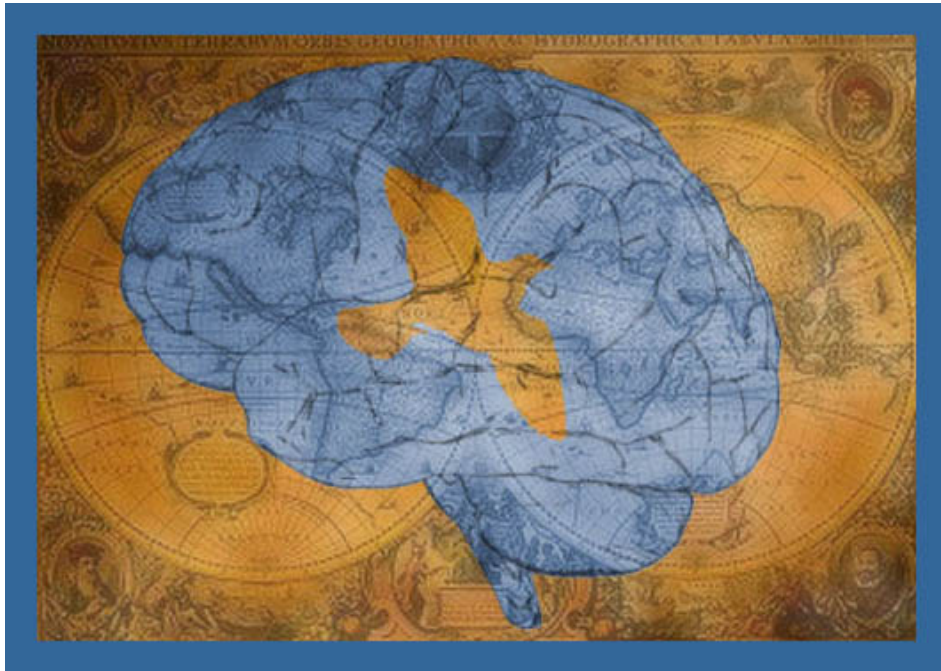


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## Animal Spatial Cognition:

Comparative, Neural & Computational Approaches

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## An Adaptationist's View of Comparative Spatial Cognition

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### Abstract

This chapter reviews some of the recent experiments investigating spatial cognition that have been predicated on adaptationist hypotheses, specifically that some animals will have faced greater selection pressure on their spatial cognitive abilities than others. In contrast to more traditional experimental psychology, adaptationists seek to explain some of the variation in cognitive abilities, rather than to reduce it via experimental control. Variation in the ways animals solve spatial problems (e.g., cues used) and in their learning and memory capabilities, at least in some situations, appear to be well explained by the demands put on them by their environment or life history. Additionally, the adaptationist approach has led to the testing of a broader range of species in a wider span of spatial contexts than previously.

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## I. Introduction

Variation in spatial cognitive ability has been both a cause for concern and enthusiastically observed in almost equal measure. The cause for concern comes, typically, from studies in which the aim is to examine performance on a task such that, as nearly as possible, only a particular cognitive ability is assessed. External factors such as time of day, time of year, temperature, light intensity and many more are controlled by the experimenter so as to have no, or negligible, effect on performance. Intrinsic factors such as motivation (e.g., appetite and thus willingness to work for food rewards) are more difficult to control but these too are manipulated so as to reduce variation both within and among subjects. Previous experience can be essentially removed as a source of variation by training animals to a pre-test criterion level. If they do not reach this level, they are excluded from experimental testing. All of this control by the experimental psychologist leads to a significant reduction in the effects by extraneous factors on task performance. To an evolutionary biologist, on the other hand, variation in a trait is of as much interest as is the level of the trait itself, not least because variation is what natural selection gets to act on. Seeking out possible sources of variation, for example, the need by one animal for more, or greater dependence on, spatial information than another, also provides an a priori basis for formulating adaptive hypotheses. Having some understanding of the source of variation in need for spatial information means that it is possible to explore whether or not natural selection has managed to mould animal cognition with the same precision as it has shaped sensory processing.

