

Review

Small-scale spatial cognition in pigeons

Ken Cheng^{a,*}, Marcia L. Spetch^b, Debbie M. Kelly^c, Verner P. Bingman^d

^a Centre for the Integrative Study of Animal Behaviour, Department of Psychology, Macquarie University, Sydney, NSW 2109, Australia

^b Department of Psychology, University of Alberta, Edmonton, Alta., Canada T6G 2E9

^c Department of Psychology, University of Saskatchewan, Saskatoon, Sask., Canada S7N 5A5

^d Department of Psychology, J.P. Scott Center for Neuroscience, Mind and Behavior,
Bowling Green State University, Bowling Green, OH 43403, USA

Received 28 August 2005; accepted 28 November 2005

Abstract

Roberts and Van Veldhuizen's [Roberts, W.A., Van Veldhuizen, N., 1985. Spatial memory in pigeons on the radial maze. *J. Exp. Psychol.: Anim. Behav. Proc.* 11, 241–260] study on pigeons in the radial maze sparked research on landmark use by pigeons in lab-based tasks as well as variants of the radial-maze task. Pigeons perform well on open-field versions of the radial maze, with feeders scattered on the laboratory floor. Pigeons can also be trained to search precisely for buried food. The search can be based on multiple landmarks, but is sometimes controlled by just one or two landmarks, with the preferred landmarks varying across individuals. Findings are similar in landmark-based searching on a computer monitor and on a lab floor, despite many differences between the two kinds of tasks. A number of general learning principles are found in landmark-based searching, such as cue competition, generalization and peak shift, and selective attention. Pigeons also learn the geometry of the environment in which they are searching. Neurophysiological studies have implicated the hippocampal formation (HF) in avian spatial cognition, with the right hippocampus hypothesized to play a more important role in the spatial recognition of goal locations. Most recently, single-cell recording from the pigeon's hippocampal formation has revealed cells with different properties from the classic 'place' cells of rats, as well as differences in the two sides of the hippocampus.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Pigeons; Landmarks; Search; Touch-screen; Hippocampus; Geometry

Contents

1. Introduction	116
2. Review	116
2.1. Pigeons on the radial maze and analogs	116
2.2. Landmark use in pigeons	117
2.2.1. Open-field tasks	117
2.2.2. Landmark use in touch-screen tasks	118
2.2.3. General principles of learning in landmark use	120
2.2.4. Averaging space and time	121
2.2.5. Images on monitors and places in the world	121
2.3. Geometry and features	121
2.3.1. Geometry, features, and pigeons	122
2.3.2. Recent research on wild bird species	122
2.4. Hippocampal control of spatial cognition in pigeons	123
2.4.1. Lesion studies	123
2.4.2. Single-cell recording in the pigeon's hippocampal formation	124

* Corresponding author. Tel.: +61 2 98508613; fax: +61 2 98509231.

E-mail address: ken@galliform.psy.mq.edu.au (K. Cheng).

3.	Discussion	124
3.1.	Themes common to other domains	124
3.2.	The role of the hippocampal formation	124
3.3.	Further research	124
4.	Conclusion	125
	Acknowledgements	125
	References	125

1. Introduction

The laboratory rat has long featured in research on spatial cognition. Even in the first half of the 20th century, its spatial performance was used to argue for latent learning (Tolman and Honzik, 1930) and inferential reasoning (Maier, 1929). Interest in the capacity of the rat's spatial memory exploded following the influential demonstration of their excellent performance on the radial maze (Olton and Samuelson, 1976). Just as influential was the swimming pool task pioneered by Morris (1981). Interest in the hippocampus of the rat also exploded with the discovery of place cells (O'Keefe and Dostrovsky, 1971), and O'Keefe and Nadel's (1978) classic, *The Hippocampus as a Cognitive Map*, has been cited over 3000 times.

In contrast, laboratory studies of spatial cognition in birds have been modest. Birds are of course known for long-distance, global scale navigation (Berthold, 2001), with the homing pigeon being the model species despite its nonmigratory nature (Wallraff, 2004; Wiltschko and Witschko, 2003). Because pigeons have a home that they return to, small-scale navigation, in the form of pinpointing their home in the last stage of the journey, is also important to them ecologically. The use of landmarks and the hippocampus are implicated in the last stage of homing (Bingman et al., 1984). Laboratory studies allow precise stimulus control and precise manipulations that are difficult with natural landmarks such as trees. Domestic pigeons have long been a favorite subject for research on animal learning. With the flourishing of comparative cognition in the 1980s came laboratory studies on spatial cognition in the pigeon. Bill Roberts played an important role in this line of work because his work on the radial-maze task in pigeons (Roberts and Van Veldhuizen, 1985) stimulated much of the research that followed. In this paper, we review this body of laboratory work on spatial cognition in pigeons, and discuss a number of themes that have arisen from the research.

2. Review

2.1. Pigeons on the radial maze and analogs

The radial maze used for rat experiments (Olton and Samuelson, 1976) consists of a central platform with long narrow arms radiating from it, typically eight in number. Food is placed at the ends of the arms. Olton and Samuelson (1976) discovered that the rats could retrieve food from the arms with very few repeat visits to already visited arms. With little training, rats could visit an average of ~ 7.5 arms in their first eight choices.

In doing this task, spatial memory is used, rather than cues left on the maze or stemming from the food (Roberts, 1984).

Bond et al. (1981) and Olson and Maki (1983) exposed pigeons directly to a radial maze and tested their spatial working memory. The birds performed poorly, much poorer than the rats. Roberts and Van Veldhuizen (1985) thought that the radial maze was an unnatural task for pigeons. Rats live in burrows with inter-connecting tunnels, and the long narrow arms of a radial maze make an analog of tunnels. Pigeons on the other hand forage over open space, and tunnel-like structures are strange to them. Roberts and Van Veldhuizen started by training their pigeons to remember just one visited arm. By gradually increasing task demands, the birds eventually managed to perform the eight-arm radial maze almost as well as rats, choosing 7.37 different arms on average out of their first eight choices of arms. A series of further experiments with the same trained birds then established many parallels between pigeons and rats in their performance on the radial maze.

This paper led to a replication with some variations by Spetch and Edwards (1986). They dispensed with arms altogether, instead placing eight feeders in an open room. In their most successful version of the task, feeders, which consisted of milk cartons with the tops cut off, were placed in a circular arrangement on the floor of the testing room (Fig. 1). The pigeons took to this task readily. Their search accuracy was well above chance on initial trials and improved to about 90% correct choices within 20 trials. Moreover, computer simulations revealed that accuracy was well above the level expected on the basis of response algorithms, and the birds transferred their accurate search to novel linear arrangements of the food sites.

Spetch and Honig (1988) used this open-field analog of the radial maze to explore characteristics of pigeons' spatial work-



Fig. 1. Example of a set up of feeders made from milk cartons used by Spetch and Edwards (1986) and Spetch and Honig (1988).

ing memory. First, they demonstrated that a stable arrangement of spatial landmarks between trials facilitates spatial working memory. The room contained four landmarks placed on the floor and three pictures placed on walls. For birds in group constant, the locations of these landmarks were constant across trials. For birds in group variable, the landmarks were randomly rearranged between trials, but in constant locations within trials. Birds in the constant-landmark group were significantly more accurate than birds in the variable-landmark group in forced-choice tests that ruled out the use of response strategies. This difference in accuracy did not appear to reflect a general disruption in performance because the time taken to complete four choices was virtually the same for the two groups. Spetch and Honig suggested that being able to form a stable map of the landmarks in the room facilitated performance. A stable map was not possible when landmarks were shifted on every trial. Thus, these results suggested that pigeons have a map-like rather than a list-like representation of spatial locations. Roberts (1984) and Mazmanian and Roberts (1983) reached the same conclusion about rats' spatial representation.

The duration of retention was also investigated. Spetch and Honig (1988) found that pigeons' memory remained accurate with retention intervals of up to 32 min but declined significantly and was not above chance level with a 2-h retention interval. Spetch (1990) found that pigeons' accuracy decreased significantly but remained above chance at a 1-h retention interval. The pigeons' accuracy in choosing between one previously visited site and one newly baited site was not affected by whether they had visited 2, 4 or 6 sites prior to the retention interval. Thus, memory load within the range of 2–6 locations was not a significant determinant of performance, but retention intervals of longer than an hour reduced working memory accuracy.

Pigeons also performed reasonably well on an operant analog of the radial maze (Zentall et al., 1990). A large panel of keys in a 5×5 array was used, five of which were lit for a trial. The bird had to peck a key a number of times. It was reinforced while the keys were extinguished for a short time. All five keys were then relit, and the bird had to peck an as yet 'unvisited' key. The pigeons performed better with the keys spread over two dimensions rather than in a line, and with each key having a distinctive hue rather than the same white color.

In the radial-maze work then, pigeons proved especially capable with discrete unconnected 'patches' of food, even when the patches were on a vertical screen of a monitor. Perhaps pigeons have evolved the ability to keep track of the foraging payoffs of patches in their natural world, and are tapping this ability in the laboratory tasks.

2.2. Landmark use in pigeons

Radial-maze studies investigated memory for multiple locations, but did not address how any location is coded. With O'Keefe and Nadel's (1978) notion of cognitive maps in rats, and a picture-like template representation suggested for bees (Cartwright and Collett, 1982, 1983), interest in how birds might code a location with respect to surrounding landmarks arose.

