

Do not ask whether they have a cognitive map, but how they find their way about

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The publication of "The hippocampus as a cognitive map" (O'Keefe & Nadel, 1978) has had a remarkable impact, stimulating a huge amount of both behavioural and neurobiological research on spatial learning and memory, involving both laboratory and field studies, and employing a variety of novel techniques. The reviews of this general area of research provided by the previous contributors to this special issue attest to the progress that has been made since 1978. No one would now doubt that the hippocampus is implicated in the use of configurations of landmarks to locate a goal - in both mammals and birds, although the precise nature of that implication remains a matter of much speculation and debate. On balance, however, the behavioural evidence does not seem to have supported O'Keefe and Nadel's original hypothesis that true spatial or locale learning is quite distinct from simple associative learning and depends on the establishment of a cognitive map of the environment.

"It's just the study of rats in mazes" was a popular description of experimental psychology in the middle of the 20th century, and the image of rats trundling their way through a maze, learning by blind trial and error, became a symbol of everything that was wrong with old-fashioned behaviourism. The publication of O'Keefe and Nadel's book, *The Hippocampus as a Cognitive Map* (1978), changed all that. The study of spatial learning and memory has flourished as never before. Over the past 25 years, psychologists, ethologists and neurobiologists have all mounted major research programs to study spatial behaviour; the ability to find their way round their world is seen as of critical adaptive significance to the animals who do so; above all, the mechanisms underlying such behaviour can now be seen to be a great deal more complex (and cognitive) than the traditional denunciation of such experiments implied. New experimental procedures and paradigms for the study of spatial learning, memory and navigation have been devised, and new theories developed. As this issue of the journal shows, much has been discovered in the past 25 years - but no doubt much remains to be learned.

What is this spatial learning and memory that we are talking about? In their natural environment, some animals navigate over long distances - from summer to winter quarters, to and from their breeding grounds, to their home

loft from a distant release point if they are homing or racing pigeons. Within their home range, which may be as small as a few square metres or as large as several hundred square kilometres, animals must find their way around, learn what the limits of that range are, who occupies neighbouring ranges, the way to food and water and the way back home, where they have stored food for later consumption, where predators may lurk, and where are suitable sites for a new home. And they must remember this information for days or months. Within the laboratory, rats have been trained to run through mazes to a single goal box, or to find the single piece of food at the end of each of eight or more maze arms radiating out from a central platform; they have learned to find food buried in the sand in one corner of a rectangular arena, and to swim to a submerged platform in a circular pool; in operant chambers they have been required to remember the location where a stimulus appeared a few seconds or minutes ago. Birds have inspected the dozens of hiding places in which the experimenter has placed a piece of food, and are tested for their retention of this information when they are allowed to come back minutes or hours later to find the food.

In the natural world, all this is achieved under an extraordinarily wide range of circumstances. Some animals travel by daylight, others by night; some through the air, others through the sea or up rivers; some through a landscape replete with landmarks, others across featureless desert. Different animals bring to the same laboratory task great differences in sensory apparatus, and their performance also differs widely. It seems obvious that spatial learning and memory must engage an equally wide variety of mechanisms. And they do. To explain all, or even most, types of such learning by appeal to a cognitive map is to rob that term of all explanatory value. We need to ask instead exactly what are the mechanisms underlying any particular example of spatially guided behaviour.

Orientation and Path Integration

The preceding sentences are not intended as any sort of comment on O'Keefe and Nadel's book - which was indeed very largely devoted to an attempt to elucidate what they termed locale or true spatial learning, i.e., behaviour based on a representation of allocentric space, or cognitive map. They contrasted this with taxon learning, which they divided into two - orientation and guidance learning. By orientation, they meant what an earlier generation of psychologists had sometimes called response learning: a rat solving a T-maze by learning to make a left turn at the choice point. They paid scant attention to another form of response learning - dead reckoning or path integration, since nearly all the elegant research demonstrating such a mechanism in a wide variety of animals has been conducted since their book was published. Rodrigo (2002) provides a review of some of this work, and I shall return to it when discussing the work of Whishaw and his colleagues on the role of hippocampus in spatial learning.

Guidance to a Beacon

The second form of O'Keefe and Nadel's taxon learning, guidance, does indeed involve learning about a place, but just as much orientation learning can be described as a form of instrumental conditioning, so guidance can be construed as Pavlovian conditioning. The rat in the maze associates the goal box stimuli with the delivery of food, and this Pavlovian association is sufficient to elicit approach. The visible platform in the Morris pool (Morris, 1981), or the beacon that Pearce and his colleagues attach to a submerged platform (e.g., Roberts & Pearce, 1999), provide just such a stimulus - here associated with escape from the water. Backward chaining of such associations will allow the rat to thread his way through a long and tortuous maze with numerous dead ends, by approaching at any point in the maze those stimuli most closely (in time) associated with the final reward (Deutsch, 1960). When people have learned a route through a map of an imaginary town, some of them (mostly females) will describe the correct route simply as a list of the street names, buildings and other landmarks in the order in which they are encountered as the route is followed (Galea & Kimura, 1993).

