



REVIEW

Animal learning and memory: an integration of cognition and ecology**

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Summary

A wonderfully lucid framework for the ways to understand animal behaviour is that represented by the four 'whys' proposed by Tinbergen (1963). For much of the past three decades, however, these four avenues have been pursued more or less in parallel. Functional questions, for example, have been addressed by behavioural ecologists, mechanistic questions by psychologists and ethologists, ontogenetic questions by developmental biologists and neuroscientists and phylogenetic questions by evolutionary biologists. More recently, the value of integration between these differing views has become apparent. In this brief review, we concentrate especially on current attempts to integrate mechanistic and functional approaches.

Most of our understanding of learning and memory in animals comes from the psychological literature, which tends to use only rats or pigeons, and more occasionally primates, as subjects. The underlying psychological assumption is of general processes that are similar across species and contexts rather than a range of specific abilities. However, this does not seem to be entirely true as several learned behaviours have been described that are specific to particular species or contexts. The first conspicuous exception to the generalist assumption was the demonstration of long delay taste aversion learning in rats (Garcia et al., 1955), in which it was shown that a stimulus need not be temporally contiguous with a response for the animal to make an association between food and illness. Subsequently, a number of other examples, such as imprinting and song learning in birds (e.g., Bolhuis and Honey, 1998; Catchpole and Slater, 1995; Horn, 1998), have been thoroughly researched. Even in these cases, however, it has been typical for only a few species to be studied (domestic chicks provide the 'model' imprinting species and canaries and zebra finches the song learning 'models'). As a result, a great deal is understood about the neural underpinnings and development of the behaviour, but substantially less is understood about interspecific variation and whether variation in behaviour is correlated with variation in neural processing (see review by Tramontin and Brenowitz, 2000 but see ten Cate and Vos, 1999).

Key words: cognitive ecology, spatial learning and memory, adaptive specialisation

Cognitive ecology and successful food storing

A more recent body of work, which is currently being loosely categorised as 'cognitive ecology', has attempted to take a broader approach to addressing questions concerning animal behaviour by integrating cognition, evolution and behaviour in the same experimental paradigm. This work largely originates from observations of animals in their natural environment and subsequent study of the cognitive abilities required for

the behaviours observed. The following are brief descriptions of some examples of work that might be construed as cognitive ecology (see also Dukas, 1998). Although we present them in a positive light, we acknowledge that Bolhuis and Macphail (2001; also Macphail and Bolhuis, 2001) have put forward a fervent critique of the approach which has since engendered much discussion (for some of the responses see Dwyer and Clayton, 2002; Flombaum et al., 2002; Hampton et al., 2002; MacDougall-Shackleton and Ball, 2002).

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One of the first cognitive ecology studies came from the observation that some animals store food in a number of different places and they appear to be extremely accurate in their recovery of these stores (Cowie et al., 1981; Stevens and Krebs, 1986). Usefully, some of these species can be induced to store food in the laboratory and this has enabled demonstration that at least some food-storing bird species can remember the locations of their caches (Sherry et al., 1981; Sherry, 1982; Shettleworth and Krebs, 1982, 1986). They appear to be able to remember more than simply location, however. For example, Sherry (1984) showed that black-capped chickadees, (*Parus atricapillus*), returned to stored food items that they preferred first and that they appeared not to return to cache sites from which they had removed the food (see also Krebs et al., 1990). They also learn to avoid sites from which the food has been pilfered by an experimenter (Hampton and Sherry, 1994). In a series of elegant experiments, Clayton, Dickinson and co-workers have shown that scrub jays *Aphelocoma coerulescens* remember not only where they have stored food but what the food was and when it was stored (Clayton and Dickinson, 1998, 1999a,b; Clayton et al., 2001). They do not visit caches that they have learned will have decayed, if the intervening time interval is appropriately long. Scrub jays learn about pilfering too (Clayton and Dickinson, 1998). The memories that scrub jays have of their caches appears to be the first animal analogue of episodic memory, a kind of memory some claim to be specific to humans (e.g., Tulving and Markowitsch, 1998). This ability is unprecedented in an animal, however, it may not be unique. Future research may find other species or contexts which involve memories that are tripartite (that is they involve where, when and what information), in the way that cache memory seems to be in scrub jays (Griffiths et al., 1999).

