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# The Homing Pigeon Hippocampus and Space: In Search of Adaptive Specialization

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## Key Words

Birds · Comparative cognition · Forebrain evolution · Hippocampal lateralization · Landmark navigation · Single unit recording

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## Abstract

The hippocampus (HF) of birds and mammals is essential for the map-like representation of environmental landmarks used for navigation. However, species with contrasting spatial behaviors and evolutionary histories are likely to display differences, or 'adaptive specializations', in HF organization reflective of those contrasts. In the search for HF specialization in homing pigeons, we are investigating the spatial response properties of isolated HF neurons and possible right-left HF differences in the representation of space. The most notable result from the recording work is that we have yet to find neurons in the homing pigeon HF that display spatial response properties similar to HF 'place cells' of rats. Of interest is the suggestion of neurons that show higher levels of activity when pigeons are near goal locations and neurons that show higher levels of activity when pigeons are in a holding area prior to being placed in an experimental environment. In contrast to the rat, the

homing pigeon HF appears to be functionally lateralized. Results from a current lesion study demonstrate that only the left HF is sensitive to landmarks that are located within the boundaries of an experimental environment, whereas the right HF is indifferent to such landmarks but sensitive to global environmental features (e.g., geometry) of the experimental space. The preliminary electrophysiological and lateralization results offer interesting departure points for better understanding possible HF specialization in homing pigeons. However, the pigeon and rat HF reside in different forebrain environments characterized by a wulst and neocortex, respectively. Differences in the forebrain organization of pigeons and rats, and birds and mammals in general, must be considered in making sense of possible species differences in how HF participates in the representation of space.

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## Introduction

From a behavioral perspective, a generally unappreciated turning point in the evolution of life occurred when organisms began to actively move through their environments in a goal-directed manner. When moving through

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space, both prokaryotic and eukaryotic (specifically members of the kingdom Animalia) organisms use a wide range of spatial behavior mechanisms that enable them to locate desirable locations and avoid potential dangers. Bacteria and unicellular eukaryotes can reach goal locations without a structured nervous system by relying on, for example, environmental chemical gradients [Eisenbach, 1991] and the earth's magnetic field [Blakemore, 1975]. In multicellular eukaryotes, nervous systems coordinate action across cells that regulate movements through space, and it is worth speculating that the survival and reproductive benefits of coordinating movements through space and memory for space were likely substantial selective forces driving the evolution of nervous systems in multicellular animals. The diversity of spatial behavior mechanisms displayed by organisms with a nervous system is large. Examples include simple taxes and kineses [Fraenkel and Gunn, 1940], which characterize many invertebrates, to more complex orientation mechanisms, like the time-compensated sun compass [Able, 1991], which characterize vertebrates as well as many invertebrates, to map-like representations of space, which appear to be a uniquely vertebrate characteristic [but see Mizunami et al., 1998].

The way individuals of a species navigate space is presumably a product of a long evolutionary history of nervous system adaptations to the ecological contingencies of that species. Some of the best examples that demonstrate this point are neural adaptations that enable species to locate stimuli in perceptual space, i.e. that portion of the environment accessible to an organism's sensory systems. Some fish species living in environments with poor visibility have evolved neural mechanisms that enable individuals to extract spatial information from variations in the ambient electric field using feedback from self-generated electric pulses [Heiligenberg, 1991]. Some species of nocturnally hunting owls have evolved neural mechanisms that enable individuals to orient toward environmental sources of sound with remarkable accuracy [Wagner et al., 1987]. Diverse neural organizational responses to the challenges of locating goals and navigating space characterize the animal kingdom. However, amid this diversity can be found striking examples of evolutionary conserved spatial behavior systems. Notable in this context is the universal participation of the hippocampal formation in the map-like representation of environmental space in birds and mammals, and likely other vertebrate groups.

## Hippocampus and Maps of Space

Birds and mammals, and likely many reptiles and anamniotes as well [Rodriguez et al., 2002], are able to learn map-like representations of environmental space that can guide goal navigation. By map-like we mean that environmental landmarks or stimulus features are combined into a single, allocentric spatial representation that veridically captures (at least approximately) the spatial relationship among the landmarks, and supports efficient and flexible navigation among goal locations. In birds and mammals, the hippocampal formation (abbreviated below as HF) is generally assumed to participate in the learning and memory of spatial representations that guide navigation when environmental landmarks are represented in a map-like fashion [O'Keefe and Nadel, 1978]. For example, HF lesions in rats lead to navigational deficits in the use of distal room cues [Eichenbaum et al., 1990] remarkably similar to the landmark navigational deficits in the field that occur in homing pigeons following HF lesions [Gagliardo et al., 1999].

Although the role of the avian and mammalian HF in the general domain of spatial cognition has been conserved, there is evidence that HF displays substantial evolutionary plasticity. Specifically, the anatomical and physiological organization of HF in a given species, and even different populations and sexes of the same species, has likely been shaped by natural selection as an adaptation to environmental spatial challenges. Evidence in support of the highly plastic nature of HF evolution can be found in a number of places. Anatomically, an examination of the HF of reptiles, birds and mammals reveals that only mammals have the well-known cytoarchitectural organization of a distinct, nicely layered Ammon's horn and dentate gyrus. The HF of birds in particular, and to a lesser extent reptiles [Lohman and Mentink, 1972], lack this striking internal organization. This observation alone suggests considerable plasticity in HF evolution, albeit of uncertain functional consequence. Stronger evidence linking variation in HF anatomy with species ecology and natural selection is the well described phenomenon of larger relative HF volume in species of birds that display exceptional spatial behaviors [Krebs et al., 1989; Sherry et al., 1989; Hampton et al., 1995], including population differences within species [Pravosudov and Clayton, 2002]. In some mammal and bird species, differences in hippocampal anatomy between males and females correlate with differences in spatial behavior and memory [Sherry et al., 1992]. Finally, studies using inbred strains of mice have found considerable variation in hippocampal mor-

phology (mossy fibers) that correlates with cognitive ability [e.g., Crusio et al., 1987].