Although such guidance learning is quite sufficient to solve many spatial problems, it is not a specifically *spatial* solution. An ordered list of landmarks encountered along a route encodes information about the temporal sequence in which they were experienced, but nothing about the spatial relationships between them. Other participants in Galea and Kimura's experiment (mostly males) did describe the route in spatial terms - as compass directions and distances between places en route. There was, moreover, a significant correlation between such performance and scores on a test of mental rotation - a standard measure of visuo-spatial ability in IQ tests.

The rat swimming towards the visible platform, or beacon attached to it, in the Morris pool, does not need to know anything about the spatial location of the platform or beacon with reference to any other feature of the pool or experimental room. He need only know that certain swimming movements cause the platform to come nearer. In order to attribute specifically spatial knowledge to the rat with any degree of confidence, we must alter the conditions of the experiment.

Off-goal Beacons

In an animal's natural environment, it must surely often be the case that his goal (whether home or food or another animal) is not conveniently marked by a salient beacon sitting right on top of it. If there is a beacon close by the goal, an animal may first approach the beacon by the guidance mechanism just outlined, but if the goal remains invisible, what is he to do next? If the goal is very close to the beacon, a random search round the beacon will find the goal soon enough. It is also clear that animals can learn, by a variety of mechanisms which differ in different species (see Rodrigo, 2002), the exact distance between beacon and goal, and thus confine their search to the appropriate distance from the beacon. But beyond a certain distance, it must often be important for animals to learn the direction from the beacon to the

goal, in order to confine their search to the correct location. Some beacons provide their own directional information, because they look quite different when viewed from different sides. But a perfectly symmetrical beacon provides no directional information, and yet there is ample evidence that rats will learn to search for a hidden goal only at the correct distance and direction from such a beacon (Biegler & Morris, 1996; Roberts & Pearce, 1998). How do they do it?

Sometimes, the experimenter's apparatus allows a simple solution. If rats are trained to swim to a submerged platform in the Morris pool, when the pool is surrounded by heavy black curtains and there are four salient landmarks round the perimeter of the pool to allow them to locate the platform, they learn about all four landmarks, and can continue to locate the platform when any two are available - but not with only one (Prados & Trobalon, 1998; Rodrigo, Chamizo, McLaren & Mackintosh, 1997). However, if one of these landmarks is immediately next to the platform, this one landmark may be enough to locate it (Chamizo, 2002). The explanation is presumably that they learn that the platform is a particular distance from the landmark, but also the same distance from the edge of the pool. This, and the fact that the platform is not outside the pool, is enough to prevent them searching in a circle round the landmark, without their needing to learn anything about the direction from the landmark to the platform as such.

However, rats can readily learn to swim direct to a submerged platform located 20cm due north of a beacon, even when the perfectly symmetrical beacon, and platform with it, are moved around the pool from trial to trial (Roberts & Pearce, 1998). This implies that they have learned not only the distance, but also the direction, from the beacon to the platform. Here then we have evidence of true spatial learning. What is its basis? How is direction computed? A wide variety of birds and insects use the sun as a directional cue under natural conditions, calculating direction by observing the angle between their goal and the sun's azimuth position (Rodrigo, 2002). In order to use the sun as a compass over any long period of time, of course, they must also make allowance for the movement of the sun during the course of the day - and over the seasons. In the laboratory, any distant, fixed source of stimulation can be used to provide a similar directional cue. In our own experience, the experimenter may have no idea what cues animals are using. When we wished to train rats to locate the submerged platform in a Morris pool by reference to four visual landmarks placed around the perimeter of the pool, we found that in order to ensure that rats were actually using these landmarks, it was necessary to rotate the landmarks (and platform with them) from trial to trial. Otherwise, they clearly used static directional cues (noises, draughts, odours in the room, perhaps even some compass sense) that we were unaware of. Presumably Roberts and Pearce's rats were using a similar, unknown directional cue. But it would surely be worth testing that rats do actually need a distant directional cue in conjunction with a beacon close to the platform, in order to find a platform that lies in a particular direction from the beacon. One could provide a specific distant cue, and in addition to moving the beacon and platform from one part of the pool to another between trials,

one could also *rotate* platform, beacon and directional cue all together from trial to trial during the course of training. Test trials on which only the directional cue was rotated should then reveal whether the rats now searched for the platform in the new direction.

Piloting: The Use of Configurations of Two or More Landmarks

The preceding case, where the rat uses a nearby beacon and a distant directional cue to locate the goal, is only a special case of the use of two (or more) distal landmarks to locate a goal - the standard procedure in experiments employing the Morris pool. Rats' ability to find the platform under such conditions, and the dependence of that ability on the integrity of the hippocampus, appeared to provide one of the strongest confirmations of O'Keefe and Nadel's hypothesis of a cognitive map located in the mammalian hippocampus. I shall usually avoid using that term, in part because it is now used in too many different ways. For O'Keefe and Nadel, of course, a cognitive map is a particular, highly developed theoretical construct. Gallistel (1990), however, regards any use of spatial information about distances and directions as evidence of a cognitive map. Others (e.g., Pearce, Roberts & Good, 1998) use the term in a relatively atheoretical way to refer to the ability to locate a goal by the use of extraneous landmarks; while Prados and Redhead (2002) move back and forth between more and less theoretical uses - although sometimes qualifying the term with further adjectives (traditional, gestaltic) when referring to O'Keefe and Nadel's theoretical use.