This difference in angle of approach to variation in spatial cognition is proving to be a fruitful one even if sometimes beset with misunderstandings (e.g., Hampton, Healy, Shettleworth, & Kamil, 2002; Macphail & Bolhuis, 2001). Some of the fruits of this approach are epitomized in the work carried out by Balda, Kamil and colleagues, described elsewhere in this volume. As a result, we can see that there is real biological variation in spatial learning and memory, and we are beginning to see what kinds of variation exist, the degree to which variation occurs and under what circumstances. Here, I will examine a more diverse literature than that described by [Balda and Kamil, this volume](#), which has also taken an adaptationist stance when addressing questions of spatial cognition, and attempt to address the value and pitfalls of such an approach.

## II. Spatial Cognition as an Adaptation



Figure 1. A blind Mexican cave fish *Astyanax fasciatus*.  
Courtesy of Theresa Burt de Perera.

Just as evolution via natural selection has acted on morphological structures (Figure 1) so it has on cognitive abilities (see also [Balda & Kamil, this volume](#)). However, one of the major problems in determining what solutions have been arrived at is that cognition itself is not as readily observed as is a morphological structure. It is a behavioural response (or lack thereof) to a stimulus and can be considerably more plastic, and its presence more difficult to confirm, than most morphological traits. It can also be difficult to differentiate between aspects of cognitive abilities that are essentially innate and those that are acquired through experience.

A useful place to begin to deal with this problem of identifying a cognitive ability, its extent and variation, is with an understanding of the specific problems an animal faces. In spatial cognition this has led to a focus on those animals that appear to face considerable, even excessive, demands on their ability to learn about and to remember locations.

An example of an animal that faces a major spatial problem, which has been more thoroughly investigated than others, is the homing pigeon, a strain of *Columba livia*, which has been selected for its ability to home to a loft over many miles. Most of the work on pigeon navigation over both familiar and unfamiliar terrain has focused on their ability to do this using magnetic and olfactory cues, largely due to the finding in the 1970's that pigeons wearing frosted contact lenses managed to reach the vicinity of their home loft (Schmidt-Koenig & Walcott, 1978). [Bingman et al. \(this volume\)](#) present the current status of the work on homing in pigeons from which it is clear that visual landmarks play a crucial role in successful homing, although the scale over which those landmarks operates means they are largely outside (as yet) experimental scope. In addition to using olfactory and magnetic information, pigeons utilize all manner of different visual landmarks, including those humans have unwittingly provided (Biro, Meade, & Guilford, 2004; Guilford, Roberts, Biro, & Rezek, 2004, Figure 2).

## III. Cue Use

A number of studies have demonstrated differences in cue use amongst animals that are compatible with predictions based on the ecology of the animals under comparison. Food-storing birds, for example, which use their memory for where they have hidden food to relocate it successfully, prefer to use the spatial arrangement of visual cues to do this (Sherry & Vaccarino, 1989). They also preferentially use these kinds of cues when returning to sites containing food previously seen but not removed (Brodbeck, 1994; Clayton & Krebs, 1994). Nonstoring species, on the other hand, tested in the same experiments, showed no particular preference for which cues they used to return to sites containing food. This difference in cue preference is consistent with the cue use predicted for animals that differ in the degree to which they are dependent on spatial information for efficient foraging or homing.

If one looks across the range of experiments carried out on cue use in vertebrates, it becomes clear that many animals use the arrangement of visual cues surrounding the goal, rather than visual features of the goal itself, especially, but not exclusively, when the goal itself is not particularly visually distinctive. This has led to a vigorous debate as to the roles of proximal or distal cues, when it seems that examining the relative value of the information provided by the cue may be more relevant. For example, whether a cue is stable, more accurate or reliable across time seems what is likely to be important and useful to a navigating animal (Gibson & Shettleworth, 2003).