2.2.1. Open-field tasks

Two papers appeared in 1988 that marked the beginning of lab-based research on the use of landmarks by pigeons. Spetch and Edwards (1988) continued to experiment with feeders made from milk cartons, but introduced cue manipulations to probe the cues used in localization. In training, three cartons were placed in a line on the floor close to one another, in an otherwise open room. The four pigeons were trained to find food in the middle one. They could use the global cues, those provided by the walls of the room, such as geometric shape (a topic reviewed in 2.3), or they could use the local cues provided by the array of feeders. The birds used both. On one test, local cues were eliminated by removing one of the incorrect feeders. With two feeders, the 'middle' cue could not be used. The birds were still largely correct. On another test, the entire array was moved to a different part of the room, rendering global cues useless. The birds persisted in choosing the middle carton, displaying use of the local cues. Finally, when local and global cues were put in conflict, the birds favored the local cues, although they also used the global cues to some extent. A similar strategy was later used to test other birds (Brodbeck, 1994; Brodbeck and Shettleworth, 1995; Hodgson and Healy, 2005), a topic that we will not review here.

In work done in Bill Roberts' laboratory, Cheng (1988) tested three pigeons extensively on their use of landmarks. The birds had to find food in a 1.6 m square arena. Removable walls surrounded three sides of the arena, and the fourth side served as an entrance with just a 10-cm high sill. The arena was covered with a thin layer of sawdust, providing a substrate for the pigeons to search in. An indentation was drilled into the floor of the wooden arena, and this served as the food well. During training, it held a number of mixed grains. The goal was thus in one constant location in the arena and in the room. Occasionally, the birds were tested without the well and the food.

With training, the birds learned to search accurately. The search distributions on control tests, which resembled the training situation except that food was absent, were clustered tightly about the goal location. When the pigeons had to measure a perpendicular distance from a surface, search accuracy followed Weber's law (Cheng, 1990, 1992). A measure of the spread of the distribution, the width of the distribution at 50% of peak search density, varied linearly with the distance to the surface. Such a pattern is found not only in many perceptual dimensions, but also in interval timing (Cheng, 1992).

Much of the Cheng (1988) paper examined how the central tendency of search, or peak place of search, shifted under various manipulations. One set of manipulations looked at changing the size of landmarks without displacing them. Neither changing the width of a strip of cardboard on the wall nor changing the height of a nearby block had any systematic effects on shifting the searching. The pigeons were evidently not matching the size of retinal projections made by landmarks, something that bees do (Cartwright and Collett, 1982, 1983). But the birds were clearly sensitive to distances from landmarks and surfaces. When a strip of cardboard on the wall, 20 cm from the target, was shifted along the wall, the pigeons shifted their searching in the direction of the landmark shift. But they maintained the 20 cm distance from

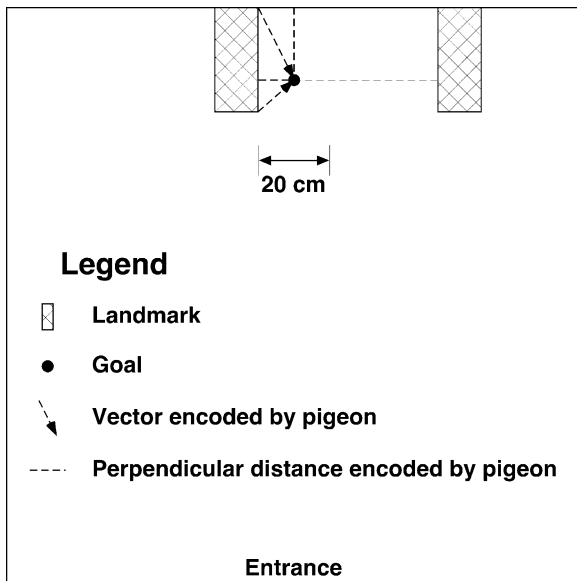


Fig. 2. An experimental set up and the information encoded by the pigeon. The set up was one found in Cheng (1989). The landmarks were unpainted wooden blocks. The goal was an indentation on the floor of the arena in which some grains were found. The entire floor was covered by a thin layer of wood chips. The pigeons learned to search the surface for hidden food by sweeping their beaks across the substrate. Results from this kind of search task suggest that the pigeon encodes two kinds of vectors. The first is a distance and direction, a classic vector, from a particular point in space, such as edges, corners, or discrete objects, shown as dashed arrows. The second is a perpendicular distance from an extended surface, shown as dashed line segments. The lighter and thinner dashed line segment indicates that this larger perpendicular distance was weighted less in the search process.

the wall. Results such as these, and further evidence (Cheng, 1989) led to the vector sum model, an idea adapted from Collett et al. (1986). The basic idea is that the pigeon encodes vectors to various landmarks. The vectors are classic algebraic vectors with components of distance and direction. Searching is based on an average of such vectors, with the use of multiple sources of information increasing search accuracy (Kamil and Cheng, 2001).

The vector sum model has had to be revised in light of later data on pigeons (Cheng, 1990, 1994, 1995; Cheng and Sherry, 1992) and other birds (Cheng and Sherry, 1992; Gould-Beierle and Kamil, 1998). But we maintain that the basic idea of encoding and using vectors measured from landmarks is still valid. Two kinds of vectors seem to be encoded by the pigeon: the distance and direction from particular objects or points in space, and the perpendicular distance to an extended surface (Fig. 2). The idea of multiple vectors to multiple landmarks has influenced other work on spatial cognition. Recently, for example, Hartley et al. (2004) found that the vector sum model proposed by Cheng (1988, 1989) accounted reasonably well for some human performance on a ‘virtual’ task of spatial localization.

Averaging the dictates of multiple vectors makes functional sense in increasing search accuracy, but pigeons do not always do this. Spetch et al. (1997) trained pigeons to search in the middle of an array of identical looking cylindrical landmarks. When the entire array was expanded in one or both dimensions

on unrewarded tests, the search peaks of the birds indicated that they generally followed individual landmarks. That is, the vector to one or two single landmarks was correct, while vectors to the rest of the landmarks mismatched those found in training. Spetch et al. pointed out, however, that the birds had not totally ignored the rest of the landmarks. Because the landmarks were identical, the configuration of landmarks had to be used to pick out the landmark whose vector they were to match. For example, if they were to search southeast of the northwest landmark, the array had to be used to figure out which landmark was the northwest landmark.

Spetch et al. (1997) used only a single array configuration in training. In more recent research, pigeons have been trained with multiple array configurations. Under such conditions, they proved able to learn abstract rules such as searching in the middle of two landmarks (Jones et al., 2002; Spetch et al., 2003), an ability previously shown in the food storing Clark’s nutcracker (Jones and Kamil, 2001; Kamil and Jones, 1997, 2000).

The open-field experiments came full circle back to Bill Roberts’ lab when Sutton (2002), under the supervision of Roberts, challenged the conclusions drawn by Spetch et al. (1997) and summarized by Cheng and Spetch (1998). Sutton thought that it would make sense for pigeons to use multiple landmarks to locate a target, as Kamil and Cheng (2001) had reasoned. She trained pigeons with two irregular configurations made of the same landmarks, with the landmarks distinct from one another in shape and color. The target location differed in the two configurations. The pigeons entered the arena from the same starting point on each trial. A number of results suggest that the configuration of multiple landmarks played a role in both identifying landmarks and the matching process of locating the goal. First, the birds discriminated readily between the two configurations made of the same set of elements and searched at the appropriate target location for each configuration, an ability also possessed by honeybees (Cheng et al., 1986). Second, when all landmarks were removed, the searching was much more scattered, indicating the important role of landmarks. The birds searched at the target locations of each configuration, as well as locations in between; these results support the vector sum model. Third, and most important, when any single landmark was shifted by 20 cm, the pigeons tended to ignore the shift, and ‘went’ with the rest of the configuration (Fig. 3). This shows that no single landmark was primary in controlling their search behavior, and that they used all the landmarks in searching for the goal.

2.2.2. Landmark use in touch-screen tasks

In the early 1990s Spetch, Cheng and colleagues set out to devise an automated task that could be used to study landmark use in pigeons. In this task, graphic landmarks were presented on a touch-screen equipped computer screen. The goal was an unmarked location on the screen, and searching behavior was defined as pecks at any location on the screen. This touch-screen task offers practical benefits: landmarks can be presented and manipulated automatically, searching locations can be recorded accurately and automatically, many trials can be given in each session, and several birds can be tested at the same time.