The evidence reviewed by Chamizo (2002) and Prados and Redhead (2002) makes it clear that many of the phenomena found in experiments on Pavlovian and instrumental conditioning and simple discrimination learning are also observed in experiments where rats are required to locate a goal by means of two or more distal landmarks. These phenomena include: blocking, overshadowing, latent inhibition, perceptual learning, and changes in attention to relevant and irrelevant cues. Standard associative theories have been advanced to explain all these phenomena (Rescorla & Wagner, 1972; Mackintosh, 1975; McLaren & Mackintosh, 2000; Pearce & Hall, 1980; Wagner, 1981). There is thus good reason to reject O'Keefe and Nadel's original claim that such spatial learning absolutely requires explanation in terms of a non-associatively acquired cognitive map. Whether there is additional evidence from such experiments that would provide support for their account is a question I return to below.

Blocking and Overshadowing

This is not to say that associative accounts of landmark learning are free of problems. As McLaren (2002) points out, there is an obvious tension between the occurrence of blocking and overshadowing between landmarks and the evidence that animals often seem to learn about all available landmarks, but navigate without error on the basis of any small sub-set. Error-correcting rules that allow the prediction of blocking naturally imply that if

four landmarks are available for locating a goal, they will share the available associative strength between them (although the more salient ones might run away with most), with the consequence that the associative value of any subset of the four will on average be substantially less than that of all four together. McLaren's model retains error correction, but solves this problem by supposing that the system uses the distribution of activation over units coding the co-ordinates of the goal location, rather than their overall level of activation, and that this distribution can be independent of the number of landmarks being processed. Thus having been trained with four equally salient landmarks, the system will respond accurately with any two. But the use of error correction ensures that it is also easy to predict blocking. Blocking is generated because learning about any newly added landmark will be slowed down, rather than prevented. As a matter of fact, many theories of blocking in Pavlovian conditioning assume that learning about the added cue is prevented rather than merely retarded. It remains to be seen whether there is any difference between blocking between landmarks and blocking between Pavlovian CSs in this respect.

Associative theories have no difficulty in accounting for the finding that intra-maze cues, or a beacon above the platform in a Morris pool, will overshadow learning about the external landmarks that also define the location of the goal (March, Chamizo & Mackintosh, 1992; Redhead, Roberts, Good & Pearce, 1997; Roberts & Pearce, 1998). It does, however, seem difficult to reconcile overshadowing of one landmark by another with the observation that rats will learn about all four landmarks when they are available, but can solve the problem with any two. McLaren's model indeed does not predict any genuine overshadowing, and he interprets the results of an experiment by Sanchez-Moreno, Rodrigo, Chamizo and Mackintosh (1999) in terms of generalisation decrement rather than competition for associative strength. Whether or not this is a reasonable account of these results, it is too soon to say whether evidence of apparent overshadowing between landmarks is a serious theoretical problem; at present, the evidence is sparse, and we do not know what are the conditions under which such overshadowing might occur. Perhaps overshadowing will not be observed when landmarks are spaced evenly round a pool, so that each provides an independent directional fix on the location of the platform. It is notable that the overshadowing observed in the experiments of Sanchez-Moreno et al. was between two immediately adjacent landmarks, where it seems plausible to argue that they really were redundant. Under other circumstances, it is possible that landmarks must differ greatly in their relative validity or in their proximity to the goal (as in the experiments by Spetch, 1995) before one can overshadow the other.

Prior Exposure

O'Keefe and Nadel's theory suggested that prior exposure to a set of landmarks will allow animals to build up a map, and that they will therefore learn to use those landmarks to locate a goal more rapidly than animals not given such exposure to them. Prados and Redhead's (2002) review finds little

support for this analysis, but rather evidence of latent inhibition, perceptual learning and changes in attention. Here too, however, there remain questions unanswered. Although many of the results they review are consistent with the associative theory of perceptual learning of McLaren and Mackintosh (2000), it is equally clear that many fall outside the scope of that model. For example, if rats have learned that a particular set of landmarks has previously signalled the location of a submerged platform in the Morris pool, they will use those landmarks to find a new location of the platform more rapidly than controls, even if the actual configuration of the landmarks, as well as the location of the platform, changes between the two phases of the experiment. Conversely, if they have learned that there is no consistent relationship between landmarks and platform, they will be slower to learn than controls who have not seen the landmarks before (Prados, Redhead & Pearce, 1999; Redhead, Prados & Pearce, 2001). These are hallmarks of the kind of attentional effect seen in other experiments on discrimination learning - such as those on intradimensional and extradimensional shifts (e.g., George & Pearce, 1999): animals have learned to attend to cues that predict reinforcement and to ignore cues that are uncorrelated with the availability of reinforcement. They are quite different from the perceptual learning effects produced by unreinforced exposure to sets of landmarks in experiments by Prados, Chamizo and Mackintosh (1999), Rodrigo, Chamizo, McLaren and Mackintosh (1994) and Sansa, Chamizo and Mackintosh (1996).