For the remainder of this paper, we operate under the assumption that species differences in HF organization occur as adaptive responses to differences in species ecology and natural history. Following from this assumption, comparisons between any two species with contrasting spatial ecology could substantially enhance our understanding of how the brain is able to create a physical memory trace of environmental space, and how species-specific variation in HF organization can influence the properties of spatial memory and behavior. HF comparisons between homing pigeons (*Columba livia*) and the laboratory rat (*Rattus norvegicus*) can be used to highlight the importance of the comparative approach. Behaviorally, the contrast between pigeons and rats could not be more striking. Homing pigeons, like most birds, have superb vision, are diurnal, move freely both on the ground and in the air in mostly open field settings, and successfully navigate over enormous distances. Rats, like most rodents, are nocturnal, tend to move on the ground in labyrinths or corridors, and successfully navigate in relatively small home ranges. It is hard to imagine that identical HF design features universally apply to the representation of space in such different species. In 300 million years of independent evolution, has natural selection shaped the HF of homing pigeons in a manner different from rats consistent with their very different spatial behavior and ecology? If yes, what form(s) does this adaptive specialization take?

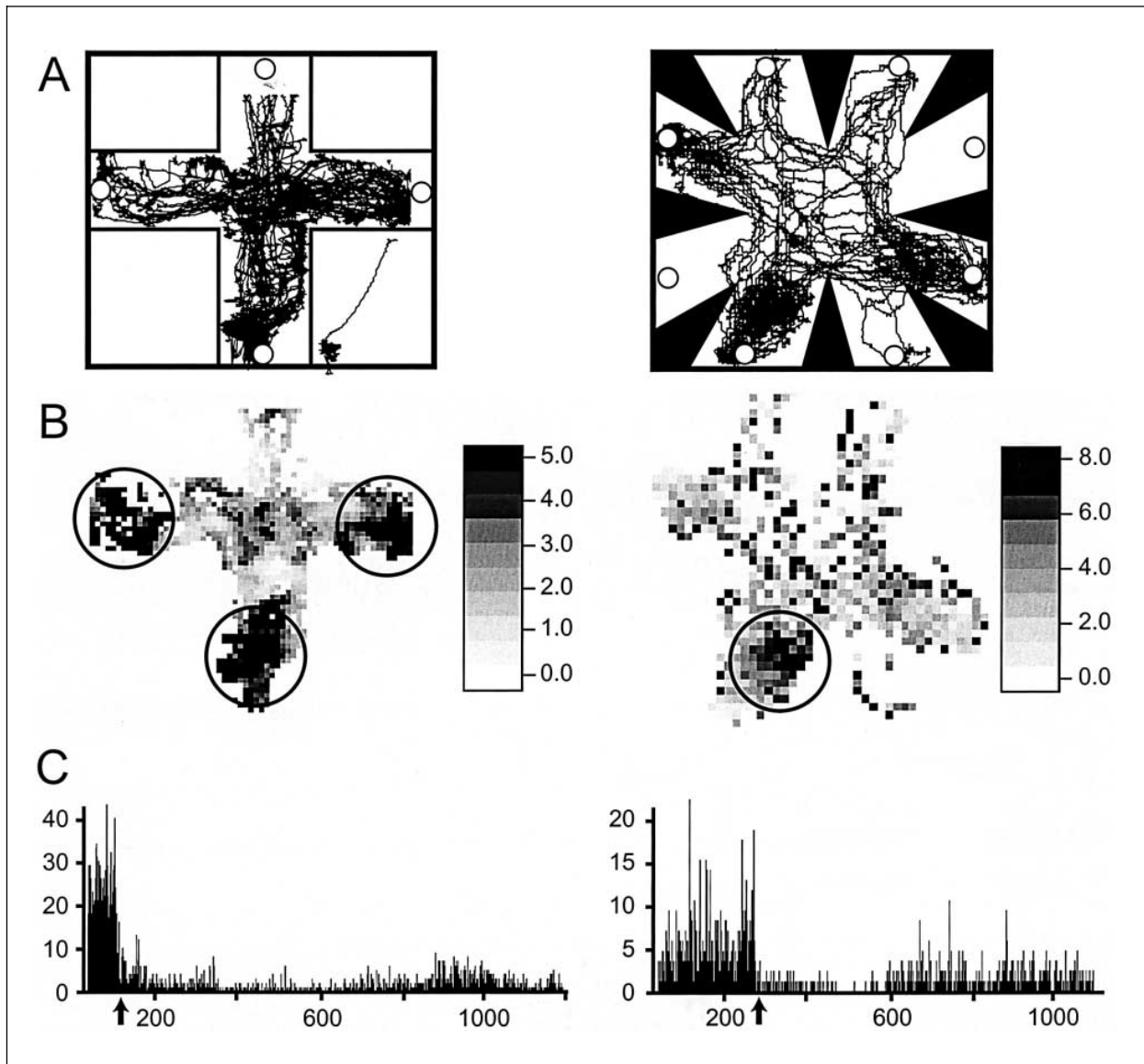
### **Spatial Response Properties of HF Neurons: A Preliminary Survey**

The landmark discovery by O'Keefe and Dostrovsky [1971] that HF pyramidal neurons, most apparent in the CA1 region, display increased firing rates of action potentials when a rat is in a restricted portion of an experimental environment has led to an industry of investigations trying to unravel how space is represented in the single and ensemble neuronal activity of the rat HF. It is impossible to summarize this vast body of literature of increasing complexity in the present paper [see Sharp, 2001 for a review]. However, so-called HF 'place cells', each sensitive to a different, sharply bounded portion of the experimental environment or 'place field', remain the most salient feature of the spatial response properties of HF neurons.

