

The hippocampus, spatial memory and food hoarding: a puzzle revisited

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Behavioural ecology assumes that cognitive traits and their underlying neural substrates are shaped by natural selection in much the same way as morphological traits are, resulting in adaptation to the natural environment of the species concerned. Recently, however, the ‘neuroecology’ approach of attempting to gain insight into brain structure and function by testing predictions about variation in brain structure based on knowledge of the lifestyle of the animal has been criticized on the grounds that such an adaptationist view cannot provide insight into the underlying mechanisms. Furthermore, the criticism has focussed on attempts to use variation in demand for spatial memory and in hippocampal size as a basis for predicting variation in cognitive abilities. Here, we revisit this critique against the field of so-called ‘neuroecology’ and argue that using knowledge of the natural history of animals has led to a better understanding of the interspecific variation in spatial abilities and hippocampal size, and to the generation of novel hypotheses and predictions.

A quarter of a century ago, O’Keefe and Nadel [1] argued that the hippocampus is a brain region that plays a crucial role in spatial memory. Their book, *The Hippocampus as a Cognitive Map*, captured the attention of several behavioural ecologists, who hypothesized that species with extreme demands on spatial memory might have adaptations in behaviour and brain for coping with these increased spatial demands. For example, Krebs [2] suggested that food-hoarding birds have enhanced spatial memory as an adaptation for efficient recovery of their scattered hoards and, concomitantly, these species will have larger hippocampal volumes to support the increased memory load. This approach, termed ‘neuroecology’ by Macphail and Bolhuis [3] and ‘brain ecology’ by Francis [4], has been affirmed by Nadel [5], who wrote: ‘I am strongly of the view that one can only understand the way an animal’s brain functions by looking at that animal’s behaviour in relatively natural conditions.’

This approach of linking the size of specific regions of the brain to adaptations in behaviour and cognition has, however, recently been the focus of considerable controversy. It has been criticized, first, for confusing proximate and ultimate mechanisms, which are, according to Tinbergen [6], two distinct levels of explanation of

behaviour. A second criticism has been levied at the way in which neuroecologists interpret the data on species differences in spatial memory and the hippocampus [3,4,7,8]. Here, we consider these criticisms from an empirical and a theoretical perspective. We argue that the approach is valid, that significant advances have been made, and that there are promising avenues to pursue. We focus the discussion on examples concerning the relationship between spatial memory and the hippocampus. However, the criticism is essentially directed to all those scientists who have proposed species-specific, or problem-specific, differences in cognitive abilities and the putative brain regions underlying those abilities, from complex social cognition and the neocortex of primates [9,10] to song learning and the song control nuclei of song birds [11,12].

The neuroecologist’s approach

Because of their training in behavioural ecology, neuroecologists presuppose that the behaviour of an animal is adapted to its natural environment, that the cognitive abilities of an animal are no exception and, therefore, these cognitive abilities will also show adaptations to the natural history of the species concerned [13,14]. Furthermore, those brain regions enabling particular cognitive abilities might occupy brain space that is proportional to the demand put upon them. The rationale behind the assumption that the increased size of a particular brain region is associated with enhanced spatial memory is that the brain is costly to maintain and, thus, specific brain regions will only be enlarged if there is a positive fitness return, or if such regions are enlarged at the expense of other regions that are reduced in size [15]. These assumptions are akin to the well known, close relationship between the sensory demands of an animal and the related neural processing; for example, the matching of the neural processing of auditory information for prey localization in the barn owl *Tyto alba*, a nocturnal hunter [16]. For the neuroecologist, there seems no *a priori* reason to suppose that what holds for sensory processing should not hold for cognitive abilities.

Thus, neuroecologists set out to test whether there is a positive correlation between the size of the hippocampus and a demand for increased spatial memory. A positive correlation has been found in a variety of situations across a range of species: food hoarding (songbirds [17] and rodents [18]), brood parasitism (songbirds [19–21]), migration (songbirds [22]) and homing (pigeons [23]) and

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home-range size (geese [24], pigs [25], mustelids, rodents [26] and sheep). Furthermore, within a species, the sex with the higher spatial demands can have the larger hippocampus, from polygynous male rodents [26] to brood parasitic female cowbirds [19–21]. Experience might also play a role. Thus, garden warblers *Sylvia borin* with migration experience have a larger hippocampal volume than do naïve birds [22] and, in species that hoard food caches for future consumption and rely on spatial memory to recover these at a later date, experienced birds have larger hippocampal volumes than do those without food-hoarding experience [27]. Black-capped chickadees *Poecile atricapilla* show geographical variation in food-hoarding behaviour: Alaskan chickadees that depend more on hoarding have larger hippocampal volumes and are more efficient at recovery of hoards than are their counterparts that live in more temperate conditions [28]. Finally, artificial selection can also result in increased hippocampal volume. For instance, homing pigeons *Columbia livia* have larger hippocampal volumes than do fantails or strassers, which have been bred for plumage characteristics rather than for their spatial capacities [23].