It is clear that one factor influencing the outcome of these experiments is whether rats have to swim to the platform in the first phase of the experiment, or are simply placed on the platform and allowed to observe the landmarks (Prados, Redhead & Pearce, 1999, Experiment 3). This makes sense. Theories of attention assume that differential reinforcement is needed to drive changes in attention, and these attentional effects are mostly observed when rats are required to swim in the pool in the first phase of the experiment. Finding the platform after active swimming must be a more reinforcing event than simply being placed on it. McLaren and Mackintosh (2000) have pointed to other cases, most notably transfer along a continuum (Lawrence, 1952), where differential reinforcement and unreinforced pre-exposure in the first phase of the experiment have quite different consequences.

Alas, the story is not quite so simple. Pearce, Roberts, Redhead & Prados (2000) found that placement on the platform in the first phase of the experiment was sufficient to produce effects on subsequent learning that would certainly not be predicted by McLaren and Mackintosh (2000), and which are better (although perhaps not perfectly) accounted for by supposing that this experience was sufficient to teach rats to attend to relevant landmarks and ignore irrelevant ones. Even so, however, they also found important differences between the effects active swimming and passive placement on the platform. If such placement is sufficient to drive some changes in attention, it is still reasonable to suppose that it is less effective than finding the platform after swimming round a pool. And the results of an earlier set of experiments by Prados, Chamizo and Mackintosh (1999), in which rats were exposed to the landmarks surrounding a pool by being placed

on a distinctive observation platform in the centre of the pool, are more consistent with McLaren and Mackintosh's (2000) theory of perceptual learning than with any theory of changes in attention to relevant and irrelevant cues. There is certainly no doubt that some of the earlier maze pre-exposure experiments of Rodrigo et al. (1994) and Sansa et al. (1996) are very much more easily explained by that theory than by theories of attention. It seems plausible to suppose that the opportunity to explore a maze is a closer approximation to wholly unreinforced pre-exposure than is placement on a small platform surrounded by water. But is also quite possible that there are other critical differences between those situations where pre-exposure seems to result in changes in attention, and those where it simply causes the sort of perceptual learning effect analysed by McLaren and Mackintosh. As Pearce et al. (2000) conclude, "it is likely that further research will reveal that the influence of landmark preexposure will depend on the interaction between a number of processes."

Geometry

We live in a geometrical world, with square rooms and rectangular corridors with right-angled turns. So it is not surprising that we locate objects by reference to geometrical features - in the near corner, in the middle of the room, at the far end, and so on. Although the natural world of rats or other rodents can hardly be so dominated by such regular right-angled shapes, the work of Cheng (1986) and Gallistel (1990) establishes that they often use geometrical information to locate a goal. If food is hidden in one corner of a rectangular arena, rats will rapidly learn to search in that corner, but will also search in the diagonally opposite corner, even though there are additional salient cues that signal which corner contains the food.

In Cheng's experiment, the geometry of the arena gained control over the rats' behaviour, even though there was another better predictor of the whereabouts of the food. In a series of experiments in the Morris pool, Pearce, Ward-Robinson, Good, Fussell and Aydin (2001) explicitly examined whether the presence of a beacon attached to the platform would overshadow or block learning about the relationship between the location of the platform and the geometrical shape of the pool, when the normally circular pool was fitted with inserts to make it triangular. They found no evidence whatsoever of blocking or overshadowing.

These results are, of course, exactly what O'Keefe and Nadel's theory might have led one to expect in experiments on multiple landmark learning. The apparent implication is that although learning about landmarks is not the province of a specialised module, independent of humdrum associative learning, geometrical information is indeed processed by just such a module - as Cheng and Gallistel have argued. It remains to be seen whether a multiplicity of salient landmarks would be equally unable to overshadow or block geometrical information. And it will also be important to see whether one source of geometrical information could block or overshadow another. This should not be too difficult. When Benhamou and Poucet (1998) trained

rats to find a platform, whose location was defined by its relationship to three distinct landmarks arranged in a triangular array, test trials revealed that the rats used the geometrical arrangement of the landmarks rather than their distinctive features to locate the platform. If rats were trained to find a platform located at the apex of a triangular shaped pool, it should therefore be possible to provide a second geometrical cue by adding a triangular array of three identical landmarks outside the pool, positioned such that the platform was midway along the base of this new triangle. Would one observe overshadowing or blocking between these two geometrical cues?

Does Use of Multiple Landmarks Imply a Map-Like Representation of Space?

Animals' ability to use information about the shape of their environment is remarkable, but although such information is surely spatial, we are not yet postulating any map-like knowledge. Similarly, although the ability to locate a hidden goal by reference to its distance and direction from a number of distal landmarks clearly implies the possession of some spatial knowledge, this knowledge still falls short of that implied by possession of a map. Someone who uses a map of a city to find his way from A to D, detouring via B and C, can also use the map to find the direct route from A to D bypassing B and C altogether. Presumably, therefore, possession of a cognitive map in O'Keefe and Nadel's sense implies that experience of the route A-B-C-D not only gives knowledge of the direction and distance between A and B, B and C, and C and D, but is also sufficient to allow deduction of the distance and direction from A to D in the absence of any experience of the direct route from one to the other.