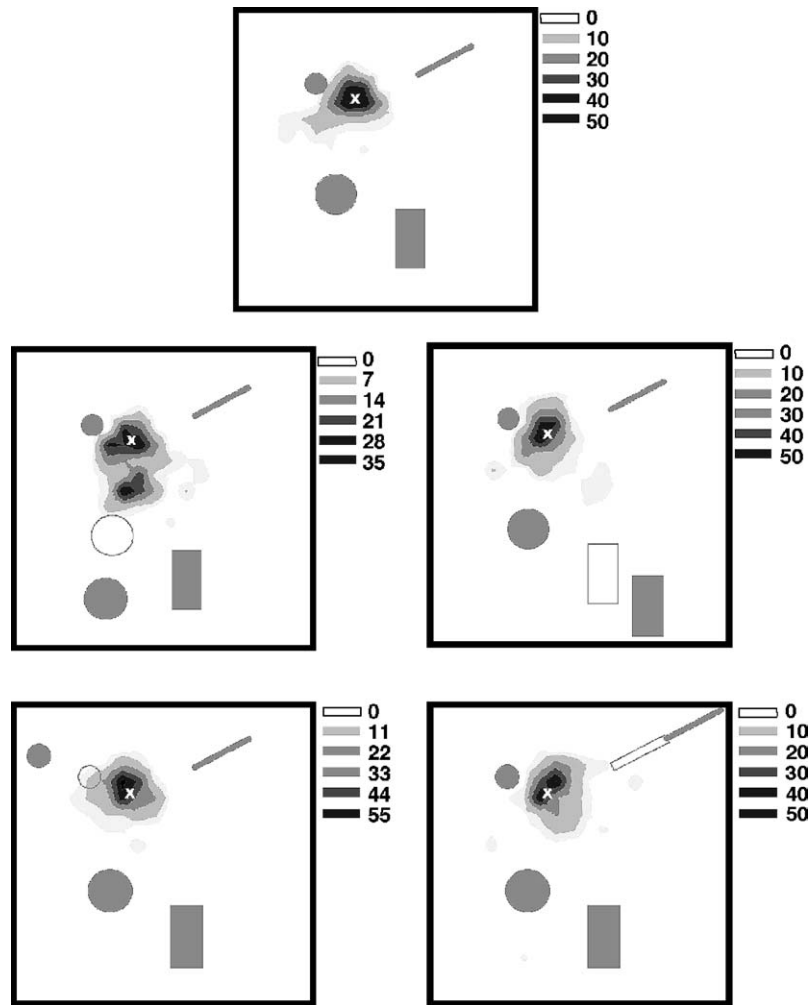


Fig. 3. Search distributions of pigeons from Experiment 2 of Sutton (2002). The top panel presents (control) tests with the training configuration, with the gray objects representing styrofoam landmarks differing in shape and color. The other panels show performance on tests with a single landmark displaced, with the unfilled shape indicating the training position of the landmark. The white xs indicate the goal location in training. The grayscale shades represent the total number of searches by all pigeons. Reprinted from Fig. 5 of Sutton (2002) with permission of the author and the publisher, American Psychological Association.

Even more important than the practical benefits, the touch-screen task provides an additional tool for assessing landmark use by pigeons, and one that differs in many ways from the tasks conducted in mazes or on the laboratory floor. First, the scale of space is an order of magnitude smaller on the touch-screen. Second, search behavior consists of pecking at a location on a screen rather than navigating through space to reach the goal. Third, the landmarks are two-dimensional (2D) images rather than three-dimensional (3D) objects. Fourth, the reinforcer appears at a feeder at a distance from the target location in the touch-screen task, whereas it appears at the target location in the open field. Fifth, the visual system employed by the pigeon is different in these two situations: Pigeons use the bilateral frontal visual field when viewing and pecking at close objects but they use the monocular lateral visual fields when viewing objects that are greater than 20 cm away (Zeigler and Bischof, 1993). These and other differences between the two tasks are important for determining the generality of spatial cognitive processes. When the same principles of landmark use are found in such differ-

ent situations, we can be more confident that they reflect central cognitive processes rather than task-specific processes.

In the first study conducted with the touch-screen spatial search task, Spetch et al. (1992) placed the unmarked target near an edge, with one landmark near it. When the goal was near the top of the screen and to the left of a graphic landmark, pigeons shifted their searching with the landmark in the horizontal dimension but not in the vertical dimension. When the goal and landmark were near the left edge, pigeons shifted vertically with the landmark but not horizontally. Birds were thus willing to shift parallel to a nearby edge, but not perpendicular to it, a pattern replicated in studies conducted on the laboratory floor (Cheng and Sherry, 1992; Gould-Beierle and Kamil, 1998). These results suggest that the distance to an edge was encoded.

Paralleling the study of Spetch et al. (1997) on an open field, Spetch et al. (1996) trained pigeons to search in the middle of an array of four landmarks. The results were also similar: pigeons' peak search locations were mostly at the correct distance and direction from just one landmark of the array, and

different birds relied on different landmarks. Both these sets of results, one in the open field and one on the touch-screen, differ from the findings of Sutton (2002) reviewed in Section 2.2.1. This in turn suggests that the differences are attributable to some procedural factors other than the differences between a touch-screen task and an open-field task. Perhaps crucial to the pattern of findings is that Sutton trained the pigeons with two configurations based on the same landmark elements. It may be that training the birds with two configurations encourages attention to configural cues, just as training the birds with multiple inter-landmark distances encourages the birds to use a relational rule. It would be interesting to replicate Sutton's study on the touch-screen.

2.2.3. General principles of learning in landmark use

Spatial cognition is often considered a specialized domain (Gallistel, 1990; O'Keefe and Nadel, 1978). A special domain might have learning principles that hold specifically for that domain (Gallistel, 2000). But it might also have learning principles that apply broadly to many domains. The search for general principles of learning in spatial cognition has shown that this indeed is the case (Chamizo, 2003; Cheng and Spetch, 1998). Spatial cognition in pigeons provides a number of cases in support.

As with studies on the lab floor, selective control by individual landmarks on a touch-screen was sometimes found. Spetch and Mondloch (1993) trained pigeons to peck at an unmarked goal that was surrounded by four distinct nearby landmarks. Pigeons relied mostly on one or two individual landmarks in this task. Interestingly, the preferred landmarks varied across pigeons. When a bird's preferred landmarks were removed, performance deteriorated, and when those landmarks were shifted relative to the other landmarks, search shifted with the preferred landmarks. Cheng and Spetch (1995) found similar selectivity when a goal was near a landmark and one edge of a graphic frame. Spetch et al. (1998) found similar idiosyncratic control by landmarks near a target on a task with digitized images of a scene. The selective control by spatial cues seen in these studies is reminiscent of a study by Reynolds (1961) on "attention" in pigeons. After discrimination training with redundant cues of color and shape, one pigeon in his study showed control by color and the other pigeon showed control by shape. Such idiosyncratic cue selection may be expected when there is little inherent difference in the information value provided by the multiple cues and when a single cue suffices for the task.

Control by landmarks is more systematic when multiple spatial cues differ substantially in their distance to the goal. For example, in a study by Spetch and Wilkie (1994) the goal was an unmarked spot on the grass in digitized images of an outdoor scene, with three landmarks at different distances from the goal. All birds showed primary control by the nearest landmark to the goal. Lechelt and Spetch (1997) provided further evidence that proximity to the goal is an important determinant of landmark use by pigeons, both in an open-field task and in a touch-screen task with digitized images of the arena and landmarks. These results from touch-screen tasks are thus consistent with evidence from open-field studies showing that nearer landmarks

are weighted more, in birds (Bennett, 1993; Cheng, 1989) and honeybees (Cheng et al., 1987).

Spetch (1995) showed that control exerted by a landmark may depend not only on its absolute proximity to the goal, but also on its proximity relative to other landmarks. For both pigeons and humans, the control exerted by a landmark of interest that was a particular distance from the goal depended on how close other landmarks were to the goal. When tested on its own, the landmark of interest exerted more control if had been the closest landmark to the goal, than if another landmark had been closer to the goal than the landmark of interest was during training. In other words, the presence of a landmark very near the goal overshadowed control by a landmark that was a medium distance to the goal.

Stimulus generalization and discrimination in the spatial domain also provide parallels with principles found with non-spatial cues. Cheng et al. (1997) trained pigeons to peck when a marker appeared at a specific location on the screen (S+). For non-differential training, the marker appeared at the S+ location on all trials. In discrimination training, the marker sometimes appeared at a location that was displaced horizontally from the S+ and pecks were not reinforced (S-). On subsequent generalization tests, the marker was presented at a range of locations. Following non-differential training, single-peaked generalization gradients around S+ were obtained. Following discrimination training, the generalization gradients were shifted toward the S+ side of the distribution. If the S+ and S- were close together, a shift in peak of responding to a value on the S+ side of the distribution was found (Fig. 4). This classic peak-shift effect has been found with other stimulus dimensions, such as wavelength, auditory intensity, and line tilt (review: Honig and Urciuoli, 1981). In a subsequent study using a computer betting game, Cheng and Spetch (2002) also found a peak-shift effect in the spatial domain with humans.