Food storers, then, appear to possess the kinds of cognitive abilities and capacities required for successful food retrieval. It may also be that all animals do but they have not been tested. However, cognitive abilities may be expected to have been selected to be closely matched to the cognitive demands posed by each species' environment (biological and physical), and if this is the case we might expect interspecific differences in cognition. The apparent difference in demand for spatial memory – food storers may hide hundreds or thousands of food items and not retrieve them for days, weeks or months – between storers and nonstorers, led to the hypothesis that a greater demand for spatial memory would be related to increased processing or memory capacity. It was predicted that this increased capability in food storers would be readily demonstrable when food storers and nonstorers were tested on spatial memory tasks.

This hypothesis gained indirect support from a handful of studies that showed that the hippocampus was involved in memory for food caches. The mammalian hippocampus is the brain region thought by many to be crucially involved in processing spatial information (e.g., Morris et al., 1982; Nunn et al., 1999). Firstly, lesions to the hippocampus of black-capped chickadees left these birds able to store and motivated to retrieve, but their retrieval performance was no better than at chance (Sherry and Vaccarino, 1989). Secondly, the hippocampus is relatively larger in food storers than it is in nonstorers, is larger in birds that store more for longer and is larger in food storers with storing experience (Hampton et al., 1995; Healy and Krebs, 1992a, 1996; Krebs et al., 1989; Sherry et al., 1989). Finally, experimental manipulation of food storing experience has shown that increases in hippocampal volume in food storers is dependent on either food storing experience or on activities that bear a strong similarity to food storing (Clayton, 1995; Clayton and Krebs, 1994). Therefore, cache memory seems to be a hippocampal-dependent, spatial, task.

The first experiments that compared spatial learning and memory of food storers with that of closely related nonstoring species did not reveal the expected differences in spatial learning and memory (e.g., Healy and Krebs, 1992b, c; Healy, 1995; Hilton and Krebs, 1990). However, in tasks that were used to test cue preferences of food storers and nonstorers, the food storers were found to rely on spatial cues (either the position or location of a feeder) to return to rewarded locations while nonstorers had no preference for spatial cues over the visual information provided by the individual colour patterns on each feeder (Brodbeck, 1994; Clayton, 1995). In these experiments birds were presented with four or seven, visually differentiable feeders in a room, only one of which contained food. Once the bird had located the rewarded feeder it was allowed to eat only part of the food before being forced to leave the room. Before the bird returned to the room, the rewarded feeder was switched with one of the others and the bird's response to this switch (i.e. the order of feeders the bird visited) when the bird returned to the room was observed. Later experiments, using tasks ranging from the semi-naturalistic involving free-flight (like those of Brodbeck and Clayton, see also examples in Healy, 1998), to the highly artificial (e.g. presenting images on touch screens, see examples in Shettleworth, 1998 and Leonard and McNaughton, 1990), have consistently found that food storers outperform nonstorers specifically on spatial learning and memory tasks (Clayton and Krebs, 1994; Hampton and Shettleworth, 1996; Hampton et al., 1998; McGregor and Healy, 1999). One of these tested birds on the duration, capacity and accuracy of their spatial memories. Birds were presented

with trials in which they were required to peck at images on a touch screen and after a retention interval of a few seconds, rewarded for correctly choosing the new of two images. The number of sample images varied (capacity), the retention interval (duration) was titrated (i.e. this was increased on the subsequent trial when the bird made a correct choice and decreased when the bird made an error) and the distance the two images in the choice phases was varied (accuracy). Food storers (coal tits *Parus ater*) could remember spatial locations for longer than could nonstorers (great tits *P. major*) but the species did not differ in the number of locations they could remember, nor in the accuracy of their memory (Biegler et al., 2001).

Food storing has also proved a source of predictions about interspecific differences in social learning. Pinyon jays *Gymnorhinus cyanocephalus*, for example, store and recover seeds even when in large flocks. Bednekoff and Balda (1996a) showed that pinyon jays remember the locations in which they have seen flock mates hide food. They went on to show that Mexican jays *Aphelocoma ultramarina* which are also a social species are as accurate at retrieving caches as the birds seen to do the caching. Clark's nutcrackers *Nucifraga columbiana*, on the other hand, which are not social, are more accurate when retrieving food they have stored than food they have seen stored by a conspecific (Bednekoff and Balda, 1996b; see also Hitchcock and Sherry, 1995).