Given that a rat's information about landmarks must initially be acquired from a limited local perspective, the critical question would seem to be whether, and if so how, such local information about the relationship between landmarks in one part of the environment is combined with information about other landmarks in other parts of the environment. Only if the representations of such local scenes are somehow linked to one another, would an animal have a single representation of an entire environment. And only if they were combined in certain ways, would that global representation be one that encoded *spatial* information about the relationship between different parts of the environment. A simple, alternative possibility is that the representations of local scenes are linked together associatively because they occur in temporal contiguity to one another as the animal moves from one part of the environment to another. Just as maze learning was explained by Deutsch (1960) by postulating the formation of an associative chain that linked together the representations of cues in the maze in the temporal order in which they were encountered, so it might in principle be possible to provide a similar associative account of landmark-based navigation that did not appeal to any knowledge of the spatial relationship between one local scene and another. The nearest to such an account is that provided by Leonard and McNaughton (1990; see also Whishaw, 1991), who do however allow the rat knowledge of

the movements required to move from one scene to another. Gallistel (1990) and Poucet (1993), on the other hand, have argued that local views are eventually combined into a single framework that encodes the spatial relationships between them.

How to decide between these alternative views? As Rodrigo (2002) notes, the traditional experimental test has been to ask whether animals are capable of taking a novel short cut. The fact that Deutsch's simple model predicted such behaviour under certain circumstances should have been warning enough that this is hardly a decisive test, and Bennett (1996) concluded that the existing evidence of short-cutting provided no grounds for attributing anything like an integrated spatial map to any animal. One critical issue has been whether cues associated with the goal are visible at the point where an animal starts to take the short cut (see the dispute between Gould, 1986, and Dyer, 1991, about whether honeybees can fly straight to a goal when displaced by the experimenter). Another is that path integration or dead reckoning provides an efficient mechanism for short-cutting under many circumstances. And a third is that the short cut may not always be novel (another problem with Gould's experiment). Thus Morris (1981) trained rats to find a hidden platform in a swimming pool, always placing them into the pool at one particular point at the start of each trial. They still swam straight to the platform on a test trial when placed in the pool at a different position. But, as Prados and Redhead (2002) note, Sutherland, Chew, Baker and Linggard (1987) showed that this probably depended on the fact that on early training trials rats had initially swum at random round the pool, and had therefore had experience of approaching the platform from all possible directions.

An alternative approach to the question has been followed in some ingenious experiments by Brown (1992) on rats in a radial maze. Brown surrounded the central platform of the maze with opaque doors, each with a small circular opening through which the rats could look before making a choice. Thus they could only see down one arm at a time, but if they simply looked down an arm they had already entered on that trial, they were allowed to retrace and look down another. The critical question was whether, having retraced, they would go directly to an arm they had *not* visited on that trial, or whether they would be equally likely to choose any arm. In fact, they chose at random - once again retracing if they happened to look down an arm they had already entered. But if a rat retraces from arm 1 because he remembers visiting it already on this trial, and if he knows the spatial relationship between arm 1 and arm 4, which he has not visited on this trial, he should go direct to arm 4 in preference to arm 6, which he has visited already. If he is just as likely to go to arm 6 as to arm 4, but retraces as soon as he looks down arm 6, this implies that he does not know the spatial relationship between arms 1, 4 and 6. A subsequent experiment (Brown, Rish, Von Culin and Edberg, 1993) suggested that rats would choose to approach and look down unvisited arms in preference to already visited arms. But unfortunately it is open to an alternative explanation. The logic of Brown's experiments requires that, when on the central platform, and before they look down an arm, rats have no cue

available to locate an unvisited arm other than its remembered spatial relationship to the arms they have visited. Although the rats could only see down one arm at a time, there may have been other unidentified directional cues available in the experimental room, such as noises, odours or sounds, that were perfectly detectable from the central platform (see above, p. xxx). In order to rule out the possibility of any such reliance on static directional cues, it would have been necessary to rotate the maze and its surrounding visual landmarks from trial to trial. This was not done.

Much remains to be learned about whether, and if so how, animals integrate information about different locations into an overall representation of their environment. The evidence described by Chamizo (2002) suggests that associative mechanisms are involved in spatial integration. But it is also worth suggesting that many laboratory experiments place rather little premium on such integration. The radial maze task does not really require the rat to do anything more than construct a list of the arms already visited or not visited on a given trial. The cost of looking down, but then withdrawing from, an already visited arm is rather low, and the memory of having recently visited it is surely most effectively retrieved by a direct inspection of the arm. Spatial integration may occur only if the cost of error is higher. This seems more likely in a larger environment than that provided by most laboratory experiments. But it is also worth suggesting that the alternative explanations of short-cutting noted by Bennett (1996) are not just an exercise in carping criticism. To the extent that there are many ways by which animals can find their way direct to their goal, they may have little need to develop an integrated map of an entire environment. As I argue below, even navigation over very long distances may be achieved by rather simpler means.