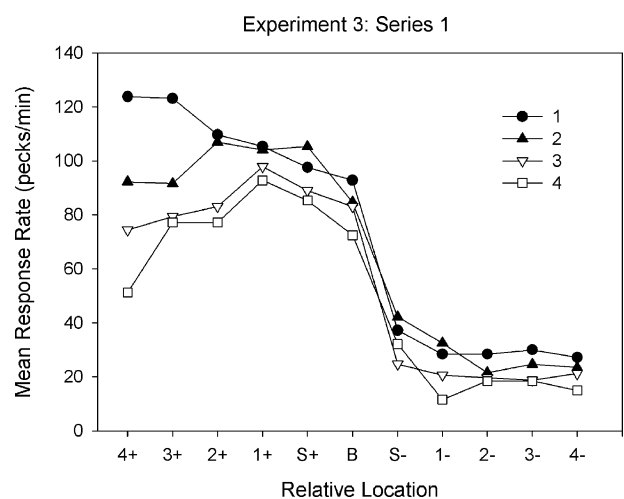


Fig. 4. Spatial peak shift in pigeons. Response rate is 4 text blocks as a function of stimulus location, from Fig. 4 of Cheng et al. (1997). The stimulus object was a graphic square on a monitor. The S+ (rewarded location in training) was constant for each animal, as was the S- (unrewarded location in training). Successive locations were 30 pixels apart in a horizontal line. Data were obtained on occasional unrewarded tests. Reprinted with permission of the publishers, American Psychological Association.

2.2.4. Averaging space and time

The touch-screen spatial task also provided an opportunity to investigate other questions. As mentioned earlier, pigeons sometimes average the dictates of multiple landmarks to determine where to search. But can information from entirely different dimensions of experience be centrally integrated? Cheng et al. (1996) investigated this question with a task in which both spatial position and elapsed time redundantly signalled reward availability. In training, a landmark moved at a fixed pace across the screen on each trial and reward became available when it reached a certain place, which was always a fixed duration of time after trial onset. Thus, both elapsed time and position of the landmark on the screen accurately predicted the availability of reinforcement for a response. On occasional unrewarded test trials, time and location were dissociated by varying the speed at which the landmark moved across the screen. Both species appeared to average the temporal and spatial information to determine a single criterion for when to respond. The weighting differed across species, with humans giving more weight to the place cues and pigeons giving more weight to the temporal cues. These results suggest that the brain may store or recode information from different dimensions of experience in terms of some common code that allows averaging to take place.

2.2.5. Images on monitors and places in the world

Another question raised by the use of the touch-screen spatial search task is whether pigeons see images of scenes as representations of actual places. Evidence that animals see pictures as representing the real world has been mixed (Fagot, 2000). One common approach has been to look for transfer of a learned discrimination from the real world to pictures or vice versa. Spetch et al. (1998) showed that under some circumstances, pigeons can transfer across novel views of a scene shown as digitized images on a monitor. But evidence that pigeons can transfer learned spatial relationships between the 2D screen and the 3D world has been less forthcoming.

Cole and Honig (1994) examined transfer of place learning between pictures (colored slides) and real locations in a room. Some birds were trained in a long room in which food was found at one end but not at the other end of the room. Other birds were trained with pictures of the two ends of the room and were reinforced for pecking the pictures of one end but not the pictures of the other end. The birds were then transferred between the two environments. The birds trained with pictures showed significant positive transfer to the room but the birds trained in the room did not transfer the discrimination to pictures. It is not clear whether the unidirectional transfer that occurred was based solely on features, such as colors or distinctive objects in the two ends of the room, or whether the spatial relationships among features in the pictures were encoded and contributed to the transfer.

In an attempt to provide specific evidence for transfer of learned spatial relationships, Lechelt and Spetch (1997) tested pigeons for transfer of landmark-based search between a real arena and digitized images of the arena. Pigeons were trained to find a hidden goal either in the arena or in images on the computer

screen. The goal location in the arena or on the screen varied across trials but was fixed relative to three local landmarks. The birds were later transferred between environments with either the same or a new spatial relationship between the landmarks and goal. Although the pigeons showed similar control by the landmarks in the two environments (e.g., more control by the nearest landmark in both), there was no evidence that the birds transferred the learned landmark-to-goal relationships between the two environments. Birds transferred with the same relationships did not learn faster or search more accurately than birds transferred with a new relationship.

Taken together with other studies that have examined spatial learning in both touch-screen and open-field tasks, the studies we have described indicate that the touch-screen task is an excellent tool for investigating spatial cognition and that it taps into some of the processes that animals use to solve real world spatial tasks. Video images of social stimuli have also proven to be effective stimuli in place of a real animal in different species (jumping spiders: Clark and Uetz, 1990; lizards: Ord et al., 2002; chickens: Evans and Marler, 1991), despite many differences between video and live stimuli (D'earth, 1998). However, we cannot conclude that pigeons see the images on the screen as representing real world three-dimensional spatial relationships, and this should be kept in mind when interpreting the results of spatial touch-screen tasks. The colors on a monitor constructed for human vision might appear quite different to a pigeon, and not correspond to the colors of real-world objects. The monitor lacks 3D depth information. And the pigeon views the monitor largely binocularly, whereas it views the larger distances of the real world mostly monocularly, thus engaging mostly different visual systems in the two paradigms.

2.3. Geometry and features

This topic has been thoroughly reviewed recently (Cheng and Newcombe, 2005), and we will keep it brief, focusing on pigeons and two recent studies on other birds that did not make it into Cheng and Newcombe's review. Almost all of this line of research took place in rectangular arenas with walls, following the shape used by Cheng (1986). The rectangular shape of the arena provides the geometric cues, while distinctive cues on or in front of the walls provide featural cues. In research on pigeons, these might be distinct panels or 3D objects in the corners. The target is typically at a corner. The corner diagonally opposite the target corner is of interest because it stands in the same geometric relations to the arena as the target, but has different featural cues. Cheng (1986) reported that rats made this error systematically, suggesting that they sometimes used only geometric cues in doing the task.

As reviewed by Cheng and Newcombe (2005), in the two decades following Cheng's initial study, many researchers have examined the encoding of geometric and featural cues across a range of species including children and adults, monkeys, birds, and fishes (Gouteux and Spelke, 2001; Gouteux et al., 2001; Hermer and Spelke, 1994, 1996; Kelly et al., 1998; Sovrano et al., 2002, 2003; Vallortigara et al., 1990). Both geometric and featural cues are used by all the species studied.

2.3.1. Geometry, features, and pigeons

Kelly et al. (1998) showed that pigeons encoded and used featural cues, when these cues were either 2D panels or 3D objects presented in the corners of a rectangular environment. On tests with all distinctive features removed, however, the pigeons searched primarily at the geometrically correct corners, thus showing that they had learned geometric cues as well. Interestingly, when featural and geometric information were placed in conflict, the responses depended on training experience. Birds trained initially in an environment with features and geometry relied primarily on features; birds trained initially in an environment with only geometry divided their choices between the featurally and geometrically correct locations.

As mentioned, Spetch et al. (1997) found that after being trained to search in the center of a square array of discrete landmarks, pigeons typically relied most on a single landmark when the array was expanded (Section 2.2.1). This means that the pigeons relied most on absolute distances to discrete landmarks. We might wonder whether continuous walls, used in ‘geometry’ studies, might induce the birds to use relative geometry. This point was confirmed by Kelly and Spetch (2001) with pigeons trained to find a corner in a rectangular enclosure, and by Gray et al. (2004) with pigeons trained to search in the middle of an enclosure.

Kelly and Spetch (2004b) further examined the encoding of geometric and featural cues by examining how these cues are used by pigeons in a vertically oriented 2D environment on a touch-screen monitor (Fig. 5). Pigeons were shown schematic images of a rectangular environment viewed from a top-down perspective. Unlike studies using a 3D environment, the subjects were oriented but the ‘arena’ was rotated on each trial. As in a 3D environment, pigeons trained with distinctive features readily encoded both the featural and geometric properties. Pigeons trained with only geometric information found the task very difficult and required significantly more training trials to learn. The geometry learned was specific to the training orientations. Presenting the environment at a novel orientation caused the pigeons to choose randomly among the four corners, suggest-

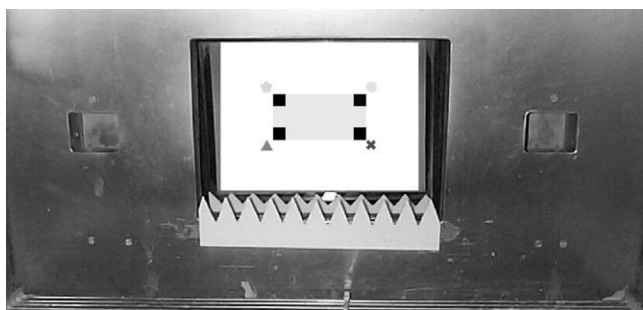


Fig. 5. A retouched photograph of touch-screen stimuli used in Kelly and Spetch (2004b). The stimuli appear on a monitor (center in the photograph). For clarity, a copy of the graphic stimuli has been superimposed on the original photograph. The gray rectangular box with the black squares in the corners defines the geometric cues, while the graphic shapes outside the box (actually in different colors rather than grayscale) provide featural cues. The recesses on the wall on either side of the monitor are food wells in which food is given for correct responses.

ing that pigeons may have encoded multiple orientation-specific ‘geometries’. Parallel results were found in adult humans on a highly similar task (Kelly and Spetch, 2004a). Humans also found geometry learning difficult and showed no transfer to new orientations. Kelly and Spetch (2004a,b) suggested that when learning geometry on a vertical surface, gravity may define a privileged axis. If this is right, then this difference between touch-screen tasks and open-field tasks in the control exerted by geometry has nothing to do with the nature of touch screens versus arena floors except for the orientation of the environment. Needless to say, the other two cells of the 2×2 matrix, horizontal touch screens and vertical open fields, are necessary to resolve this issue.