We have recently been exploring the field potential activity [Siegel et al., 2000], as well as the electrophysiological profile [Siegel et al., 2002a] and spatial response properties [Siegel et al., 2002b] of single (isolated) HF neurons in freely moving homing pigeons. That work has shown that the homing pigeon HF regularly displays rhythmic field potential activity in the 4-Hz range that resembles so-called hippocampal theta rhythm in rat [usually 8–10 Hz; e.g., Vanderwolf, 1969]. We have also found general similarity in the electrophysiological profile (firing rates, rhythmicity, and tendency to burst or not to burst) of different neuronal types in the homing pigeon compared to rat HF [Fox and Ranck, 1981; Quirk et al., 1992; Sharp and Green, 1994]. However, together with the general pattern of similarity, differences between pigeon and rat HF were also found with respect to the details of these electrophysiological dimensions. The significance of the differences for understanding the relationship between HF and the memory representation of space remains to be understood.

From a behavioral and cognitive perspective, clearly the spatial response properties of HF neurons in freely-moving homing pigeons is of most potential interest in identifying possible adaptive differences in the relationship between space and the homing pigeon and rat HF. We are still in the preliminary stages of this work, having recorded the spatial receptive fields of about 60 isolated HF neurons, recorded from 10 pigeons, in two distinct environmental settings. About 35 of the neurons were recorded in a plus maze (fig. 1), where food was made repeatedly available in four food bowls at the end of each arm. About 25 of the units were recorded in an analog 8-arm radial maze (fig. 1), where food was made repeatedly available in food bowls in four of the arms, which were cued by a unique color card above each food bowl. Thus, only in the radial arm maze was there a difference in the reward properties of different food bowls, and therefore, a memory component for the differential distribution of food across the food bowls. Many of the details of the recording equipment, acquisition and analysis software can be found in Siegel et al. [2002a].

The most striking result of the preliminary work has been the absence of neurons whose spatial response properties resemble the prototypical place cell of the rat HF [see, for example, Muller et al., 1987]. None of the neurons, which were sampled from various subdivisions within the pigeon HF, displayed a well-defined environmental spatial receptive field where the firing rate was substantially increased above baseline. The working conclusion from this finding is that the homing pigeon HF



**Fig. 1.** Examples of two isolated HF neurons that displayed significantly higher levels of activity at or near food bowls, and two other isolated HF neurons that displayed substantially higher levels of activity while the pigeon was being held in the holding area just prior to running a maze. **A** Experimental environments and paths taken by birds as they ran in the two types of experimental maze (different bird for each environment). The environment on the left was a 4-m<sup>2</sup> space that enclosed a plus maze. A food bowl (circles) was located at the end of each arm. All four food bowls were baited repeatedly during a recording session. The environment on the right was a 4-m<sup>2</sup> space that enclosed an analog 8-arm radial maze. Food bowls (circles) were located at the end of each arm, but food was repeatedly baited at only four of the arms, which remained constant across all the recording sessions of a given bird. A unique color card also marked

the end of each arm with a baited food bowl. The lines within each maze identify the path taken by the pigeon while the activities of the neurons presented in B were being recorded. **B** Rate maps of isolated, single neuron activity recorded during the sessions depicted in A. The unit recorded in the left arena preferentially responded near three of the food bowls (circles), while the unit recorded in the right arena preferentially responded only near one bowl (circle in SW arm). The firing rate (spikes/sec) of the neuron at each pixel can be read off the gray scale to the right of each rate map. **C** Response rate (y-axis in spikes/s) time (x-axis in seconds) histograms of two isolated neurons that fired preferentially in the holding area, but became silent while the pigeons ran the mazes (left neuron plus maze, right neuron radial maze). Transition between holding area and maze is identified by the arrows on the x-axes.

participates in spatial cognition in a manner less reliant on neurons representing the location or place of an animal in a familiar environment. However, we need to emphasize that we only attempted to correlate a bird's location in an environment with changes in neuronal activity. But place is not the only possible spatial reference frame that could best define the spatial receptive field of a HF neuron. For example, the critical spatial dimension that might best define the spatial receptive field of homing pigeon HF neurons is a bird's gaze direction (where it is looking rather than where it is). Something like this, so-called 'spatial view cells', has been observed in monkey HF [Rolls, 1999]. The analyses we carried out would have been insensitive to changes in neuronal activity that would have correlated with gaze direction, because a pigeon's gaze direction could change even while its location or place in the environment did not. Therefore, it is possible that a gaze direction analysis, or an analysis based on some other spatial reference, could still reveal robust space-specific activity that resembles place cell-like behavior.

Although the discovery of a prototypical place cell in the homing pigeon HF has so far eluded us, we routinely record from neurons that show modestly higher levels of activity at locations distributed throughout the test environments during a recording session. Most of the neurons recorded in the plus maze and radial maze displayed significantly higher levels of activity (at least one standard deviation above a neuron's mean firing rate) at scattered locations (so-called 'patches', each covering at least nine contiguous pixels) in the test environments. The generally patchy spatial response profile of these neurons, ranging from one to five patches for any given neuron, are reminiscent of a type of neuron encountered in the rat HF [Kubie et al., 1990]. Some HF interneurons in the rat show multiple regions of increased activity within a given environment. The complex response properties of these interneurons seem to reflect an interaction between a rat's location in space and some accompanying, but unspecified behavioral/motivational correlate(s). Similarly, an interaction between location in space and some as yet unspecified behavioral, motivational or environmental correlate(s) may best explain the patchy spatial response profile of many homing pigeon HF neurons.

Of interest, however, was that many of the neurons had patches occupying locations at or near food bowls in the plus maze and radial maze. Occasionally, the increased level of activity of HF neurons near food bowls was striking (fig. 1). Speculating on this finding, it appears that some homing pigeon HF neurons are tuned (sensitive) to

the association (conjunction) of locations in space with 'events' that occur at those locations. We appreciate that intuitively the repetitive experience of food at the same location would gradually diminish the quality of the experience as an event. However, we are still struck by the routine occurrence of neurons with patches at food bowls and propose that neurons of this type might be encoding something like 'event space', which would have a distinctive episodic quality.