From the evidence to date, food storing appears to support the general notion that cognitive abilities are matched, at least roughly, to demands posed by the animal's environment. There are several other cases of apparent increased demand for spatial learning and memory that appear to support this theory. An increased demand for spatial learning and memory may be proposed for a situation in which the animal is faced with having to navigate either over larger, familiar areas than other animals (as in home range size variation), or be required to remember many more locations (as in food storing). Migration fits this criterion only in so far that the migrant is required to learn two or more familiar sites, as in locations of regular stopover sites en route or the locations of breeding and overwintering grounds. The distance the migrant flies does not necessarily impose any extra spatial learning and memory demands (see Healy et al., 1996). For example, in meadow voles (*Microtus pennsylvanicus*) males have larger ranges, and larger hippocampal volumes relative to the entire brain, than females (Jacobs et al., 1990), while there is no sex-linked variation in either range or hippocampus size in pine voles (*M. pinetorum*). There is also direct behavioural support for a matching of cognition and niche – male meadow voles perform better than females on spatial tasks, while there are no differences in

the performance of male and female pine voles (Gaulin and Fitzgerald, 1986). Another example is found in cowbirds, where some species are brood parasites, which face increased spatial demands because they have to remember the location of potential host nests. Brood-parasitic cowbird species have relatively larger hippocampal volumes than non-parasitic species (Reboreda et al., 1996), and in species such as the brown-headed cowbird (*Molothrus ater*), in which only females search for nest sites, females have larger hippocampal volumes than do males (Sherry et al., 1993). Experience of migration also appears to be correlated with variation in hippocampal volume – garden warblers *Sylvia borin* that have migrated at least once have a larger hippocampus than inexperienced birds (Healy et al., 1996). The experienced birds are, however, also older and it is not yet clear how age and experience contribute to this increased hippocampal volume. It does appear to be related to migration in some way as there is no age-related hippocampal variation in a closely related non-migratory species the Sardinian warbler *S. melanocephala*.

While there is behavioural support for sex differences in spatial learning and memory to match the differences in hippocampal volumes in voles, this is not yet the case for work on migration and brood parasitism in birds. Indeed, in the sole study to examine learning and memory in shiny cowbirds, females do not appear to outperform males on spatial memory tasks (Astié et al., 1998). There is the potential for much more behavioural work addressing the relationship between hippocampal variation and variation in demand for spatial information processing.

Cognitive ecology in the field?

Any deep understanding of animal behaviour must eventually enable explanation of the behaviour we see animals performing in their natural environment. And yet, nearly all studies of learning and memory are carried out in the laboratory. Laboratory studies, which offer a high degree of control, are essential to our understanding of learning and memory and yet such conditions may bear little resemblance to the natural conditions in which individuals live. One of the obvious reasons that field tests of cognitive ability in non-human vertebrates are almost non-existent is that such tests are not logistically straightforward. One needs to be sure, among other things, that (1) the same animal is being tested, (2) experience is either known or able to be manipulated, (3) animals perform naturally while being observed.

Foraging by nectarivorous rufous hummingbirds (*Selasphorus rufus*) on their breeding territories is one example of a tractable system for investigating cognition

in an ecological context. Male rufous hummingbirds set up breeding territories in the Rocky Mountains in Canada and defend them vigorously from conspecifics. They can be marked individually to ensure that the same bird is being tested, although their territorial defence is such that successful intrusion is fleeting, if at all. They can be trained to feed from artificial flowers within an hour or so and many aspects of these flowers can be manipulated (colour, location, number, nectar amount and concentration, height, size and so on). They will feed from such artificial flowers every 10–15 minutes throughout the day and in all weather. Finally, they can be observed from close quarters as they are minimally disturbed by the presence of humans. Logistically, then, these birds provide a way to begin investigating cognitive abilities in the field. Although their learning and memory abilities have, to date, been tested only with adapted laboratory paradigms using artificial flowers, wild-living rufous hummingbirds have been shown to use spatial memory for locating those flowers (Brown and Gass, 1993; Healy and Hurly, 1995, 1998; Sutherland and Gass, 1995). Birds' foraging efficiency is increased through avoidance of recently visited flowers, during which time replenishment of nectar can take place. These birds do avoid recently emptied flowers but return to flowers that were not emptied on the previous visit (Hurly and Healy, 1996). The birds pay attention to the visual characteristics of the flowers but the flower's location plays a much more important role in decisions about which flowers to visit and which to return to (Collias and Collias, 1968; Healy and Hurly, 1998; Henderson et al., 2001; Hurly and Healy, 2002; Miller and Miller, 1971; Miller et al., 1985). These and other results can be explained in the context of the advantages to a territorial hummingbird of being able to remember his foraging experiences in order to make subsequent choices that will optimise the return he gets from his defended flowers.