Of course, these correlational studies do not provide unequivocal evidence that the hippocampus is the dominant brain region for spatial memory. Rather, these correlations show that at least one region that is thought to be essential for spatial memory varies in size in a manner that is consistent with an adaptationist interpretation. These correlations are compelling and they do demand explanation.

The data

There are ten avian studies that demonstrate a positive relationship between the size of the hippocampus and the degree of food hoarding between species [17,29–36], or populations within a species [28], one study does not [37] and one study is inconclusive [38].

All the authors interpreted their results as implicating the hippocampus in remembering the location of food hoards. However, in a meta-analysis based on a subset of these data (from the avian families Corvidae and the Paridae), combined with new data, Brodin and Lundborg [7] found no significant correlation between hippocampal volume and the degree of food hoarding. The authors interpreted the lack of a relationship as the consequence of moving four of the species from one category of food-hoarding behaviour to another (e.g. from the moderate to the intense food-hoarding category) and of analysing a larger data set and, thus, reducing the chance of a type I error. They further pointed out that the field observations on which food-hoarding classifications have been based might be prone to bias, largely owing to the paucity of data on the dependence on hoards for most of the species in the analyses.

However, Lucas *et al.* [36] re-analysed the data set used by Brodin and Lundborg, and found that North American corvid and parid species had significantly smaller hippocampal volumes than did Eurasian ones. When they controlled for this ‘continent effect’, the correlation between hippocampal volume and the degree of food hoarding was clearly significant in both the parids and the corvids. In

addition, Garamszegi and Eens [35] conducted an independent meta-analysis, including many more (nonhoarding) species, and they confirmed that food hoarders have larger hippocampal volumes than do nonhoarders. In short, 12 of 15 studies support the hypothesis that species that do a lot of food hoarding have larger hippocampal volumes than those that do not. Incidentally, the one of the studies that fails to support this hypothesis [37] is based on a different group of food-hoarding birds, namely the woodpeckers (all of the other species are songbirds). Little is known about hoarding behaviour of woodpeckers or even if they rely on spatial memory for recovery of hoards.

In addition to adopting a correlational approach, neuroecologists have used experimental manipulations of food-hoarding behaviour to determine whether these behavioural changes affect hippocampal size. In at least four studies that we are aware of, changes in day length were used to manipulate food hoarding. Although all of the studies found appropriate alterations in food-hoarding intensity [39–42], the two studies that looked for them did not find concomitant changes in hippocampal volume [39,42]. Changes in food availability and predictability will also trigger changes in food-hoarding intensity and, although the hoarding intensity is correlated with spatial memory performance, this manipulation does not bring about changes in hippocampal volume [43]. By contrast, manipulations of hoarding behaviour in juveniles (mountain chickadees *Poecile gambeli* [44], coal tits *Parus ater* [45] and marsh tits *Parus palustris* [27]) suggest that experience of food hoarding is necessary for the normal development of the hippocampus. Juveniles denied this experience have abnormally small hippocampal volumes. Although experience-dependent changes in hippocampal volume have not been found in adult birds [28,43,46], volumetric changes are a gross measure of function and finer scale investigation is required. For example, immediate early genes (IEGs) are activated during hoarding and retrieval [47], and temporary inactivation of the hippocampus affects spatial memory [48]. It might be that intra- and interspecific differences in retrieval and spatial memory abilities are correlated with qualitative or quantitative variation in IEG activation.

The other source of contentious data comes from testing the cognitive performance of animals in spatial memory tasks. The most consistent results come from rodents: male meadow voles *Microtus pennsylvanicus* and deer mice *Peromyscus maniculatus* outperform their conspecific females on maze tasks, a finding that is consistent with the fact that males have larger home ranges than do females and supposedly a larger demand for spatial memory [49,50]. However, rodents also provide equivocal data, as male rats do not always perform better than do females [51], although females never outperform males. Tests of cue preference have also produced clear results: food-hoarding species pay more attention to so-called ‘spatial’ cues than they do to visual landmarks at the goal itself, whereas nonhoarders do not [52]. Male rats (which have larger home ranges than do their females) also use spatial cues rather than visual landmarks, whereas females exclusively use visual landmarks [53] (this result is mirrored in humans [54], although sex differences

in hippocampal volume are not consistent between studies [55,56]).