In ‘geometry’ studies, cue competition between featural and geometric cues is typically not found (Cheng and Newcombe, 2005). Kelly et al. (1998) trained pigeons with redundant and potentially competing geometric and featural cues. Given that the geometric cues specified two of four corners as correct, whereas featural cues specified a unique corner, the featural cues were better cues. Although these are ideal conditions for features to overshadow geometry, this did not happen. As mentioned, the birds learned the geometric cues well, as indicated by tests with the featural cues removed. In contrast, among landmark cues, cue competition is rife (Section 2.2.3).

2.3.2. Recent research on wild bird species

Almost all vertebrate species examined in the ‘geometry’ literature to date have been laboratory reared, and invertebrate species have not been examined at all. The two exceptions are both food storing birds, the Clark’s nutcracker (*Nucifraga columbiana*) and the mountain chickadee (*Poecile gambeli*). Examining the use of geometric cues in wild captured birds allows us to examine the role of experience with constructed rectilinear environments, something that all domestic species have plenty of exposure to (Cheng and Newcombe, 2005). Kelly et al. (2004) trained Clark’s nutcrackers in an open-field task analogous to the paradigm used by Kelly and Spetch (2004b). Four objects were arranged in a rectangular configuration and centered in an open room. Located in front of each object was a covered tin container. Nutcrackers were trained to locate a target container that was provisioned with pine nuts. On each trial the configuration of landmarks was presented in a new orientation (but always centered in the room). For one group of nutcrackers the four objects each had a different color and shape, providing featural cues. For another group all the four objects were identical, limiting this group to geometric cues. The group trained with the identical objects had great difficulty learning the task. After over 100 training trials none of the birds were able to limit their searching to the geometrically correct locations with an accuracy of 80% or better. In one study, 3–4-year-old children also had similar difficulties in learning geometry composed of separate objects (Gouteux and Spelke, 2001). The birds trained with distinct objects readily learned the task. Interestingly, when these featurally trained birds were subsequently tested with the unique objects replaced by identical objects, thus removing all useful featural cues, the birds were able to rely on geometric cues. Far from cue competition then, the featural cues

might well have facilitated the learning of geometric cues in this case.

Using the more traditional fully enclosed rectangular environment Gray et al. (2005) examined the encoding of featural and geometric cues by mountain chickadees. Rather than using discrete objects, the unique color of one of the walls of the arena provided featural information. Three groups of birds were trained in this task: one group had four identical walls and thus only geometric information, a second group had its rewarded corner near the uniquely colored wall, and the third group had its rewarded corner distant from the uniquely colored wall. The birds trained with only geometry learned to search at a geometrically correct corner. The birds trained with the colored wall distant from the reinforced location also showed an encoding of geometry when tested with all four walls colored the same way (thus removing the distinct feature). The birds trained with the reinforced location near the colored wall, however, were unable to use the geometric properties of the environment when the distinct feature was removed. This demonstrated for the first time the overshadowing of geometric cues by a featural cue. Note that the good performance of the birds in using geometric cues when the target was far from the distinctive wall rules out a host of attentional and motivational explanations such as an adverse reaction to a changed environment. Thus, it appears that when featural information can be used as a beacon, the wild caught chickadees did not encode the geometric properties of the target corner. We note, however, that the mountain chickadees were not disoriented on the task. In contrast, disoriented pigeons tested in a similar paradigm readily learned both geometric and featural cues (Vargas et al., 2004, reviewed in Section 2.4.1). At this point, too few studies have focused on wild caught birds to be confident of the differences between species, let alone ascertaining the bases for the differences. But these initial results suggest that comparative research may be a useful avenue of research.

2.4. Hippocampal control of spatial cognition in pigeons

Complementary to the behavioral studies reviewed so far, neurophysiological studies have added to our understanding of spatial cognition in birds. Located in the dorsomedial region of the avian telencephalon is a brain structure identified by early comparative anatomists as the avian homologue of the mammalian hippocampal formation (HF). By now a large experimental and theoretical literature has identified the mammalian HF as crucial for representing environmental (allocentric) spatial properties (review: Jeffery, 2003). Both lesion studies and single-cell recording have implicated the hippocampus in avian spatial cognition as well.

To get home from tens or hundreds of kilometres, a pigeon has to get to the area of its home, and then recognize its home. We call these processes spatial *navigation* and spatial *recognition*, respectively. Whereas recognition can occur in the absence of navigation, navigation is typically dependent on recognition processes for computing goal-directed trajectories. It is now clear that the avian HF is recruited in support of both spatial recognition and navigational processes (Bingman et al., 2003).

With respect to navigation in the homing pigeon, Bingman et al. (2005) has recently reviewed the important role played by the HF in navigation by familiar landmarks, but less so in other types of navigation. We thus concentrate our review on the relationship between HF and goal recognition.

2.4.1. Lesion studies

We have made the distinction between geometric and featural cues. If featural cues are at the goal, they provide a beacon, and an animal heading to the goal does not need to process *spatial* relations at all. In contrast, geometric cues are a kind of spatial cue in which spatial relations or the goal's position in space relative to many cues are important to process. A goal may thus be recognized by its features or its position. The HF in pigeons (and other birds) is important for the positional recognition but not the featural recognition of goal locations.

In birds, this dissociation was first found in the food storing black-capped chickadee. Sherry and Vaccarino (1989) found that birds with HF lesions could not re-locate cached food by position, but could still recognize goals cued by distinctive beacons (black or white cards). Hampton and Shettleworth (1996) reported similar findings in a study carried out in an operant chamber. Similar results were found in homing pigeons. Strasser and Bingman (1999) trained birds on a one-trial match-to-sample task in an open field. Birds were exposed to a rewarded food bowl once, and had to return to it after intervals ranging from 10 min to 24 h. While both control and HF-lesioned pigeons readily recognized the previously rewarded food bowl without any explicit training, conflict probe trials revealed that pigeons with HF lesions relied more on featural cues to recognize a goal, while controls relied more on positional cues.

More recently, Vargas et al. (2004) trained control and HF-lesioned pigeons to locate a food bowl at a corner of a rectangular arena. One wall was distinctly colored. The target could thus be recognized by both its geometric and featural properties. Again, both groups learned the task easily, although the HF-lesioned pigeons appeared to have learned more quickly. On conflict probe trials, control birds relied largely on geometry to recognize the goal location, whereas the HF-lesioned birds preferred to rely on the prominent featural cue.

The avian visual system exhibits strong functional lateralization (Güntürkün, 2002), with visual information from each eye going almost exclusively to the contralateral hemisphere. Therefore, the HF itself may reflect the functional lateralization of its visual inputs. Kahn and Bingman (2004) found that homing pigeons with the right HF lesioned relied less on distal spatial information and more on featural information to recognize a goal. Pigeons with left HF lesions, by contrast, behaved like controls, relying preferentially on distal spatial information for goal recognition. Using eye covers on tests (but not in training) Prior et al. (2002) tested how each hemisphere encoded global cues provided by the shape of the room and local cues in the form of nearby landmarks. They concluded that the right hemisphere relied mostly on global cues, whereas the left hemisphere relied on both global and local cues.

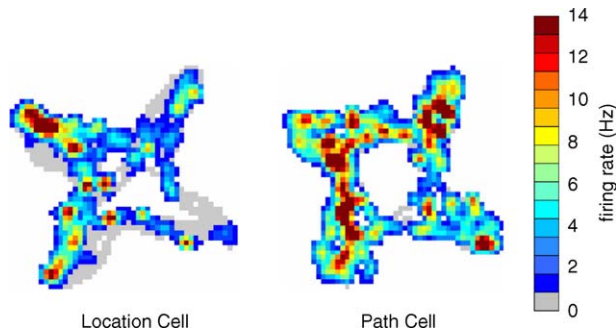


Fig. 6. Representative rate map of a right-hippocampal location cell (left, which can also be found in the left HF) and a left-hippocampal path cell (right) recorded while a pigeon moved through an analog eight-arm maze. Food goal locations are found at the terminal ends of the four visible arms. Firing rate scale is on the far right. For the location cell, note the higher firing rate when the pigeon was in the goal location at the upper left. For the path cell, note the higher firing rate in the corridor connecting the upper left goal location to the lower left goal location, and less so the upper left and the upper right. Courtesy of Gerald Hough, II.

2.4.2. Single-cell recording in the pigeon's hippocampal formation

Electrophysiological recordings of HF neurons in freely moving homing pigeons have recently been reported (Hough and Bingman, 2004; Siegel et al., 2005, 2006). Despite their relatively poor temporal reliability and stability, many right HF cells displayed patches of higher activity at goal locations (with food reward) placed at the terminal end of the maze arms (Fig. 6, left). These neurons were not just responding to food, as many neurons would respond at only one or two of the goal locations (Fig. 6, left). Right HF neurons appear more responsive to the interaction between the momentary occurrence of biologically significant stimuli (such as food) and location, than to location per se. They seem well suited for representing the spatial properties of goal locations.

Although this type of sensitivity to location is also present in some left HF neurons (Siegel et al., 2006), many left HF neurons are more responsive when pigeons are moving along corridors that connect goal locations, a spatial response profile rarely seen in right HF neurons (Fig. 6, right). Left HF neurons, and the left HF in general, may be more involved in navigational aspects of HF function than the right HF (see also Bingman et al., in press).