Spatial Learning and the Hippocampus

O'Keefe and Nadel's theory was, of course, a neurobiological one, and it has generated a huge body of research on the role of the hippocampus in spatial learning and memory. The reviews by Macphail (2002), Rehbein and Moss (2002), and Good (2002) in this issue make it clear that the hippocampus is implicated in such behaviour in both birds and mammals, but it is clearly misleading to describe the hippocampus simply as the locus of a cognitive map.

Mammalian Evidence

There is no doubt that damage to the mammalian hippocampus can disrupt learning that has no obvious spatial content at all - the most striking example being trace eyeblink conditioning in the rabbit (Rawlins, 1985). But there can be equally little doubt that the hippocampus is also implicated in some specific aspects of spatial learning. The critical and best known observation is that, although hippocampal lesions do not impair rats' ability to use a localised beacon to find their goal, such lesions have a drastic effect on their ability to swim to the invisible platform in a Morris pool (Morris,

Garrud, Rawlins & O'Keefe, 1982; Pearce, Roberts & Good, 1998; Sutherland, Whishaw & Kolb, 1983). The obvious interpretation must surely be that such lesions have an effect on their ability to use configurations of distal landmarks to locate a goal.

Several lines of evidence have suggested to some commentators, however, that this conclusion may require at least some qualification. Thus Eichenbaum, Stewart and Morris (1990) and Whishaw, Cassel and Jarrard (1995) both found that if lesioned rats were given extensive training to swim directly to a visible platform, they continued to perform reasonably well when the platform was made invisible, and spent as much time as controls searching in the platform quadrant of the pool on test trials when the platform was absent. Whishaw et al. interpreted their results as evidence of "a dissociation between getting there and knowing where": lesioned rats, they proposed, could use external landmarks to define the location of the platform (they knew where it was), but could not learn to swim directly to it. They attributed this failure to an inability to use path integration or dead reckoning. Eichenbaum et al., however, showed that lesioned rats were not using the configuration of external landmarks to locate the platform in the way that normal rats do, but were rather relying on one or two prominent landmarks that were directly in line with the platform from the fixed starting point. When these landmarks were moved, the lesioned rats still swam straight towards them, while control rats continued to swim to the platform.

In both studies, lesioned rats were seriously impaired when required to learn a new place task with the invisible platform located in a different quadrant of the pool. Whishaw and Tomie (1997) confirmed this, and showed that this was because they persisted in searching for the platform in its original location. This seems most plausibly interpreted as another instance of hippocampal lesions impairing spatial reversal learning (see Rehbein & Moss, 2002) rather than any failure of path integration. Indeed, it is not entirely clear in what sense learning to swim to an invisible platform should actually depend on path integration or dead reckoning. But Whishaw and his colleagues have tested rats on a different task where path integration may certainly be involved. As described by Good (2002), rats were trained to leave their home base, located just below one of eight holes distributed round the edge of a large circular platform, in order to find a large piece of food hidden somewhere near the centre of the platform, which they then took back to their home base to eat. Both control and lesioned rats learned this task (Maaswinkel, Jarrard & Whishaw, 1999; Whishaw & Maaswinkel, 1998), but when the location of the home base was moved for a probe test, control animals, after an initial return to their old home location, immediately went to the new location, and went there directly on subsequent trials. Their behaviour on the first test trial implies that they knew the location both of their old home base and of the new one. The former knowledge must have been based on landmarks, the latter might have been based on dead reckoning. Lesioned rats, however, did not learn to return to the new home base. Once again, of course, they were being asked to learn a reversal, and the fact that they persisted in returning to the old base suggests that their problem was indeed one of

reversal learning. But when rats were blindfolded for a series of test trials with the home base in a new location, control rats always went immediately back to the new base, but lesioned rats chose at random. This does seem to suggest a failure of path integration. But it is possible that the loss of flexibility implied by inefficient reversal learning extends to an inability to switch strategies. Lesioned rats presumably relied on a prominent nearby landmark to identify the location of their home base during initial training, but may have been unable to switch to dead reckoning when that became the only feasible strategy on the blindfold tests. The critical test would be to see if lesioned rats were capable of returning directly home if trained blindfolded from the outset.

There is other evidence that hippocampal damage does not impair path integration or dead reckoning (Alyan & McNaughton, 1999), but one reason for questioning whether a failure of path integration contributes to the effects of hippocampal lesions on spatial learning and navigation is the accumulation of evidence that hippocampal lesions affect performance on a much wider range of discrimination problems, none of which require animals to navigate to a goal at all. This evidence has, of course, been used to argue that although hippocampal lesions undoubtedly disrupt rats' ability to use configurations of landmarks to locate a hidden goal, this is not a deficit in spatial learning *per se*, but rather a special case of a wider problem. Thus Eichenbaum and Cohen (2001) have argued that hippocampal animals are unable to solve relational discriminations; Sutherland and Rudy (1989) that their difficulty is with any kind of configural discrimination; and Hirsh (1974), Rehbein and Moss (2002), and Good and Honey (1991) that their problem is one of contextual retrieval.