That cue use for solving apparently spatial problems may be context dependent is further supported by data from a cue test in which migratory and resident dark eyed juncos (*Junco hyemalis* and *J. h. carolinensis*, respectively) were compared (Cristol et al., 2003). Although the migratory subspecies outperformed the resident subspecies in the duration over which they could remember which was the correct feeder, both groups of animals showed a marked preference for the spatial cues over the colour of the feeder. These data are not consistent with the hypothesis that cue preference is ecologically determined, at least, not in a simple, across-context fashion as in this situation, it might be predicted that the migrants would be more dependent on spatial information than the residents. It is also not clear why the outcome of this experiment was different from the cue use found in comparisons of migrant juncos with chickadees (Brodbeck, 1994; Brodbeck & Shettleworth, 1995). In a more recent, larger scale test of spatial memory, the two subspecies did not differ in their ability to home from distances of up to 40km (Keiser, Ziegenfus, & Cristol, 2005). This result shows that demonstrating a clear relationship between ecological demands and cognitive performance is far from straightforward. The junco data from both labs also shows that performance as shown under laboratory conditions may not be representative of what animals do when tested in the wild.

One of the few paradigms in which cue use has been tested repeatedly in both laboratory and field conditions, is that of homing in pigeons (see Bingman et al., and Phillips et al., this volume). However, most of the work has been directed at determining whether directional cues such as the sun compass are used or, whether information that the pigeons garner when flying can help them, subsequently, to discriminate among photographs of a variety of locations (Dawkins, Guilford, Braithwaite, & Krebs, 1996; Wilkie, Willson, & Kardal, 1989). It would be interesting to carry out experiments on pigeons similar to those done with the juncos.

Aside from the homing pigeon literature, there have been few field experiments on the use of visual cues by vertebrates to return to rewarded sites. One exception is a series of tests done using rufous hummingbirds. The choice of this species was based on both logistical and biological features. The first comprises such useful attributes as the birds coming to feed every 10-15 minutes, strong territorial defence and birds being readily trained to feed from artificial flowers. The biological rationale is based on the territorial defence by the males of a number of flowers coupled with the relatively small amount of time spent foraging and the fact that the bird empties the flowers he visits. It is, therefore, plausible that it might be efficient for these birds to remember, in order to avoid, flowers they have recently visited (as they are now empty).

It seems that territorial hummingbirds, like food-storing birds and juncos, rely more heavily on spatial information than on visual cues borne by flowers themselves when returning to rewarding flowers (Healy & Hurly, 1998; Hurly & Healy, 1996; Miller, Tamm, Sutherland, & Gass, 1985, Figure 3). This finding appears to contrast with claims that the red coloration of the Californian flora is due largely to the fact they are, almost exclusively, pollinated by hummingbirds (Grant, 1966). It is possible to reconcile the experimental findings with the pollination hypothesis, if the birds in question are territorial in the first instance and migratory in the second. Spatial memory is only useful in familiar situations while using colour as a cue to locate new sources of food is useful in unfamiliar places. Thus, the same animal may pay attention to different cues depending on the situation in which it finds itself. Territorial hummingbirds can, and do, pay attention to the colour of flowers but only under certain circumstances (Healy & Hurly, 1998; Hurly & Healy, 1996).

#### IV. Species Comparisons

One of the potential problems with basing adaptationist predictions concerning cue preference on the extent to which species rely on spatial information, is that those species will also tend to differ in a variety of other ways. It is possible, for example, that an explanation for the difference in cue use between black-capped chickadees and dark-eyed juncos may be found in the placement of the feeders on the walls of the experimental room. Although chickadees are familiar with feeding on vertical substrates, this is uncommonly so for juncos. One of the differences between the Brodbeck studies (Brodbeck, 1994; Brodbeck & Shettleworth, 1995) and those by Cristol et al. (2003) is that juncos were tested on the floor of the experimental room in Cristol's tests. While it is not clear why this would result in a change in cue use, it is at least possible that experimental context is relevant. Even those experiments that have examined cue use with much more closely related species that appear to occupy very similar habitats and niches within them (e.g., Clayton & Krebs, 1994), face this problem. It is entirely possible that there are other differences between these species that cause them to pay more or less attention to visual cues (for example), or aspects of those cues. If their visual processing differed in some way, for example, or one species put more emphasis on other sensory cues, then this may be the cause of the variation in cue and not the apparent variation in dependence on spatial information.