In summary, substantial evidence demonstrates that the avian HF is crucial for representing the spatial properties that characterize transient but significant biological events, and forming spatial representations that can support subsequent recognition. The right HF may be more important for this function, and 'location' cells in the right HF may be a necessary element of its neuronal implementation.

3. Discussion

In this section, we briefly discuss a number of themes emerging out of this body of research. The themes include the use of multiple cues, principles of associative learning found in the spatial domain, and the central role of the hippocampal formation in spatial cognition. We end by suggesting some lines of research.

3.1. Themes common to other domains

Themes shared by spatial domains and other domains of learning are discussed elsewhere (Cheng, in press), and thus we will be brief. One theme is that in using landmarks, pigeons often rely on multiple cues (e.g., Cheng, 1988). This is common in many domains of learning and cognition. One good functional reason for using multiple landmarks is that the encoding and memory of the target's relation to each landmark is inaccurate to some degree. Simulations show that with such inaccuracies, the use of multiple landmarks cuts down on overall errors in localization (Kamil and Cheng, 2001). We suggest in Section 3.3 further research to investigate how optimal the use of multiple landmarks is.

A second theme is that principles of associative learning that have been amassed in the conditioning literature can sometimes apply to landmark-based searching in pigeons. We reviewed overshadowing, generalization, peak shift, and selective use of cues in the use of landmarks by pigeons. All these principles are found in traditional paradigms of classical and operant conditioning. These principles of learning are not always found in landmark-based searching. Thus, beacon cues do not overshadow the learning of geometric cues (Cheng and Newcombe, 2005), except in mountain chickadees (Gray et al., 2005). Then again, principles such as overshadowing are not universal in classical conditioning either. For example, biologically significant cues are less subject to cue competition (Denniston et al., 1996; Miller and Matute, 1996).

3.2. The role of the hippocampal formation

As reviewed in Section 2.4, it is the encoding of spatial relations, such as geometric relations, in which the HF in birds plays a major role. The HF is not necessary for remembering object characteristics such as a distinctive color. This is likely to be a homologous trait found widely across vertebrate animals. The role of the hippocampus in spatial cognition in rats has been well documented (Jeffery, 2003; O'Keefe and Nadel, 1978). The proposed homologue of the hippocampus of birds and mammals seems to serve a spatial function in what are considered more ancient vertebrates as well, such as turtles and fish (Salas et al., 2003). In recent single-cell recordings from pigeons done in Bingman's lab (2.4.2) however, classic place cells found in rats (O'Keefe and Nadel, 1978) are infrequently encountered. Although the properties of hippocampal place cells in rats have proven to be more complex in recent work (Jeffery, 2003; Mizumori et al., 2004), it is possible that the spatial response properties of mammalian and avian HF neurons have undergone some divergent evolution.

3.3. Further research

We noted that pigeons often use multiple landmarks in localization. Further work can examine how they weight different sources of information, and how optimal the weighting scheme is. This theme has received considerable recent attention in human spatial perception and cognition. Numerous studies have

shown that humans weight different sources of spatial information in a near optimal fashion (reviews: Deneve and Pouget, 2004; Kersten and Yuille, 2003). How should sources of spatial information such as landmarks be weighted? Optimal is to weight each source in proportion to its reliability, or better put, in proportion to the inverse of its unreliability. The unreliability of a single cue source can be estimated by the scatter (SD) of the search distribution when that cue is the only one available. Functionally, we might expect all animals to have evolved near-optimal weighting strategies. But to our knowledge, this Bayesian approach to the integration of information has only been tested on humans.

Another topic of current research is geometry. Indeed, the three authors who have active pigeon labs (MLS, DMK, VPB) are all concerned with this topic, and the remaining author (KC) has produced recent theoretical contributions (Cheng, 2005; Cheng and Gallistel, 2005; Cheng and Newcombe, 2005). Two strands of research seem especially pertinent to us. One strand is the question of what is coded about geometry. Cheng (2005) and Cheng and Gallistel (2005) suggest that some global shape parameters are used, but what, if any, these might be remains theoretical speculation at the moment.

A second strand concerns the role of experience and species differences. As Cheng and Newcombe (2005) pointed out, all the species studied (up to the time of the publication of their paper) have been species with large amounts of exposure to rectilinear spaces. This applies to humans, as well as laboratory-raised monkeys, rats, pigeons, chicks, and even fish. Wild caught mountain chickadees have produced a notable exception to the literature in the first ‘geometry’ study on the species: they exhibited overshadowing of geometric cues by a featural cue (Gray et al., 2005). Pigeons, especially homing pigeons, make a good bird model whose developmental experience can be controlled to a large extent. For example, they can be raised entirely indoors, in environments of various shapes and sizes, or they can be given plenty of exposure to the world outdoors.

Mention of homing pigeons brings us to another theme for current research. Modern satellite tracking technology has meant that the flight paths of homing pigeons can be tracked with good accuracy. Within their familiar territory, at distances of tens of kilometres from home, the use of familiar landmarks for homing has been implicated in studies from two different groups (Biro et al., 2004; Lipp et al., 2004). Theoretical analyses of such paths have also begun (Guilford et al., 2004; Roberts et al., 2004). It would be valuable to determine how pigeons use landmarks over the natural scale of distances that they travel.

Finally, while the role of the avian hippocampus has been much studied by lesioning the HF, there have been few studies recording the ‘performance’ of single cells in the avian HF. The pigeon is an ideal model in these studies because their neuroanatomy is well known, and the requisite recording techniques have been worked out. The studies so far show that cells in the pigeon HF do not represent space in the same way as place cells in rats (Hough and Bingman, 2004; Siegel et al., 2005, 2006). Further investigations are certainly needed. It would be informative to record from the brains of free-flying birds.

4. Conclusion

We have presented the research on spatial cognition in pigeons roughly in historical order. The thread ran from radial-maze studies with rats to radial-maze studies with pigeons to mechanisms of landmark use in pigeons, then expanding to other topics of landmark use and studies on the touch-screen, on to geometry and features, and culminating in recent work on single-cell recordings from the hippocampal formation of freely moving pigeons. Bill Roberts has been influential in this line of work. His study with pigeons on the radial maze (Roberts and Van Veldhuizen, 1985) played a key role in launching the work of Ken Cheng and Marcia Spetch on spatial cognition in pigeons, work that spread to touch-screen studies, ‘geometry’ experiments, and neurophysiological investigations. We dedicate this review to Bill Roberts.

Acknowledgements

This paper expanded from a presentation by Ken Cheng, entitled *Pigeon spatial cognition: some common principles*, at a symposium “In Honor of the Contributions of William A. Roberts” at the Annual International Conference on Comparative Cognition, Melbourne Beach, Florida, March 18, 2005.

References

- Bennett, A.T.D., 1993. Spatial memory in a food storing corvid. I. Near tall landmarks are primarily used. *J. Comp. Physiol. A* 173, 193–207.
- Berthold, P., 2001. *Bird Migration. A General Survey*, second ed. Oxford University Press, Oxford.
- Bingman, V.P., Bagnoli, P., Ioalé, P., Casini, G., 1984. Homing behavior of pigeons after telencephalic ablations. *Brain, Behav. Evol.* 24, 94–106.
- Bingman, V.P., Hough II, G.E., Kahn, M.C., Siegel, J.J., 2003. The homing pigeon hippocampus and space: in search of adaptive specialisation. *Brain, Behav. Evol.* 62, 117–127.
- Bingman, V.P., Siegel, J.J., Gagliardo, A., Erichsen, J., in press. Representing the richness of avian spatial cognition: properties of a lateralized homing pigeon hippocampus. *Rev. Neurosci.*
- Bingman, V.P., et al., 2005. The avian hippocampus, homing in pigeons and the memory representation of large-scale space. *Integr. Comp. Biol.* 45, 555–564.
- Biro, D., Meade, J., Guilford, T., 2004. Familiar route loyalty implies visual pilotage in the homing pigeon. *Proc. Natl. Acad. Sci.* 101, 17440–17443.
- Bond, A.B., Cook, R.G., Lamb, M.R., 1981. Spatial memory and performance of rats and pigeons in the radial-arm maze. *Anim. Learn. Behav.* 9, 575–580.
- Brodbeck, D.R., 1994. Memory for spatial and local cues: a comparison of a storing and a nonstoring species. *Anim. Learn. Behav.* 22, 119–133.
- Brodbeck, D.R., Shettleworth, S.J., 1995. Matching location and color of a compound stimulus: comparison of a food-storing and a nonstoring bird species. *J. Exp. Psychol.: Anim. Behav. Proc.* 21, 64–77.
- Cartwright, B.A., Collett, T.S., 1982. How honey bees use landmarks to guide their return to a food source. *Nature* 295, 560–564.
- Cartwright, B.A., Collett, T.S., 1983. Landmark learning in bees. *J. Comp. Physiol. A* 151, 521–543.
- Chamizo, V., 2003. Acquisition of knowledge about spatial location: assessing the generality of the mechanism of learning. *Q. J. Exp. Psychol.* 56B, 102–113.
- Cheng, K., 1986. A purely geometric module in the rat’s spatial representation. *Cognition* 23, 149–178.
- Cheng, K., 1988. Some psychophysics of the pigeon’s use of landmarks. *J. Comp. Physiol. A* 162, 815–826.