The obvious weakness of this interpretation is the question of why we should include space as a defining response property of neurons with patches at food bowls? Why not simply call what we think might be event-space neurons 'food cells'? First, numerous lesion studies [e.g., Gagliardo et al., 1996; Strasser and Bingman, 1999] have demonstrated that HF lesions interfere with the ability of pigeons to associate food with locations defined by the sun compass or environmental landmarks, but have no effect on the ability of birds to identify food or even associate feature cues with food. Therefore, it is hard to imagine that food alone could control the activity of HF neurons. We have also recorded from neurons with patches of higher activity near one food bowl but not others (fig. 1). Such a response profile would not be expected if food was the critical stimulus driving the increased firing rates at patches. Finally, it is worth noting that what makes food-storing birds with their larger HF so interesting is their remarkable ability to remember the locations of sometimes hundreds of stored seeds. The sensitivity of some HF neurons to locations at or near food bowls in homing pigeons may be a critical feature of how birds generally represent food locations in memory, a behavioral ability that appears to be most highly developed in food-storing species.

If the presence of event-space neurons in the avian HF proves to be a reality, would that represent a dramatic difference in how the HF of homing pigeons and rats represent space? The place field of a prototypical place cell in the rat is generally thought to be uninfluenced by the behavioral/motivational salience of the place field location [e.g., McNaughton et al., 1996]. However, several recent studies have shown that rat HF place cells can over-represent the location of an escape platform in a water maze [Hollup et al., 2001] and be sensitive to the interaction among spatial and non-spatial environmental variables [Wood et al., 1999]. The response properties of these neurons in the rat HF resemble what we are calling event-space neurons in pigeons. Therefore, as things stand now, the pigeon and rat HF do not seem to differ in the occurrence of neurons sensitive to the salience of environmen-

tal space. However, they may differ in the lack of salience-indifferent, space-sensitive neurons (i.e., prototypical place cells) in pigeons.

In addition to HF neurons with patches at food bowls, we have also recorded from a small number of HF neurons that show the interesting property of displaying increased levels of activity while a pigeon is being held in a holding area adjacent to a maze. Such neurons display higher levels of activity just prior to a pigeon being placed into a test environment. Once a pigeon is placed in and running the maze, these neurons show a dramatic reduction in activity (fig. 1). We admit that the relevance of this response profile for the representation of space is not obvious, but we would like to offer one speculation. HF neurons that display increased levels of activity prior to a pigeon being placed in an experimental environment may participate in representing something resembling anticipation of running the maze. For example, such neurons could participate in a process in which contextual, perhaps spatial contextual, information from the environment would activate retrieval of a representation of stored spatial relationships among locations in the maze. If true, then neurons of this type could be described as 'context setting' cells. Consistent with the possible existence of context-setting neurons is the finding that, under some experimental conditions, HF lesions in homing pigeons can result in behavior suggestive of a loss of sensitivity to contextual stimuli [Strasser and Bingman, 1997].

Again, if we demonstrate the presence of context-setting neurons in the avian HF, would that represent a dramatic difference in how the HF of homing pigeons and rats represent space? Probably not. In rats, hippocampal lesion effects on context sensitivity have been regularly reported [see Holland and Bouton, 1999 for a recent review]. Perhaps of more interest is a study by Gothard et al. [1996] in which recordings of HF neurons were taken as rats moved through an experimental arena. Relevant for the present discussion is that they described a type of neuron with increased levels of activity at or near the arena start box, regardless of the location of the start box in the test environment. If we assume that the start box can serve as a contextual cue preparing the animal for running the maze, then HF neurons active near the start box may participate in the representation of that context sensitivity. We are intrigued by the similarity in the spatial response properties of their start-box neurons and the neurons we have found that are preferentially active while a pigeon is held in the holding space prior to running a maze.

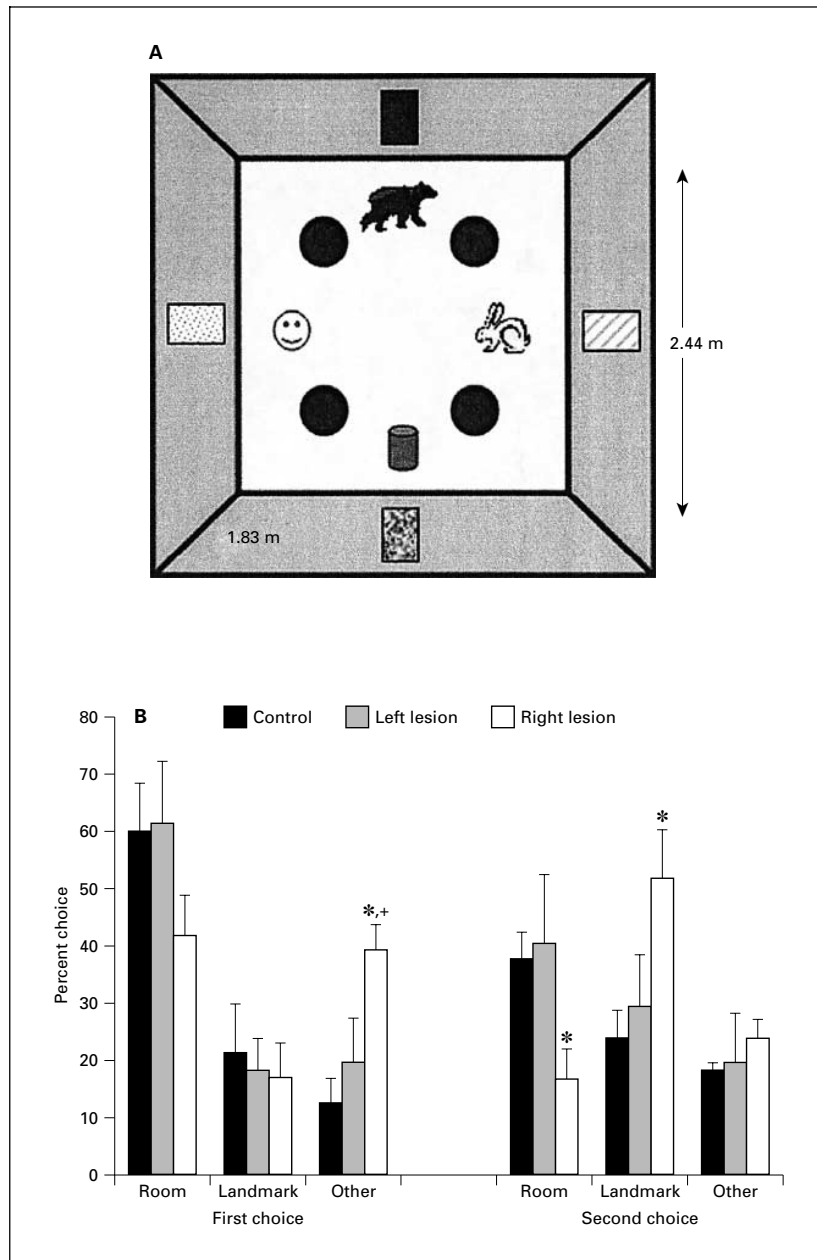
## Lateralization of Hippocampal Function