Each of these authors can point to evidence of deficits in non-navigational tasks in support of their theory (see Good, 2002, and Rehbein & Moss 2002). My own difficulty with Eichenbaum and Cohen's account is that it is not easy to discern the common thread that unites the range of problems they describe as relational. The success of their theory seems to hinge on the vagueness of their characterisation of relational learning. As Good (2002) argues, there is certainly evidence consistent with Sutherland and Rudy's configural theory, but a sufficient number of studies have been able to dissociate a specifically spatial deficit from a more general configural one to question whether it can be correct. Whether their subsequent modifications will rescue it, or simply make it harder to evaluate remains an open question. The suggestion that hippocampal lesions disrupt contextual retrieval finds direct support in a number of studies reviewed by Good (2002), and one strong argument in its favour is that appropriate contextual retrieval is what is required by tests of episodic memory with which human amnesic patients have such difficulty. What is perhaps lacking, however, is direct evidence of the role of contextual retrieval in spatial navigation tasks.

Much has been learned about the functions of the mammalian hippocampus in the past 25 years – and much remains to be learned. Some of the disputes between rival accounts will no doubt be resolved by more refined

and incisive behavioural experiments, but some will certainly be resolved by further advances in neuroscientific techniques. I have talked glibly about the effects of lesions to “the hippocampus”, when a variety of different techniques have been employed by different experimenters to destroy a variety of different structures. It is beyond my competence to pass judgment here, but it is now abundantly clear, as Good (2002) establishes, that “the hippocampus” is not a unitary system and that selective damage to particular structures within the hippocampal system often have quite different effects. It is worth suggesting that similar dissociations may be found as more precise lesions are developed in studies of “the avian hippocampus”.

Food-Storing Birds

In birds, a quite different line of evidence suggests a role for the hippocampus in spatial learning and memory. As Macphail notes, those species that store food in a variety of different caches have a relatively larger hippocampus than related species that do not store food (e.g., Krebs, Sherry, Healy, Perry & Vaccarino, 1989). There is also seasonal variation in the size of the hippocampus in storing species that coincides with the increase in autumn in the amount of storing they engage in, and evidence that it is the experience of storing that drives this increase (Clayton, 1996; Healy, Clayton & Krebs, 1994). A similar seasonal variation in the size of the hippocampus is seen in brood parasitic birds, such as cowbirds, as they search for suitable host nests in spring (Clayton, Reboresda & Kacelnik, 1997). But Macphail points to what he sees as a significant problem in what seems, on the face of it, to be a straightforward and compelling story. Differences in food storing in the wild may be associated with differences in the relative size of the hippocampus, but they are not, he argues, associated with consistent differences in spatial learning or memory in the laboratory.

A variety of experiments with parids has examined whether food storing species (e.g., marsh tits and willow tits) outperform non-storing species (e.g., great tits and blue tits) in experimental tests of spatial learning and memory. In general, they have not (see Macphail & Bolhuis, 2001, for a more detailed review). However, given a task that can be solved either by learning about the location of a target or about its colour or shape, storing species have consistently responded to its location significantly more than non-storing species (Brodbeck & Shettleworth, 1995; Clayton & Krebs, 1994a). The second family of birds that has been extensively studied is corvids - although a problem here is that most corvid species engage in storing food to a greater or lesser extent. One exception is the jackdaw, which has performed significantly more poorly than storing species in two different spatial memory tasks (Clayton & Krebs, 1994b; Gould-Beierle, 2000). The four North American corvid species that have been studied, Clark's nutcracker, pinyon, Mexican and scrub jays, all store food, but are usually placed in this rank order for their dependence on storing. Clark's nutcrackers, for example, store up to 30,000 pine seeds in the autumn, which they retrieve during the course of the winter, while scrub jays tend to cache food for only a few hours or days

at a time. Whether this should lead one to expect a similar ranking of their performance in laboratory tasks which test spatial memory over a few minutes or at most hours, is not at all obvious. And, as Macphail shows, no consistent picture has emerged from such studies.

My own reading of this literature leads me to a rather different conclusion from Macphail's. The comparison of storing and non-storing parids reveals that the former are more likely than the latter to respond to the location of a target stimulus rather than to its visual appearance. The comparison of storing and non-storing corvids reveals that the former outperform the latter on tests of spatial learning or memory. At the very least, this suggests that storing species are more likely than non-storers to attend to, and therefore learn about, the spatial location of a target. This may not mean that storers have a superior spatial memory as such (located in the hippocampus), but it will not really do to dismiss these results, as Macphail and Bolhuis (2001) do, on the grounds that they prove only that spatial cues are more salient for storers than for non-storers, just as visual stimuli are more salient for diurnal than for nocturnal animals. What is the difference in peripheral sensory systems that would make spatial cues more salient for one species than another?

Macphail does point to an important and consistent finding from studies of "window shopping", where birds are initially allowed to see, but not collect, food placed in various locations, and then return some minutes or hours later to collect it. There is no consistent difference between storers and non-storers when the food is visible, but not obtainable, in the first phase of the experiment; but storers outperform non-storers when the food is hidden in this first phase and the birds have to search many different sites to find it. In this case, the non-storers, unlike the storers, make errors on test by going back to sites they examined in the first phase of the experiment - even when those sites never contained food. Since they do not make errors by going to previously unvisited sites, Macphail concludes that they must therefore "recall locations as efficiently as storers - that, in other words, their spatial memory is as efficient as that of storers". Leaving aside the possibility that they are not recalling previously visited sites at all, but simply have consistent preferences for some sites over others, it hardly seems an efficient memory system that is unable to remember whether or not there was food in a particular location. As the work of Clayton and Dickinson (1999; Clayton, Yu & Dickinson, 2001) has shown, scrub jays remember not only where they cached food, but also whether they later retrieved it, what kind of food it was, and how recently they cached it.