- Cheng, K., 1989. The vector sum model of pigeon landmark use. *J. Exp. Psychol.: Anim. Behav. Proc.* 15, 366–375.
- Cheng, K., 1990. More psychophysics of the pigeon's use of landmarks. *J. Comp. Physiol. A* 166, 857–863.
- Cheng, K., 1992. Three psychophysical principles in the processing of spatial and temporal information. In: Honig, W.K., Fetterman, J.G. (Eds.), *Cognitive Aspects of Stimulus Control*. Lawrence Erlbaum Associates, Hillsdale, NJ, pp. 69–88.
- Cheng, K., 1994. The determination of direction in landmark-based spatial search in pigeons: a further test of the vector sum model. *Anim. Learn. Behav.* 22, 291–301.
- Cheng, K., 1995. Landmark-based spatial memory in the pigeon. In: Medin, D.L. (Ed.), *The Psychology of Learning and Motivation*, vol. 33. Academic Press, San Diego, pp. 1–21.
- Cheng, K., 2005. Reflections on geometry and navigation. *Connection Sci.* 17, 5–21.
- Cheng, K., in press. Common principles shared by spatial and other kinds of cognition, in: Dolins, F., Mitchell, R. (Eds.), *spatial perception, spatial cognition: mapping the self and space*. Cambridge University Press, Cambridge.
- Cheng, K., Collett, T.S., Pickhard, A., Wehner, R., 1987. The use of visual landmarks by honeybees: bees weight landmarks according to their distance from the goal. *J. Comp. Physiol. A* 161, 469–475.
- Cheng, K., Collett, T.S., Wehner, R., 1986. Honeybees learn the colours of landmarks. *J. Comp. Physiol. A* 159, 69–73.
- Cheng, K., Gallistel, C.R., 2005. Shape parameters explain data from spatial transformations: comment on Pearce et al. (2004) and Tommasi and Polli (2004). *J. Exp. Psychol.: Anim. Behav. Proc.* 31, 254–259.
- Cheng, K., Newcombe, N.S., 2005. Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychon. Bull. Rev.* 12, 1–23.
- Cheng, K., Sherry, D.F., 1992. Landmark-based spatial memory in birds (*Parus atricapillus* and *Columba livia*): the use of edges and distances to represent spatial positions. *J. Comp. Psychol.* 106, 331–341.
- Cheng, K., Spetch, M.L., 1995. Stimulus control in the use of landmarks by pigeons in a touch-screen task. *J. Exp. Anal. Behav.* 63, 187–201.
- Cheng, K., Spetch, M.L., 1998. Mechanisms of landmark use in mammals and birds. In: Healy, S. (Ed.), *Spatial Representation in Animals*. Oxford University Press, Oxford, New York, pp. 1–17.
- Cheng, K., Spetch, M.L., 2002. Spatial generalization and peak shift in humans. *Learn. Motiv.* 33, 358–389.
- Cheng, K., Spetch, M.L., Johnston, M., 1997. Spatial peak shift and generalization in pigeons. *J. Exp. Psychol.: Anim. Behav. Proc.* 23, 469–481.
- Cheng, K., Spetch, M.L., Miceli, P., 1996. Averaging temporal duration and spatial position. *J. Exp. Psychol.: Anim. Behav. Proc.* 22, 175–182.
- Clark, D.L., Uetz, G.W., 1990. Video image recognition by the jumping spider, *Maevia inclemens* (Araneae: Salticidae). *Anim. Behav.* 40, 884–890.
- Cole, P.D., Honig, W.K., 1994. Transfer of a discrimination by pigeons (*Columba livia*) between pictured locations and the represented environments. *J. Comp. Psychol.* 108, 189–198.
- Collett, T.S., Cartwright, B.A., Smith, B.A., 1986. Landmark learning and visuo-spatial memories in gerbils. *J. Comp. Physiol. A* 158, 835–851.
- D'earth, R.B., 1998. Can video images imitate real stimuli in animal behaviour experiments? *Biol. Rev.* 73, 267–292.
- Deneve, S., Pouget, A., 2004. Bayesian multisensory integration and cross-modal spatial links. *J. Physiol. Paris* 98, 249–258.
- Denniston, J.C., Miller, R.R., Matute, H., 1996. Biological significance as determinant of cue competition. *Psychol. Sci.* 7, 325–331.
- Evans, C.S., Marler, P., 1991. On the use of video images as social stimuli in birds: audience effects on alarm calling. *Anim. Behav.* 41, 17–26.
- Fagot, J. (Ed.), 2000. *Picture Perception in Animals*. Psychology Press, New York.
- Gallistel, C.R., 1990. *The Organization of Learning*. MIT Press, Cambridge, MA.
- Gallistel, C.R., 2000. The replacement of general-purpose learning models with adaptively specialized learning modules. In: Gazzaniga, M.S. (Ed.), *The New Cognitive Neurosciences*. MIT Press, Cambridge, MA, pp. 1179–1191.
- Gould-Beierle, K., Kamil, A.C., 1998. Use of landmarks in three species of food-storing corvids. *Ethology* 104, 361–378.
- Gouteux, S., Spelke, E.S., 2001. Children's use of geometry and landmarks to reorient in an open space. *Cognition* 81, 119–148.
- Gouteux, S., Thinus-Blanc, C., Vauclair, J., 2001. Rhesus monkeys use geometric and nongeometric information during a reorientation task. *J. Exp. Psychol.: Gen.* 130, 505–519.
- Gray, E.R., Bloomfield, L.L., Ferrey, A., Spetch, M.L., Sturdy, C.B., 2005. Spatial encoding in mountain chickadees: features overshadow geometry. *Biol. Lett.* 1, 314–317.
- Gray, E.R., Spetch, M.L., Kelly, D.M., Nguyen, A., 2004. Searching in the center: pigeons (*Columba livia*) encode relative distance from walls of an enclosure. *J. Comp. Psychol.* 118, 113–117.
- Guilford, T., Roberts, S., Biro, D., Rezek, I., 2004. Positional entropy during pigeon homing II: navigational interpretation of bayesian latent state models. *J. Theor. Biol.* 227, 25–38.
- Güntürkün, O., 2002. Ontogeny of visual asymmetry in pigeons. In: Rogers, L., Andrew, R.J. (Eds.), *Comparative Vertebrate Evolution*. Cambridge University Press, Cambridge, pp. 247–273.
- Hampton, R.R., Shettleworth, S., 1996. Hippocampal lesions impair memory for location but not color in passerine birds. *Behav. Neurosci.* 110, 831–835.
- Hartley, T., Trinkler, I., Burgess, N., 2004. Geometric determinants of spatial memory. *Cognition* 94, 39–75.
- Hermer, L., Spelke, E.S., 1994. A geometric process for spatial reorientation in young children. *Nature* 370, 57–59.
- Hermer, L., Spelke, E., 1996. Modularity and development: the case of spatial reorientation. *Cognition* 61, 195–232.
- Hodgson, Z.G., Healy, S.D., 2005. Preference for spatial cues in a non-storing songbird. *Anim. Cogn.* 8, 211–214.
- Honig, W.K., Urciuoli, P.J., 1981. The legacy of Guttman and Kalish (1956): twenty-five years of research on stimulus generalization. *J. Exp. Anal. Behav.* 36, 405–445.
- Hough II, G.E., Bingman, V.P., 2004. Spatial response properties of homing pigeon hippocampal neurons: correlations with goal locations, movement between goals, and environmental context in a radial-arm arena. *J. Comp. Physiol. A* 190, 1047–1062.
- Jeffery, K.J. (Ed.), 2003. *The Neurobiology of Spatial Behaviour*. Oxford University Press, Oxford.
- Jones, J.E., Antoniadis, E., Shettleworth, S.J., Kamil, A.C., 2002. A comparative study of geometric rule learning by nutcrackers (*Nucifraga columbiana*), pigeons (*Columba livia*), and jackdaws (*Corvus monedula*). *J. Comp. Psychol.* 116, 350–356.
- Jones, J.E., Kamil, A.C., 2001. The use of relative and absolute bearings by Clark's nutcrackers, *Nucifraga columbiana*. *Anim. Learn. Behav.* 29, 120–132.
- Kahn, M., Bingman, V.P., 2004. Lateralization of spatial learning in the avian hippocampal formation. *Behav. Neurosci.* 118, 333–344.
- Kamil, A.C., Cheng, K., 2001. Way-finding and landmarks: the multiple-bearings hypothesis. *J. Exp. Biol.* 204, 103–113.
- Kamil, A.C., Jones, J.E., 1997. The seed storing corvid Clark's nutcracker learns geometric relationship among landmarks. *Nature* 390, 276–279.
- Kamil, A.C., Jones, J.E., 2000. Geometric rule learning by Clark's nutcrackers (*Nucifraga columbiana*). *J. Exp. Psychol.: Anim. Behav. Proc.* 26, 439–453.
- Kelly, D.M., Robak, E., Kamil, A.C., 2004. Encoding of geometric and featural cues in an open environment by Clark's nutcrackers. In: Paper Presented at the Meeting of International Conference on Comparative Cognition, Melbourne, Florida, March, 2004.
- Kelly, D.M., Spetch, M.L., 2001. Pigeons encode relative geometry. *J. Exp. Psychol.: Anim. Behav. Proc.* 27, 417–422.
- Kelly, D.M., Spetch, M.L., Heth, C.D., 1998. Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *J. Comp. Psychol.* 112, 259–269.
- Kelly, D.M., Spetch, M.L., 2004a. Reorientation in a two-dimensional environment: I. Do adults encode the featural and geometric properties of a two-dimensional schematic of a room? *J. Comp. Psychol.* 118, 82–94.