A survey of the rat HF literature is surprising in revealing, to the best of our knowledge, no evidence of left and right HF differences in the representation of space [e.g., Fenton and Bures, 1993; but see Roof and Havens, 1992, for evidence of sex dependent hemispheric differences in HF anatomical organization, and LaMendola and Bever, 1997, for evidence of cerebral asymmetries in spatial cognition]. It is surprising because right-left HF differences are well known in man [Smith and Milner, 1981; Maguire et al., 1998]. In birds, functional cerebral lateralization has been known for decades [see Rogers, 1996]. Of particular interest are studies carried out in food-storing birds and pigeons demonstrating, through the use of eye caps, that the two cerebral hemispheres participate differently in the memory representation of food locations [Clayton and Krebs, 1994; Prior et al., 2002]. Because memory for food stores involves the HF [Sherry and Vaccarino, 1989], the functional lateralization found in the eye cap studies implicates HF as one cerebral structure characterized by left and right hemispheric differences.

Motivated by the eye-cap studies, some recent investigations have looked at the effects of unilateral HF lesions on homing behavior [Gagliardo et al., 2001, 2002]. The results from that work identified the left, but not right HF as critical for navigational map learning. However, both hemispheres seemed to participate in learning to navigate over previously experienced terrain reliant on familiar landmarks. It was this latter result that motivated an ongoing study [Kahn et al., 2002] designed to investigate whether the left and right HF make different contributions to the representation of familiar landmarks used to navigate space.

Control, left and right HF lesioned pigeons were trained to locate food in an experimental room (fig. 2) containing four identical (purple) food bowls, four distinctive three-dimensional landmarks (toys), four distinctive two-dimensional landmarks (posters) on the walls of the room and the global room cues (lights, ceiling marks, etc.) that surrounded the experimental space. During training for any given pigeon, food was located in one bowl only, and that bowl was defined by its location with respect to the two-dimensional and three-dimensional landmarks within the experimental space, and the global room cues surrounding the experimental space. After learning the location of the correct food bowl, three types of unreinforced probe trials were introduced among training trials. On probe trials, the two-dimensional and three-dimensional landmarks were rotated either together or

**Fig. 2.** A schematic diagram of the training environment and first and second food bowl choices of the pigeons pooled across all three probe trial types. **A** Training environment. Walls were 1.83 m high and 2.44 m wide and included one-way windows for observation of the animals and small doors at the bottom of each wall for the animals to enter the experimental space. Rectangles on each wall represent four unique two-dimensional landmarks (posters), circles on the floor represent four identical food bowls, and objects on the floor represent four unique three-dimensional landmarks (toys). **B** Food-bowl choices that were ‘correct’ relative to the global room cues (room), ‘correct’ relative to the two and/or three dimensional cues within the experimental space (landmark) and choices to the other bowls (other) of the control (black), left HF lesioned (gray), and right HF lesioned (white) pigeons shown as percent of total choices. First choices during probe trials are shown on the far left (choices to room on the left, choices to landmark in the middle, and choices to other on the right), and second choices during probe trials are shown on the far right. Percent choice data has been collapsed across four trials of three different probe trial types for a total of twelve probe trials for each pigeon. There were six birds in each group. There were significant (\*) differences between the control and right HF lesioned pigeons on first choice to other [ $t(10) = -4.23, p < 0.01$ ], second choice to room [ $t(10) = 2.83, p < 0.05$ ], and second choice to landmark [ $t(10) = -2.76, p < 0.05$ ]. There was a significant (+) difference between left and right HF lesioned pigeons on first choice to other [ $t(10) = -4.34, p < 0.05$ ], and the differences between these groups approached significance for second choice to room [ $t(10) = 3.54, p = 0.053$ ] and second choice to landmark [ $t(10) = 3.53, p = 0.054$ ].



separately with removal of the other landmark type, and thus set in conflict to the global room cues with respect to defining the location of the correct food bowl. The probe trials were designed to determine whether the landmarks, and possibly which type of landmarks, or the global room cues were preferentially used by the pigeons to locate the

correct food bowl, and whether there were any right-left HF differences.