Long Range Navigation: Homing Pigeons

Kramer's "map and compass" hypothesis, as both Rodrigo (2002) and Macphail (2002) make clear, remains the most popular account of the ability of migrating birds to navigate over long distances, or of pigeons' ability to head off in a homeward direction when released many kilometres from home at a location they have never seen before. Clock-shift experiments establish

beyond doubt that pigeons, like honeybees, use the sun as a compass; but unless pigeons know that their home loft is, say, due north of the release site, a compass that tells them which way north is will not get them home. Equally relevant here is Perdeck's (1958) demonstration that adult migrating starlings, if captured and transported several hundred kilometres south from their normal autumnal migration route, will compensate for this displacement and still end up in their traditional winter quarters, but that young, inexperienced birds simply carry on flying in their original direction and end up several hundred kilometres south of where they should be. The adults have both a map and a compass; the young birds have only a compass.

Once again, however, we should not be misled by a particular choice of words. The "map" that tells a pigeon that home is north of a novel release site cannot possibly be the same as the "map" that uses a configuration of distal landmarks to locate a hidden goal. As Pearce (1997) rightly remarks, they have had no opportunity to construct a map containing information about landmarks at a release site they have never seen before. Bingman's hippocampal lesion data confirm the distinction: lesioned pigeons can still head off in a homeward direction from a novel release site, but have great difficulty in actually finding their home loft once they have arrived in its vicinity (Bingman, Bagnoli, Ioale & Casini, 1984). The final location of the home loft is achieved by the use of visual landmarks surrounding it, as Schmidt-Koenig (1979) showed many years ago, in much the same way that the location of a hidden platform in the Morris pool is based on the configuration of landmarks surrounding the pool. In both cases, the ability to locate the goal depends on the integrity of the hippocampus. But the "map" that tells the pigeon that home is north of a novel release site is not based on landmarks at all. It does not need to be, because all it needs to provide is rather crude directional information. In fact, of course, if the release site is novel, the pigeon's knowledge must be based on extrapolation. A plausible story would be as follows: if a pigeon flies 10km south from the home loft on initial training flights and, as he does so, finds himself flying up a gradient of increasing odour from a distant petrochemical factory, or increasingly loud infrasounds from waves beating on a distant shore, then if he is released at a site 100km from home where there is a strong petrochemical odour, or louder than usual infrasound, it is a reasonable bet that he is again south of home. Sometimes such extrapolation will get it wrong, but there is good evidence that some release sites cause paradoxical, but systematic, errors in initial orientation (Keeton, 1974).

A further lesson from the homing pigeon research should by now be familiar. It is important to remember that the psychologist's attempts to isolate different mechanisms underlying spatial learning and navigation do not imply that animals will rely on only one of these mechanisms to solve a particular problem. Homing pigeons certainly learn to use nearby visual landmarks to locate their home loft, but clock-shift experiments can sometimes cause them to head off in the wrong direction even if they are released only 1 or 2 km from home, where they must surely be able to recognise some landmarks associated with home (Keeton, 1974). Similarly, the first time they are

released from a new distant site, they must presumably rely on their crude directional map, plus compass, to head off in the correct direction. But if the same release site is used again, they will start learning to follow a route home defined by visual landmarks (Bingman, Ioale, Casini & Bagnoli, 1987). And although shifting their clock will cause normal birds to head off in the wrong direction, even from a familiar release site, anosmic clock-shifted birds will head off in the correct homeward direction by relying on this learned visual route (Gagliardo, Ioale & Bingman, 1999). So it is clear that pigeons learn to use both visual landmarks and an odour-based map (plus compass) to find their way home both from near and from far release sites. Does this imply that there is no interaction or competition between alternative solutions, as studies of blocking and overshadowing have led us to expect in the case of Pavlovian conditioning or many other cases of spatial learning? Not necessarily, of course. But it would be interesting to see whether or not evidence of blocking could be obtained here. If pigeons were trained to fly home from a whole series of novel release sites north of home, but were then repeatedly released from a new site further north of home, would they be less likely to learn about the visual landmarks associated with this new release site than birds that had received no earlier training with the initial series of northern release sites?

CONCLUSIONS

The contributions to this issue of *Psicologica* provide eloquent testimony to the vigour and ingenuity of recent research on spatial learning and memory, and on the functions of the hippocampus and related structures. That research has transformed our perception of spatial cognition, in addition to significantly advancing our understanding of the diverse range of mechanisms that underpin animals' ability to find their way around their world. There is no doubt that the impetus for much of this research was provided by O'Keefe and Nadel's book. Not all of their theoretical ideas have survived the onslaught of this research unscathed, but if the value of a theory is to be found in the new ideas and findings it generates rather than its ultimate truth, then *The Hippocampus as a Cognitive Map* deserves its status as a modern classic.

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