We do not know whether the hippocampus plays any role in the attention given to spatial information over visual landmarks, but it is important in learning and memory [57]. However, it is in the attempt to demonstrate a learning and memory advantage to the bearers of an enlarged hippocampus that the support for the adaptationist approach appears the slimmest, and it is this aspect that has attracted the most criticism. This is because food-hoarding species do not always outperform nonhoarding species in tasks in which they are required to remember locations of food [58]. However, the lack of consistency in outcome is now being criticized in a way that is strongly reminiscent of the critique that the early optimal foraging literature faced. That is, the lack of support from a few experiments in favour of species-specific differences in cognitive abilities is sufficient evidence to conclude that there are no differences. We agree with Nadel [5], who, after reviewing some of the above results, concluded that: 'All these results *could* (italics original), one supposes, be part of a more abstract story, wherein increased hippocampal size relates to improved 'relational' learning, but there is no evidence whatever to support this position.'

The conclusion of Bolhuis and Macphail [59] that there is no evidence to support the hypothesis that food hoarders do perform better on spatial memory tasks is premature for several reasons. First, and most importantly, food-hoarding species have, in several experiments, outperformed nonhoarders, but they have never performed significantly worse than nonhoarders. Second, with the benefit of hindsight, we now recognize at least two problematic assumptions inherent in the earlier testing. First, the difference in hippocampal volume led to an expectation of clear memory differences. However, the hippocampus of nonhoarders is far from vestigial and, therefore, nonhoarders should have been expected to do well, especially on those tests that did not 'push' the birds hard (often birds had to remember only a single rewarded location in an experimental room). Second, the use of wild-caught birds, combined with attempts to capture the essential elements of the memory required for successful food retrieval, meant that the experiments were designed to be as 'natural as possible'. This emphasis on keeping the tasks naturalistic might have reduced the efficacy of those tasks for assessing learning and memory differences, particularly when the animals might have used different strategies to solve the tasks. For example, great tits *Parus major* (a nonhoarding species) were just as good as coal tits (a hoarding species) at returning to previously rewarded locations. The two species differed, however, in the kind of mistake they made: great tits also revisited locations that they had seen to be empty, whereas coal tits tended to visit new locations, which might or might not have contained food [58].

Lessons from experimental psychology

Recently, several neuroecologists have capitalized on the rigorous experimental designs used by experimental psychologists to study learning and memory. The result

has been a more careful dissection of the kinds of learning and memory that might be required for solving spatial problems, resulting in several interesting insights into the cognitive abilities of these animals. The first is directly associated with the components of memory that are required for accurate food retrieval: capacity, duration and accuracy. For instance, in a task in which all three of these components were tested, the hoarders were better than the nonhoarders only in memory duration [60]. Even when only a single item was to be remembered, the food hoarders could do so for significantly longer than could nonhoarders. This result suggests that the cognitive advantage to increased hippocampal size in these birds is specifically concerned with memory duration, rather than with other aspects of memory that are required in cache retrieval. Intriguingly, this ability to remember information for long periods of time can also be seen in an experiment in which there was no overall difference between hoarders and nonhoarders. Two species of food hoarder, marsh tits and coal tits, were compared with three species of nonhoarders, great tits, blue tits *Parus caeruleus* and green finches *Carduelis chloris* [61]. Their ability to remember several food locations was tested after 30 s, two h and 24 h. Although there was no overall difference among the species, only the food hoarders had a better than chance performance after 24 h. That the demands of retrieval require, and the advantage to an enlarged hippocampus is to aid in, increasing the duration of memories needs much closer investigation, not least because there are other experiments that do not show this effect. We give credence to the results of Biegler *et al.* [60] because the technique that they used (images presented on a touch screen) enabled the manipulation of multiple memory features simultaneously, allowing a degree of control over the ways in which an animal can solve the task that is not readily achieved via a naturalistic method (e.g. involving flying around an experimental room).

The second insight comes from a close examination of how food hoarders use information about the spatial arrangements of landmarks delineating a goal. Although it remains to be seen whether this ability is unique to food-hoarding species, Clark's nutcrackers *Nucifraga columbiana* appear to be able to do basic geometry: they can find new hidden goals when the rule they have been trained on is to search halfway between two landmarks [62]. However, when compared with Mexican jays *Aphelocoma ultramarina*, a species that is less dependent on food hoards, the Clark's nutcracker perform poorly on some spatial memory tasks, namely ones in which they are required to remember the locations of hoards made by conspecifics [63]. Mexican jays are just as good at remembering the location of hoards that they have seen others make as they are at remembering the location of their own hoards, whereas Clark's nutcrackers are not. These results highlight how cautious one needs to be when attempting to compare cognitive abilities. The prediction that Clark's nutcrackers would be better at all memory tasks compared with species that are less dependent on food hoards is much too simplistic. Knowledge of aspects of the natural history of these two species, other than their food hoarding, might provide a clue as to why the two

species differ in this aspect of spatial memory. The Clark's nutcracker is a solitary species, so might rarely observe another nutcracker hoarding food, whereas the Mexican jay is highly social and thus has ample opportunity to observe other conspecifics hoarding and, subsequently, to pilfer those hoards. The critics might claim that there is too much *post-hoc* justification for results that did not fit the initial predictions [59]. We would say that getting results that do not fit predictions makes one think more carefully about the problem.