Looking at the first food bowl chosen by the pigeons on the probe trials showed that the distribution of choices of the left HF lesioned pigeons did not differ from controls; both overwhelmingly preferred the ‘correct’ food bowl

defined by the global room cues (fig. 2). By contrast, pigeons with right HF lesions, although still preferring the 'correct' bowl defined by the global room cues, nonetheless showed less of a preference for the global room cues and a stronger preference for choosing bowls that were 'incorrect' food locations defined by either set of spatial cues. Second choice data on the probe trials were perhaps even more interesting. The control and left HF lesioned pigeons continued to behave similarly, and continued to preferentially respond to the 'correct' bowl, although less strongly, defined by the global room cues (fig. 2). By contrast, pigeons with right HF lesions overwhelmingly responded to the 'correct' food bowl defined by location with respect to the landmarks (fig. 2, the two-dimensional and three-dimensional landmarks had similar control over their behavior). Interestingly, the similarity between the control and left HF lesioned pigeons broke down for the latency to respond data. The control lesioned pigeons displayed substantially longer first choice response latencies on probe trials compared to training trials whereas the left HF lesioned pigeons did not.

The data summarized above offer a clear indication that the right and left HF make different spatial memory contributions toward representing a goal location. The behavior of the right HF lesioned pigeons, in particular their use of landmarks for navigation reflected in their second choices on probe trials, suggests that the left HF is able to support a representation of goal locations reliant on landmarks within bounded, experienced space. By contrast, the behavior of the left HF lesioned pigeons, and their exclusive use of global room cues and complete indifference to the rotation and removal of the landmarks (recall the latency data), suggests that the right HF is exclusively involved in representing goal locations reliant on global spatial features. Control pigeons, although never using the landmarks to locate a food bowl, were still sensitive to both sources of spatial information as reflected by their preference for global room cues when making choices and longer response latencies when global room cues were set in conflict with landmarks.

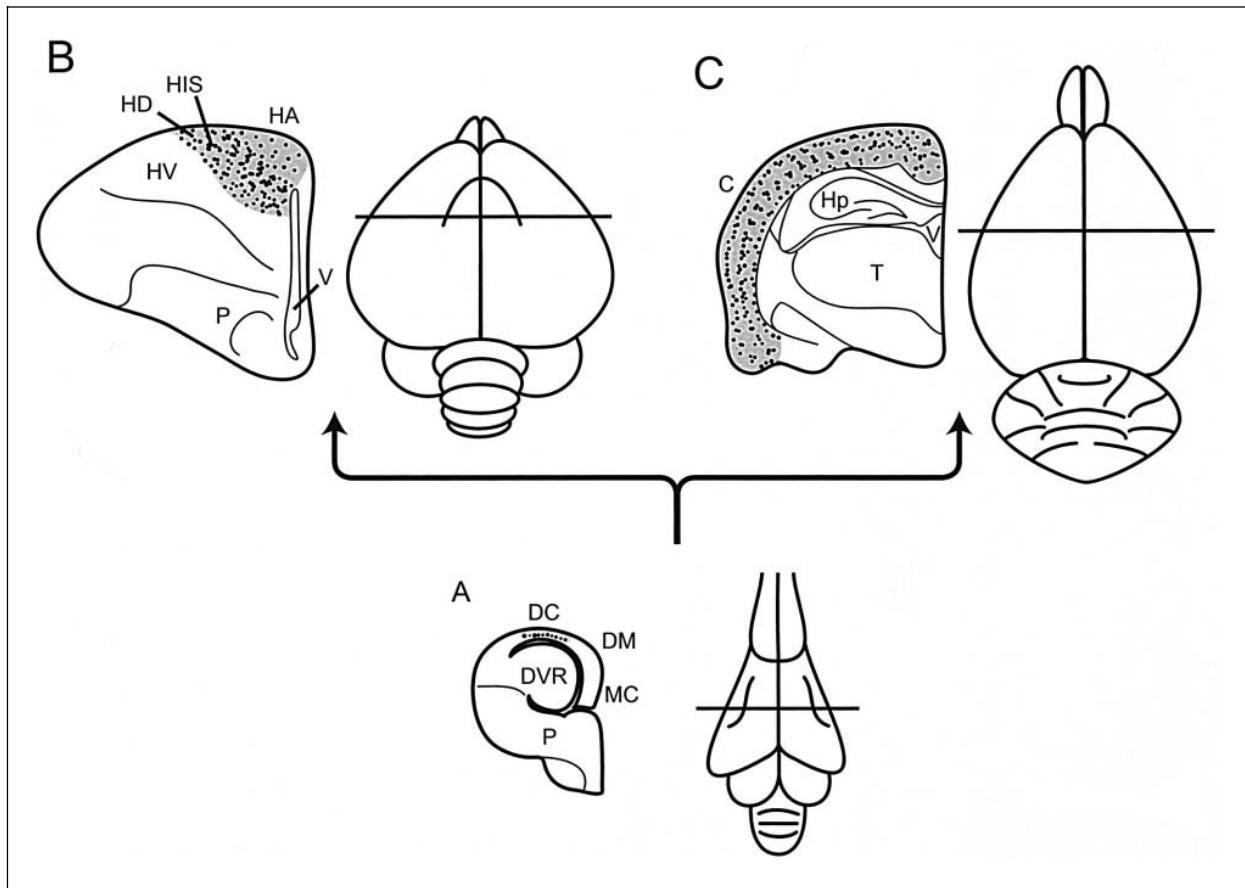
Does the indication of left and right HF differences in the memory representation of space offer a possible departure point for understanding how the homing pigeon and rat HF may be different? Acknowledging that a lot of work needs to be done before one can be confident about describing the lateralized differences in the homing pigeon HF, the data presented are nonetheless intriguing. It has been reported that it is very difficult to train rats to locate goal locations using landmarks centered in a test environment [Cressant et al., 1997]. Similarly, it is diffi-