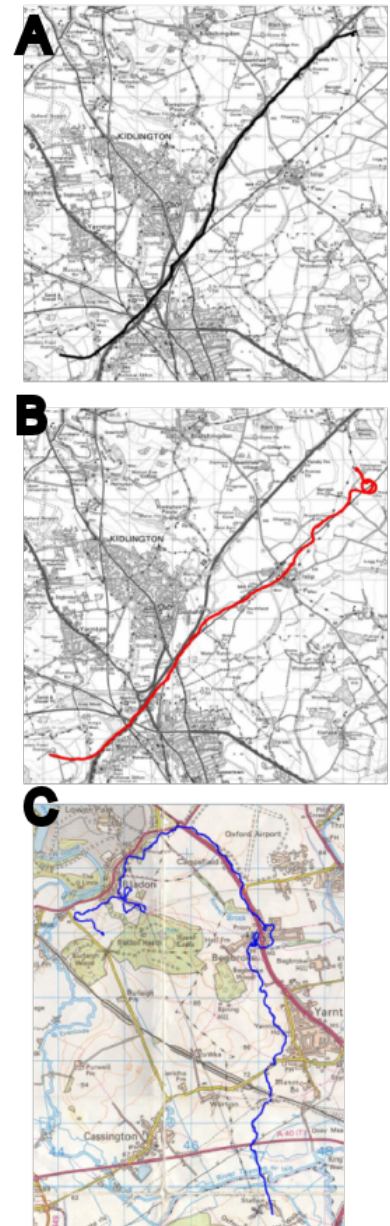


Figure 2. The bold lines in each figure represent the flight paths of three homing pigeons (a-c), superimposed on Ordnance Survey maps, showing the roads and rail lines (pigeon b flew along the railway line). Courtesy of Dora Biro.

## V. Within-species Comparisons

Pond dwelling sticklebacks *Gasterosteus aculeatus*, for example, prefer to use visual cues to locate a reward in mazes while sticklebacks from fast-flowing rivers prefer to use water flow direction or the turn direction of their bodies, possibly based on the relative stability of each environment and thus the value of depending on visual cues (Braithwaite & Girvan, 2003; Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003). Further work with this system provides evidence for this cue dependence arising both from the environment in which the fish has been raised as well as there being some genetic basis to the preference (Girvan & Braithwaite, 2000). Discriminating the cause of cue preferences is rarely done, with little regard given to the relative roles of experience versus an innate component. However, this issue seems particularly pertinent to adaptationist interpretations of cue preference as it is only on the genetic component that natural selection will act.

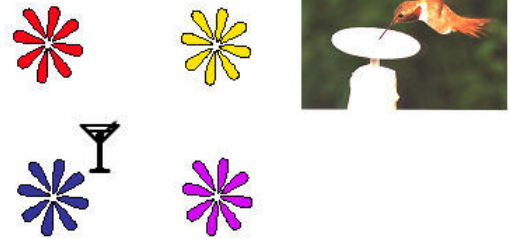


Figure 3. Spatial and visual feature cue use in rufous hummingbirds. The percentage of choices made to the four possible flowers, showing that the birds overwhelmingly returned to the flower in the original location (marked with a martini glass), in spite of the change in the flower's visual features between the first and return visits. After Healy & Hurly (1995).