The third insight comes from studies investigating the psychological processes underlying memory for food hoards in one species of corvid, the western scrub jay *Aphelocoma californica*. In a series of experiments, Clayton and Dickinson [64] showed that the recovery behaviour of western scrub jays is not consistent with an associative account of memory retrieval. By contrast, these birds appear to remember the 'what-where-and-when' of specific past events, so-called 'episodic-like' memory because it captures the behavioural criteria for recalling specific events ('episodes') that happened in the past [65]. Furthermore, the jays can use their past experience to adjust their future hoarding strategies [66], suggesting that they are capable of mentally travelling forwards in time (planning) as well as backwards in time (episodic memory), an ability that was thought to be unique to humans [67]. The advantage of the discovery of an animal model for this memory type is potentially enormous because damage to the hippocampus, such as occurs early in many forms of dementia, particularly affects this kind of memory in humans. Although there is debate as to whether scrub jays have 'episodic' memory, and whether or not an enlarged hippocampus contributes to the kinds of memory that a scrub jay has, no experimental psychologist had even an approximate potential model for this kind of memory. Work with rats has come near with demonstrations that rats could remember what and where [57,68]. However, it was the recognition that hoarding of ephemeral food types requires the what, where and when of a hoarding episode that inspired investigation of the cognitive abilities of these animals. Further experiments are required to establish whether other animals are also capable of episodic-like recall.

Theoretical considerations

Macphail and Bolhuis [3,59], and more recently Francis [4], have argued that an understanding of the behaviour of an animal in the wild cannot inform questions about brain structure and function because it mixes levels of analysis: in other words, the function of a particular behaviour cannot be taken to explain the underlying causal mechanisms. Given that Tinbergen identified causation and function as different questions, one should not necessarily expect that answers to one would provide answers to the other. Indeed, Hogan [69] argues that cause and function are logically independent concepts and, thus, cannot be used to explain each other. If neuroecology were based on the assumption that function explains cause, then it would be mistaken. But neuroecologists make no such claim. Instead they take functional considerations as providing

clues as to what the structure of the causal mechanisms might be. For example, Sherry and Schacter [70] suggested that if the functional demands of remembering two different types of information were incompatible, then one would predict that these memories would be subserved by two different mechanisms. Of course, the existence of a functional incompatibility does not provide any insight into the nature of the causal mechanisms, but it does suggest that some difference exists and, thus, provides a starting point for experiments that are designed specifically to investigate the differences in causal mechanism. Put simply, to ignore 'why' questions when constructing 'how' hypotheses is to ignore wilfully much potentially useful insight (as Macphail and Bolhuis acknowledge).

Consider the case of the population differences in the food-hoarding intensity of black-capped chickadees described previously [28]. Populations in Alaska are more dependent on the recovery of their hoards for survival than are their counterparts from more temperate regions. When housed in identical conditions in the laboratory, the Alaskan birds continue to hoard more than do the Colorado birds; they are more accurate at hoard recovery and have a larger hippocampus. These results do not provide any insight into the causal mechanism underlying the population difference in hippocampal volume or the increased performance on spatial memory tasks or hoarding intensity, but they do provide a good starting point for hypotheses about causal mechanisms. The Alaskan birds are likely to be under more stress as a result of living in a harsher climate, and corticosterone levels are higher in birds maintained on limited and unpredictable food. One can directly test a hypothesis about the effects of corticosterone on hoarding, memory and the hippocampus by experimentally manipulating corticosterone levels in birds in captivity. Indeed, birds with corticosterone levels that are elevated experimentally to the levels found in birds stressed by limited and unpredictable food do perform better at spatial memory tasks [71].

In conclusion

It is our opinion that the neuroecological approach to hippocampal function is far from fatally flawed. There is evidence for species-specific differences in both the size of the hippocampus and performance on spatial tasks that is concordant with variation in food-hoarding behaviour. Additionally, an understanding of the problems that animals face in the real world has led to discoveries of cognitive abilities in animals that were thought previously to be exclusive to humans (e.g. geometry and an episodic-like memory). We conclude, therefore, that neuroecologists have made, and will continue to make, a significant contribution to the understanding of animal cognition.

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