cult to observe HF place cells with place fields defined by landmarks centered in a test environment [Cressant et al., 1997]. Typically, distal placed stimuli have more control over behavior and the place fields of place cells. Overall, the data summarized above suggest that, under the testing conditions described, pigeons also preferentially rely on global or distally placed cues to locate a goal. However, the left HF is able to support a spatial representation of landmarks within the experimental space that rats may not readily learn. Speculating further, do the data hint that in homing pigeons, but not rats, the HF of the different cerebral hemispheres are differentially suited to some scalar property of space? Specifically, is the left HF more sensitive to smaller scale space of local landmarks, whereas the right HF is more sensitive to a larger scale space of distal, global cues? If true, the finding that either right or left HF lesions interfere with landmark navigational learning in homing pigeons [Gagliardo et al., 2002] could indicate that such learning is dependent on the integration of a prevaingly right HF representation of larger scale space, such as that provided by the sun compass [Bingman and Jones, 1994], with an exclusively left HF representation of smaller scale space made up of familiar landmarks. Such a scalar parceling of space between the left and right HF, together with robust inter-HF connections mediated by the hippocampal commissure, might be a critical design feature of a memory-based navigational system in which, in the field, global cues from the sun or earth's magnetic field are exploited to interpret the spatial relationship among landmarks that will be represented as a map [Gagliardo et al., 1999]. Of course, a difference in sensitivity to spatial scale may not be the only way to conceptualize how the left and right HF differ. Rather than scale per se, the difference could perhaps be a prevaingly right HF sensitivity to global reference frames, like room geometry or environmental directional cues, and an exclusively left HF sensitivity to discrete landmarks/feature elements.

### Search Summary

We have explored possible differences in the homing pigeon and rat HF that could offer some insight into what, if any, species specific specialization(s) in HF organization could explain differences in how homing pigeons and rats behave in and represent space. The survey of the electrophysiological data revealed one striking difference, the apparent absence of prototypical place cells in homing pigeon, and some other suggestive observations of neu-





**Fig. 3.** Schematic representations of coronal sections through the telencephalon of a turtle (**A**, serving only to approximate the brain of the last common ancestor of modern birds and mammals), a pigeon (**B**) and a rat (**C**). Adjacent to the coronal sections are dorsal views of the whole brain of each animal. Highlighted in gray are the pallial wulst of pigeons and pallial neocortex (isocortex) of rats, both presumably evolving from the same dorsal cortex (in gray) region of

their last common reptilian ancestor. Abbreviations: DC = dorsal cortex; DM = dorsomedial cortex; DVR = dorsal ventricular ridge; Hp = hippocampus; HA = hyperstriatum accessorium; HD = hyperstriatum dorsale; HIS = hyperstriatum intercalatus superior; HV = hyperstriatum ventrale; MC = medial cortex; NC = cortex; P = paleostriatum; T = thalamus; V = ventricle. Lines across the dorsal views indicate approximate location of coronal sections.

ronal responsiveness to perhaps event space and context. It is difficult to evaluate these comparative data other than to say they promise of interesting things to come. At this point the challenge is to conceptualize how a visually guided spatial representational system, such as that which includes the avian HF, can operate in the absence of neurons sensitive to the properties of allocentric space independent of what happens in that space.

A notable species-specific difference (specialization?) in HF organization is the finding of functional HF lateralization in homing pigeons that is apparently lacking in

rats. It is curious that HF lateralization is also found in humans. The temptation is to speculate that a spatial ecology with an emphasis on vision, shared by humans and birds, promotes the evolution of HF lateralization. However, we suspect that the HF lateralization seen in humans and birds reflects independent evolutionary responses to different cognitive-environmental challenges. Regardless of the evolutionary origins of hemispheric specialization in humans, language, its importance for memory and its left hemispheric emphasis presumably influenced lateralization of HF function. By contrast, HF lateralization in

birds is presumably a reflection of the challenges of navigating often enormous distances in a global, open field. Finally, the finding of lateralization in homing pigeons raises the expectation of left and right HF differences in the response properties of neurons, a possibility we are currently exploring.

### Epilogue: Beyond the Hippocampus

We have emphasized possible species differences in how the HF participates in the representation of space. However, the relationship between brain and space does not begin and end with HF. In comparing the HF of rats and pigeons we are motivated by the search for differences that would be meaningful in an evolutionary/ecological context; and we have highlighted what we think are some exciting indications of such differences. However, it is undeniable that there are numerous similarities between the rat and homing pigeon HF across a variety of neurobiological and behavioral/functional dimensions. What should not be left out of the discussion, however, is the brain environment in which the homing pigeon and rat HF reside. Many of the telencephalic and sub-telencephalic projections to and from HF are very similar in homing pigeons and rats [e.g., Casini et al., 1986]. However, pallial sensory inputs into HF, other than olfaction, are anatomically very different in homing pigeons and rats. In particular, we want to emphasize differences in the anatomical organization of visual projections into HF, which are presumably critical in shaping how HF comes to participate in the representation of space.

Figure 3 offers a schematic representation of forebrain evolution in modern birds and mammals from their last common reptilian ancestor some 300 million years ago. The most striking feature of brain evolution in birds and mammals is the massive enlargement of the cerebral

hemispheres [Jerrison, 1973], which primarily takes the form of neocortex (isocortex) in mammals and in part the anterior forebrain wulst in birds. Regions within neocortex (via entorhinal cortex) and wulst are the sources of visual input into HF, and the targets of feedback projections from HF. These regions process and structure the visual information exploited by HF in representing space in memory. The critical point is that, although neocortex and wulst may have similarly evolved from ancestral, reptilian dorsal cortex, they then likely followed different evolutionary trajectories to reach their current form [Medina and Reiner, 2000; Puelles, 2001]. The well known laminar and columnar organization of mammalian neocortex is not characteristic of the avian wulst, whose organization is perhaps better characterized as a collection of discrete nuclei. The consequence of this discussion could be profound when considering the possibility of specialization(s) in homing pigeon and rat brain that might account for species differences in spatial behavior and how the brain comes to represent maps of space. HF is currently the focus of discussion on species specialization in spatial cognition, and justifiably so. However, when the dust settles it may be specialization(s) in the properties of visual and other sensory inputs into the homing pigeon and rat HF, in part because of differences in the wulst and neocortex, that best explains why homing pigeons and rats, and perhaps birds and mammals in general, successfully navigate space in a species-specific, adaptive fashion.