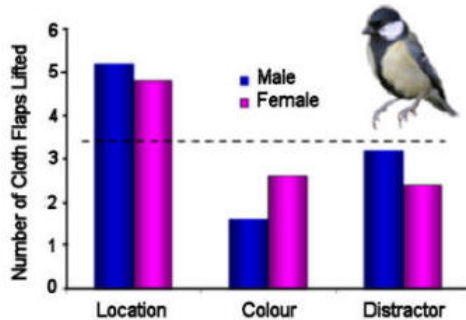


Figure 4. Cue use by male and female great tits. Both sexes preferentially used the spatial cue to relocate the rewarded well. Birds were trained with repeated visits to the rewarded well before being tested with three possible wells, all empty. After Hodgson and Healy (2005).

Milun, 1998; moving around a virtual maze, Sandstrom, Kaufman, & Huettel, 1998; real world navigation tasks, MacFadden, Elias, & Saucier, 2003). Similarly, in maze testing, male and female laboratory rats prefer to use these different cues (Kanit et al., 1998, 2000; Williams, Barnett, & Meck, 1990). Little has been done to investigate sex differences in cue use in other vertebrates, although in one of the few bird comparisons, there was no difference in cue preference between male and female great tits (Hodgson & Healy, 2005). This lack of difference might have been an outcome of the experimental design: birds were required to visit a rewarded location multiple times before being tested for cue preference. Although it is not clear whether there would be a sex difference in these birds if preference was tested after a single experience of the rewarded site (as has been done in previous cue preference tests in birds), this finding emphasises the point made earlier that cue preference may be highly responsive to experimental design (Figure 4).

## VI. Spatial Cognition

A second way to make comparisons of spatial cognition is to assess learning and memory, rather than cue preferences. Ideally, one would have some understanding of the cue preferences when comparing learning and memory, although examining factors such as the ease with which animals reach a criterion before performance is assessed may provide this to some extent.

Tests of cognitive ability followed the cue preference tests in rufous hummingbirds. The question was then, what would one predict these birds to use for ready remembrance of flowers if one was to follow an adaptationist train of thought? Although the hummingbirds prefer spatial (an arrangement of unspecified visual cues) over beacon-like, visual cues does not mean the birds should not learn and remember the visual information provided by flowers. However, if the bird has to remember a flower for several hours, it seems more likely that the flower's visual features are far more likely to have altered than its spatial location. In fact, it appears that even over the course of far shorter periods of time, birds trained to find several neighbouring rewarding flowers in an array failed to show any evidence of having learned the visual cues of the flowers when trained on a similar array that had been moved 2m from the original location (see Figure 5, Hurly & Healy, 2002). It made no difference to the birds' learning which were the rewarded flowers in the new array, whether the flowers in this second array were of the same or different colour patterns as those in the first array, as long as the flowers were in the same relative positions. Not until the shape of the test array, as well as its location, were altered from the training situation did it become clear that the birds had learned the colour patterns of the flowers in addition to their positions in the array.

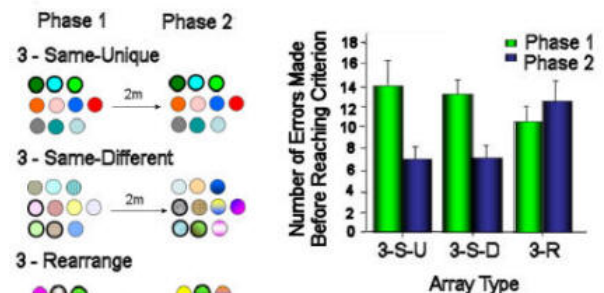


Figure 5. Use of spatial rather than visual cues by hummingbirds in an array of flowers, three of which were rewarded (marked by heavy black lines). Birds were trained with arrays as seen in the left hand column. The arrays were then moved 2m and birds trained with rewarded flowers in the same or new positions, bearing the same or new colour patterns. Birds did not appear to have learned, or to use, the colour patterns of the flowers in Phase 1 when learning which were the rewarded flowers in Phase 2. After Hurly & Healy (2002).