Problems with cognitive ecology

At its best, cognitive ecology provides a rationale for the careful formulation and testing of hypotheses. However, sometimes the cognitive ecology approach seems to be so seductive that hypotheses are produced to explain behaviour without the consequent predictions being clearly stated and then thoroughly tested. An example of this can be found in the literature on sex differences in spatial learning and memory in mammals. Males tend to outperform females on spatial tasks in humans, meadow voles, deer mice (*Peromyscus maniculatus*) and laboratory rats (e.g., Halpern, 1992; Gaulin and Fitzgerald, 1986; Galea et al., 1996; Dawson et al., 1975). There are, currently, at least six evolutionary

scenarios that have been proposed to account for these observations (reviewed in Sherry and Hampson, 1997). These scenarios include the 'dispersal' hypothesis (Silverman and Eals, 1992), which proposes that spatial ability is linked to dispersal distance and so any sex differences in dispersal should result in sex differences in spatial ability. This hypothesis is completely untested. Similarly untested is the 'female choice' hypothesis (Sherry and Hampson, 1997), which proposes that spatial ability is a sexually selected trait.

The 'fertility and parental care' hypothesis (Sherry and Hampson, 1997) proposes that female spatial ability is reduced compared to males' during reproductive periods in order to save energy and reduce predation risk. As high levels of estrogens tend to be associated with reproductive periods one of the predictions that comes from this theory is that high levels of estrogens will reduce female spatial ability. However, the evidence for this is inconsistent. Some behavioural studies find reduced spatial ability when estrogens are high (e.g., Galea et al., 1996; Phillips and Silverman, 1997), but some do not (e.g., Epting and Overman, 1998; Healy et al., 1999). Estrogens have been shown to affect the hippocampus by increasing its volume, causing cell proliferation in certain regions, and increasing the density of dendritic spines on hippocampal CA1 pyramidal cells and the synaptic plasticity of these neurones (Galea and McEwen, 1999; Galea et al., 1999; Warren et al., 1995; Woolley et al., 1990). Such changes might be expected to be associated with increased, rather than decreased, spatial ability. The only hypothesis for the evolution of spatial ability that has undergone any substantial testing is the 'range size' hypothesis (Gray and Buffery, 1971). The 'range size' hypothesis states that spatial ability is linked to range size, therefore if there are sex differences in range size one of the predictions is that there will also be sex differences in spatial ability. This prediction is generally supported by the data (Gaulin and Fitzgerald, 1986, 1989; Galea et al., 1996; Langley, 1994).

Sex differences in spatial ability seems to be an area for which many explanations have been proposed but little work has been done to test them. The value of such explanations cannot be evaluated without such tests. The study of sex differences in spatial ability could act as a warning to other areas of cognitive ecology against the tendency to formulate new hypotheses before testing and rejecting the old ones.

Conclusions

Cognitive ecology is a useful approach to animal behaviour that draws together previously separate disciplines, allowing hypotheses to be tested about how cog-

nitive abilities are shaped by the evolutionary pressures imposed by an animal's environment. In the examples we have chosen here we have emphasised the potential value of integration between mechanistic and functional explanations. It would also be valuable to address these questions at both the phylogenetic and ontogenetic levels. One such avenue which seems worthy of exploration is suggested by the data showing a relationship between timing and levels of sex hormones in utero, sex and subsequent spatial learning and memory abilities (e.g., Galea et al., 1994; Lewis and Diamond, 1995).

Cognitive ecology hypotheses tend to be based on observations of animals under natural conditions, which are then tested by experimental manipulations or cross-species comparisons, either in the lab or, if the species is particularly amenable, in the field. In order to draw useful conclusions, it is important to test and discard existing hypotheses as well as formulating new ones.

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