- Kelly, D.M., Spetch, M.L., 2004b. Reorientation in a two-dimensional environment: II. Do pigeons (*Columba livia*) encode the featural and geometric properties of a two-dimensional schematic of a room? *J. Comp. Psychol.* 118, 384–395.
- Kersten, D., Yuille, A., 2003. Bayesian models of object perception. *Curr. Opin. Neurobiol.* 13, 150–158.
- Lechelt, D.P., Spetch, M.L., 1997. Pigeons' use of landmarks for spatial search in a laboratory arena and in digitized images of the arena. *Learn. Motiv.* 28, 424–445.
- Lipp, H.-P., et al., 2004. Pigeon homing along highways and exits. *Curr. Biol.* 14, 1239–1249.
- Maier, N.R.F., 1929. Reasoning in white rats. *Comp. Psychol. Monogr.* 6, 1–93.
- Mazmanian, D.S., Roberts, W.A., 1983. Spatial memory in rats under restricted viewing conditions. *Learn. Motiv.* 14, 123–129.
- Miller, R.R., Matute, H., 1996. Biological significance in forward and backward blocking: resolution of a discrepancy between animal conditioning and human casual judgment. *J. Exp. Psychol.: Gen.* 125, 370–386.
- Mizumori, S.J.Y., Yeshenko, O., Gill, K.M., Davis, D.M., 2004. Parallel processing across neural systems: implications for a multiple memory system hypothesis. *Neurobiol. Learn. Mem.* 82, 278–298.
- Morris, R.G.M., 1981. Spatial localization does not require the presence of local cues. *Learn. Motiv.* 12, 239–260.
- O'Keefe, J., Dostrovsky, J., 1971. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Res.* 34, 171–175.
- O'Keefe, J., Nadel, L., 1978. *The Hippocampus as a Cognitive Map*. Clarendon Press, Oxford.
- Olson, D.J., Maki, W.S., 1983. Characteristics of spatial memory in pigeons. *J. Exp. Psychol.: Anim. Behav. Proc.* 9, 266–280.
- Olton, D.S., Samuelson, R.J., 1976. Remembrance of places passed: spatial memory in rats. *J. Exp. Psychol.: Anim. Behav. Proc.* 2, 97–116.
- Ord, T.J., Peters, R.A., Evans, C.S., Taylor, A.J., 2002. Digital video playback and visual communication in lizards. *Anim. Behav.* 63, 879–890.
- Prior, H., Lingenauber, F., Nitschke, J., Güntürkün, O., 2002. Orientation and lateralized cue use in pigeons navigating a large indoor environment. *J. Exp. Biol.* 205, 1795–1805.
- Reynolds, G.S., 1961. Attention in the pigeon. *J. Exp. Anal. Behav.* 4, 203–208.
- Roberts, S., Guilford, T., Rezek, I., Biro, D., 2004. Positional entropy during pigeon homing I: Application of bayesian latent state modelling. *J. Theor. Biol.* 227, 39–50.
- Roberts, W.A., 1984. Some issues in animal spatial memory. In: Roitblat, H.L., Bever, T.G., Terrace, H.S. (Eds.), *Animal Cognition*. Lawrence Erlbaum Associates, Hillsdale, NJ, pp. 425–443.
- Roberts, W.A., Van Veldhuizen, N., 1985. Spatial memory in pigeons on the radial maze. *J. Exp. Psychol.: Anim. Behav. Proc.* 11, 241–260.
- Salas, C., Broglio, C., Rodriguez, R., 2003. Evolution of the forebrain and spatial cognition in vertebrates: Conservation across diversity. *Brain, Behav. Evol.* 62, 72–82.
- Sherry, D.F., Vaccarino, A.L., 1989. Hippocampus and memory for food caches in black-capped chickadees. *Behav. Neurosci.* 103, 308–318.
- Siegel, J.J., Nitz, D., Bingman, V.P., 2005. Spatial-specificity of single-units in the hippocampal formation of freely moving homing pigeons. *Hippocampus* 15, 26–40.
- Siegel, J.J., Nitz, D., Bingman, V.P., 2006. Lateralized functional components of spatial cognition in the avian hippocampal formation: evidence from single-unit recordings in freely moving homing pigeons. *Hippocampus* 16, 125–140.
- Sovrano, V.A., Bisazza, A., Vallortigara, G., 2002. Modularity and spatial reorientation in a simple mind: encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition* 85, B51–B59.
- Sovrano, V.A., Bisazza, A., Vallortigara, G., 2003. Modularity as a fish (*Xenotoca eiseni*) views it: conjoining geometric and nongeometric information for spatial reorientation. *J. Exp. Psychol.: Anim. Behav. Proc.* 29, 199–210.
- Spetch, M.L., 1990. Further studies of pigeons' spatial working memory in the open-field task. *Anim. Learn. Behav.* 18, 332–340.
- Spetch, M.L., 1995. Overshadowing in landmark learning: touch-screen studies with pigeons and humans. *J. Exp. Psychol.: Anim. Behav. Proc.* 21, 166–181.
- Spetch, M.L., Cheng, K., MacDonald, S.E., 1996. Learning the configuration of a landmark array: I. Touch-screen studies with pigeons and humans. *J. Comp. Psychol.* 110, 55–68.
- Spetch, M.L., et al., 1997. Use of landmark configuration in pigeons and humans: II. Generality across search tasks. *J. Comp. Psychol.* 111, 14–24.
- Spetch, M.L., Cheng, K., Mondloch, M.V., 1992. Landmark use by pigeons in a touch-screen spatial search task. *Anim. Learn. Behav.* 20, 281–292.
- Spetch, M.L., Edwards, C.A., 1986. Spatial memory in pigeons (*Columba livia*) in an open-field feeding environment. *J. Comp. Psychol.* 100, 266–278.
- Spetch, M.L., Edwards, C.A., 1988. Pigeons', *Columba livia*, use of global and local cues for spatial memory. *Anim. Behav.* 36, 293–296.
- Spetch, M.L., Honig, W.K., 1988. Characteristics of pigeons' spatial working memory in an open-field task. *Anim. Learn. Behav.* 16, 123–131.
- Spetch, M.L., Kelly, D.M., Lechelt, D.P., 1998. Encoding of spatial information in images of an outdoor scene by pigeons and humans. *Anim. Learn. Behav.* 26, 85–102.
- Spetch, M.L., Mondloch, M.V., 1993. Control of pigeons' spatial search by graphic landmarks in a touch-screen task. *J. Exp. Psychol.: Anim. Behav. Proc.* 19, 353–372.
- Spetch, M.L., Rust, T.B., Kamil, A.C., Jones, J.E., 2003. Searching by rules: pigeons' (*Columba livia*) landmark-based search according to constant bearing or constant distance. *J. Comp. Psychol.* 117, 123–132.
- Spetch, M.L., Wilkie, D.M., 1994. Pigeons' use of landmarks presented in digitized images. *Learn. Motiv.* 25, 245–275.
- Strasser, R., Bingman, V.P., 1999. The effects of hippocampal lesions in homing pigeons on a one-trial food association task. *J. Comp. Physiol.* A 185, 583–590.
- Sutton, J.E., 2002. Multiple-landmark piloting in pigeons (*Columbia livia*): landmark configuration as a discriminative cue. *J. Comp. Psychol.* 116, 391–403.
- Tolman, E.C., Honzik, C.H., 1930. Introduction and removal of reward, and maze performance in rats. *U. California Publications in Psychol.* 4, 257–275.
- Vallortigara, G., Zanforlin, M., Pasti, G., 1990. Geometric modules in animal's spatial representations: a test with chicks (*Gallus gallus domesticus*). *J. Comp. Psychol.* 104, 248–254.
- Vargas, J.P., Petruso, E.J., Bingman, V.P., 2004. Hippocampal formation is required for geometric navigation in pigeons. *Eur. J. Neurosci.* 20, 1937–1944.
- Wallraff, H.G., 2004. Avian olfactory navigation: its empirical foundation and conceptual state. *Anim. Behav.* 67, 189–204.
- Wiltschko, R., Witschko, W., 2003. Avian navigation: from historical to modern concepts. *Anim. Behav.* 65, 257–272.
- Zeigler, H.P., Bischof, H.-J. (Eds.), 1993. *Vision, Brain, and Behavior in Birds*. MIT Press, Cambridge, MA.
- Zentall, T.R., Steirn, J.N., Jackson-Smith, P., 1990. Memory strategies in pigeons' performance of a radial-arm-maze analog task. *J. Exp. Psychol.: Anim. Behav. Proc.* 16, 358–371.