If the array is moved such that part of it overlays the location of the

original, the birds can be shown to encode which are the rewarded flowers relative to the distance among the flowers: flowers that are further than 40cm apart are encoded relative to cues surrounding the array, while flowers that are closer together than this are encoded relative to each other (see Figure 6, Healy & Hurly, 1998). With regard to the adaptationist model, it is not clear that these latter results would have been predicted, even with greater knowledge of the animal's behaviour. However, it is the case that without the original ecological rationale that hummingbird foraging might be a fertile field for investigation into spatial learning and memory, it is unlikely that findings such as the scale of cue use would have come to light. Variation in hummingbird foraging style (territory defence and traplining, where animals travel a repeated route around widely spaced food sites) might provide further insights into both the ways that animals use visual and spatial information as well as offer the possibility that the different foraging styles are accompanied by differences in cognition. Traplining hummingbirds forage in a markedly different way from that of territorial hummingbirds. For example, they feed on flowers that decrease nectar production during the day, a pattern that the birds mimic in their visitation rates whereas territorial birds feed at a relatively constant rate throughout the day (Garrison & Gass, 1999; Gass & Garrison, 1999). As a result, traplining birds may be particularly good, for example, at learning the sequence of places (Crystal & Shettleworth, 1994), or may only encode food sites in a sequence (de Perera, 2004), rather than in some more flexible way that would allow birds to access sites at any time from any place (a.k.a. a cognitive map).

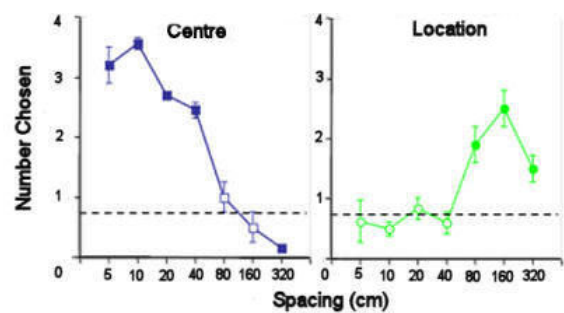


Figure 6. Rufous hummingbirds were trained to feed from the central flower in an array of flowers and the array was then moved such that the new centre was in the same location as one of the outer flowers. When the flowers in the array were 40cm apart or closer, the birds returned to the flower in the centre. When they were further apart, the birds returned to flowers in the original location. After Healy & Hurly (1998).

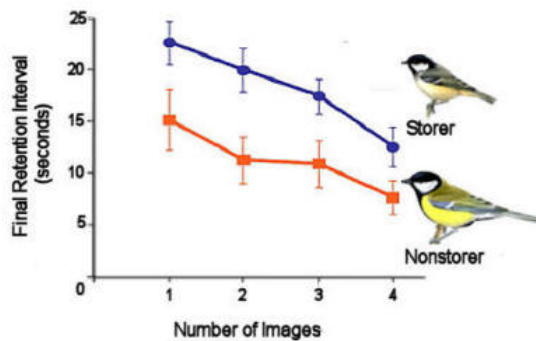


Figure 7. Coal tits (a food storing species) and great tits (a nonstoring species) were trained and tested on a spatial delayed non-matching-to-sample task presented on a touch screen in which the number of samples, the duration of the retention interval and the distance the choice images were apart were all manipulated. The outcome was that coal tits were better at remembering even a single location for longer than were the great tits. After Biegler et al. (2001).

