-storing, efforts to demonstrate a link between an enlarged hippocampus and enhanced spatial memory have been unsuccessful.

The data available to date have not demonstrated that the function of the avian hippocampus in learning and memory differs in any significant way from that of the mammalian hippocampus. It would, of course, be premature to conclude that there are no such differences, but it may be worth considering the implications of the possibility that there are extensive parallels between avian and mammalian hippocampal function. First, of course, it would suggest that whatever function the hippocampus carries out, the processes involved evolved over 300 million years ago; second, it would support the notion that the non-spatial deficits seen following hippocampal damage form part of a coherent syndrome, and are likely to be the consequence of damage to a process (or processes) involved in both spatial and non-spatial tasks. It would, then, argue against the notion (O'Keefe & Nadel, 1978) that the hippocampus contains a spatial map.

It may be appropriate to end with some propaganda on behalf of work on the avian hippocampus. As we have seen, there have already been many valuable insights from avian investigations, but it is equally clear that much remains to be done in all three areas surveyed here. The avian hippocampus is of interest not only intrinsically, but also because it throws light on mammalian hippocampal function. The behavioural repertoire of birds allows exploration in them of spatial processes - homing and cache recovery - that allow detailed exploration of specific spatial demands that are less easily explored in mammals. Finally, work on avian hippocampus and spatial behaviour has recently been used, along with work on the avian brain and song-learning, to support arguments concerned with the proper analysis of the intelligence of non-human animals in general: specifically, do animals solve problems by using problem-specific modules or by using a set general processes, used for problems of many different sorts? (Bolhuis & Macphail, 2001). Comparative research on learning and memory using non-mammals (and birds in particular) can contribute in unique ways to an understanding of mammals, the group that is understandably of the greatest interest; such research merits encouragement - and probably more attention than it has received in the past.

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