Another example in which cue preference was known, food storing, provided an ecological rationale for the hypothesis that scatter-storing (as opposed to larder storing) animals, with their greater dependence on spatial memory for successful retrieval of their stores, would outperform nonstorsers on spatial memory tasks, a hypothesis seemingly strengthened by the volumetric hippocampal data. However, the demonstration that food storers were, indeed, better at spatial tasks was not readily come by. Most of the early experiments, at least those comparing tit/chickadee species, did not show compelling differences between the two groups, although the trends were always in the predicted direction (e.g., Hilton & Krebs, 1990; Krebs, Healy, & Shettleworth, 1990; Shettleworth, Krebs, Healy, & Thomas, 1990). However, work on the corvids was more promising (see Kamil et al. this volume), and more recently, so have the results of experiments on the Paridae. Food-storing tits and chickadees remember spatial locations better than do nonstorsers while the groups do not differ in their ability to remember colours (e.g., Hampton & Shettleworth, 1996a, 1996b). Food-storing coal tits *Parus ater* can also remember even single locations for longer than do nonstoring great tits (see Figure 7 - Biegler, McGregor, Krebs, & Healy, 2001; McGregor & Healy, 1999). These results are consistent with predictions from the early adaptationist hypothesis. It is unclear why the earlier experiments did not show such clear differences. It is possible that the explanation lies in the difficulty of the tasks the birds had to solve; perhaps the earlier tasks were too simple and the differences only became apparent when the task really taxed their memory capabilities. If, as is supposed, the

variation in hippocampal underlies the difference in spatial cognition, it should also be remembered that the nonstorsers have a hippocampus, which is far from vestigial. Additionally, they have to remember some spatial information such as territory boundaries, nest and rewarding food locations, so it was never going to be the case that the comparison would be all or nothing. Yet again, it seems that the choice of task is important. While some have suggested that this implies that the adaptationist approach is at fault, an alternative interpretation is that natural selection has affected more subtle aspects of spatial cognition than was expected.

The issue of the specificity of experimental paradigm is a substantial issue in the literature investigating differences in spatial cognition in humans. Almost every lab uses a different test to compare men and women, and although most have reached a similar conclusion as to where the difference lies (i. e., in spatial superiority by men over women, e.g., Moffat, Hampson, & Hatzipantelis, 1998; Silverman et al., 2000), there is much less consensus in the views as to the details of those differences, resulting in the plethora of supposedly evolutionary hypotheses proposed as functional explanations. In this field, unlike the comparisons in birds, the adaptationist explanations have almost always followed the demonstration of a sex difference. Much more comparative data need to be collected, based on *a priori* predictions, in order to differentiate which is the most likely among the possible explanations currently proposed (for suggestions, see Jones, Braithwaite, & Healy, 2003). There are also a number of studies that have found no sex difference or a difference in which females seem to outperform men (Duff & Hampson, 2001; James & Kimura, 1997; McBurney, Gaulin, Devineni, & Adams, 1997; Postma, Izendoorn, & De Haan, 1998), which seems, yet again, to imply that exposing cognitive differences is dependent on the specifics of the task. This makes intuitive sense if one recognises that spatial cognition is not a single entity but is made up of multiple components, and in only some of these are men superior to women. The issue of task dependence has not yet arisen in comparisons between the sexes in rodents: males invariably outperform females and certainly never perform more poorly, but these comparisons have been made either in multi-arm dry mazes or in the Morris water maze. Thus, there is vastly less variation in experimental design than in the human studies.

## VII. Hormones and Spatial Cognition

A complication with all of the mammalian work, to date, is that there is a clear role being played in spatial cognition by hormones, especially sex and stress hormones. These hormonal effects act both at an organisational level (during prenatal development) and at an activational level (during the animal's lifetime), with the former bringing about the most marked effects (Williams, Barnett, & Meck, 1990; Williams & Meck, 1991). Variation in the level of testosterone during an animal's time in utero will have marked effects on that animal's spatial ability as an adult, with the sexes being affected differently: if females receive more testosterone than is usual, they will have better spatial cognition, whereas extra testosterone for a male will lead to decreased ability. Changes in oestrogens occurring across menstrual or oestrous cycles cause short term fluctuations in spatial ability (and in hippocampal morphology; see Figure 8), while seasonal changes in testosterone cause changes in male spatial ability: typically males have better spatial ability in the breeding than in the non-breeding season (e.g., Galea, Kavaliers, Ossenkopp, Innes, & Hargreaves, 1994a; Galea & McEwen, 1999; Healy, Braham, & Braithwaite, 1999; Ormerod & Galea, 2003; Warren & Juraska, 1997).

Stress also affects spatial cognition in mammals, particularly females who perform more

poorly with increasing stress (Galea, Saksida, Kavaliers, & Ossenkopp, 1994b; Kavaliers & Galea, 1995; Kavaliers et al., 1996). It is not inconceivable that at least some of the evidence for sex differences in spatial cognition in mammals, then, is due to effects of stress caused by poor handling, novel environments and so on, and not to natural selection. Studies in which rats were handled extensively prior to testing are among those that have not found a sex difference (e.g., Healy et al., 1999; Perrot-Sinal, Kostenuik, Ossenkopp, & Kavaliers, 1996).

## VIII. Variation in Hippocampal Volume

Neither species comparisons nor tests of spatial learning and memory will enable complete avoidance of the issue of possible sensory variation but they do reduce it considerably. Ultimately, the only way to demonstrate that variation in spatial ability is not explained by the capabilities of exterior sensory structures is to conduct psychophysical or signal detection experiments. Few, if any, of these have been carried out on any of the species in which current comparative spatial cognition is being examined. Such variation does exist, even within species, often, but not always between the sexes (e.g., New World monkeys, Osorio, Smith, Vorobyev, & Buchanan-Smith, 2004; e.g., blennies, White, Goncalves, Partridge, & Oliveira, 2004). There has even been a suggestion that such variation can occur seasonally, within the same individual. It would be useful, then, it seems, to do some of this type of investigation, if only to show that a sensory explanation is insufficient.

One of the reasons that this sensory explanation has been accorded less than, perhaps, its due weight, is that differences in cue preference and in spatial cognition have been correlated with variation in the hippocampus, the area of the brain commonly thought to be predominant in the processing of spatial information. Black-capped chickadees, coal and marsh tits, and jays all have relatively larger hippocampal volumes than do great and blue tits, dark-eyed juncos and jackdaws (Healy, Clayton, & Krebs, 1994; Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989). Damage to the hippocampus in food-storing birds, at least, does not impair their ability to solve food finding tasks that require colour-vision/colour-learning but birds with hippocampal lesions are unable to retrieve food stores with more than chance accuracy, nor are they able to relocate unmarked rewarded sites (Sherry & Vaccarino, 1989). Hippocampal lesions also impair spatial cognition in both black-capped chickadees and dark-eyed juncos, such that there are not species differences following the lesion (Hampton & Shettleworth, 1996b), whereas such lesions do not impair memory for colour in either species (Hampton & Shettleworth, 1996a). It is not clear whether hippocampal lesions affect cue preferences.

## IX. Summary

I have reviewed some of the recent literature that has incorporated adaptationist hypothesis testing as a way of investigating variation in spatial cognition. Although there are still relatively few studies to determine the extent to which natural selection has shaped spatial cognition, there are sufficient data to believe that the adaptationist framework continues to be useful for formulating hypotheses (and therefore for producing testable *a priori* predictions) as to causes for variation in cognition. In this way, it adds substantially to our understanding of comparative spatial cognition.

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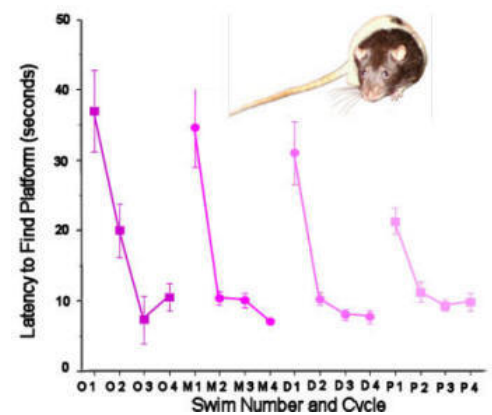


Figure 8. Female rats tested in a spatial working memory task in a Morris water maze differed in their ability to learn the location of the hidden platform across their oestrous cycle. On oestrous days they required an extra swim before reaching asymptotic performance. After Healy et al. (1999).

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