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### References

- Able KP (1991) Common themes and variations in animal orientation systems. *Am Zool* 31:157–167.
- Bingman VP, Jones T-J (1994) Sun compass based spatial learning impaired in homing pigeons with hippocampal lesions. *J Neurosci* 14:6687–6694.
- Blakemore RP (1975) Magnetotactic bacteria. *Science* 190:377–379.
- Casini G, Bingman VP, Bagnoli P (1986) Connections of the pigeon dorsomedial forebrain studied with WGA-HRP and (3H)-proline. *J Comp Neurol* 245:454–470.
- Clayton NS, Krebs JR (1994) Memory for spatial and object-specific cues in food-storing and non-storing birds. *J Comp Physiol A* 174:371–379.
- Cressant A, Muller RU, Poucet B (1997) Failure of centrally placed objects to control the firing fields of hippocampal place fields. *J Neurosci* 17:2531–2542.
- Crusio WE, Schwegler H, Lipp H-P (1987) Radial-maze performance and structural variation of the hippocampus in mice: a correlation with mossy fiber distribution. *Brain Res* 425:182–185.
- Eichenbaum H, Stewart C, Morris RGM (1990) Hippocampal representation in place learning. *J Neurosci* 10:3531–3542.
- Eisenbach M (1991) Signal transduction in bacterial chemotaxis. *Mol Cell Biol* 10:137–208.

- Fenton AA, Bures J (1993) Place navigation in rats with unilateral tetrodotoxin inactivation of the dorsal hippocampus: place but not procedural learning can be lateralized to one hippocampus. *Behav Neurosci* 107:552–564.
- Fox SE, Ranck Jr JB (1981) Electrophysiological characteristics of hippocampal complex-spike and theta cells. *Exp Brain Res* 41:399–410.
- Fraenkel GS, Gunn DL (1940) *The Orientation of Animals*. Oxford: Clarendon Press.
- Gagliardo A, Ioalé P, Bingman VP (1999) Homing in pigeons: the role of the hippocampal formation in the representation of landmarks used for navigation. *J Neurosci* 19:311–315.
- Gagliardo A, Mazzotto M, Bingman VP (1996) Hippocampal lesion effects on learning strategies in homing pigeons. *Phil Trans R Soc Lond B* 263:529–534.
- Gagliardo A, Ioalé P, Odetti F, Bingman VP, Siegel JJ, Vallortigara G (2001) Hippocampus and homing in pigeons: left and right hemispheric differences in navigational map learning. *Eur J Neurosci* 13:1617–1624.
- Gagliardo A, Odetti F, Ioalé P, Bingman VP, Tuttle S, Vallortigara G (2002) Bilateral participation of the hippocampus in familiar landmark navigation by homing pigeons. *Behav Brain Res* 136:201–209.
- Gothard KM, Skaggs WE, Moore KM, McNaughton BL (1996) Binding of hippocampal CA1 neural activity to multiple reference frames in a landmark-based navigational task. *J Neurosci* 16:823–835.
- Hampton RR, Sherry DF, Shettleworth SJ, Khurigel M, Ivy G (1995) Hippocampal volume and food-storing behavior are related in parids. *Brain Behav Evol* 45:54–61.
- Heiligenberg W (1991) *Neural Nets in Electric Fish*. Cambridge, MA: MIT Press.
- Holland PC, Bouton ME (1999) Hippocampus and context in classical conditioning. *Curr Opin Neurobiol* 9:195–202.
- Hollup SA, Molden S, Donnett JG, Moser M-B, Moser EI (2001) Accumulation of hippocampal place fields at the goal location in an annular watermaze task. *J Neurosci* 21:1635–1644.
- Jerrison HJ (1973) *The Evolution of Brain and Intelligence*. New York: Academic Press.
- Kahn MC, Bingman VP (2002) Lateralization of landmark spatial learning strategies in the hippocampus of homing pigeons. Program No. 585.16, 2002. Abstract viewer/Itinerary planner. Washington DC: Soc. Neurosci., CD-ROM.
- Krebs J, Sherry DF, Healy SD, Perry VH, Vaccarino AL (1989) Hippocampal specialisation of food-storing birds. *Proc Natl Acad Sci USA* 86:1388–1392.
- Kubie JL, Muller RU, Bostock E (1990) Spatial firing properties of hippocampal theta cells. *J Neurosci* 10:1110–1123.
- LaMendola NP, Bever TG (1997) Peripheral and cerebral asymmetries in the rat. *Science* 278:483–486.
- Lohman AHM, Mentink GM (1972) Some cortical connections of the Tegu lizard (*Tupinambis teguixin*). *Brain Res* 45:325–344.
- Maguire EA, Burgess N, Donnett JG, Frackowiak RS, Frith CD, O'Keefe J (1998) Knowing where and getting there: a human navigation network. *Science* 280:921–924.
- McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung MW, Knierim JJ, Kudrimoti H, Qin Y, Skaggs WE, Suster M, Weaver KL (1996) Deciphering the hippocampal polyglot: the hippocampus as a path integration system. *J Exp Biol* 199:173–185.
- Medina L, Reiner A (2000) Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends Neurosci* 23:1–12.
- Mizunami M, Weibrecht JM, Strausfeld NJ (1998) Mushroom bodies of the cockroach: their participation in place memory. *J Comp Neurol* 402:520–537.
- Muller RU, Kubie JL, Ranck Jr JB (1987) Spatial firing patterns of hippocampal complex-spike cells in a fixed environment. *J Neurosci* 7:1935–1950.
- O'Keefe J, Dovstrovsky 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*. London: Oxford University Press.
- Pravosudov VV, Clayton NC (2002) A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behav Neurosci* 116:515–522.
- Prior H, Lingnauer F, Nitschke J, Güntürkün O (2002) Orientation and lateralized cue use in pigeons navigating a large indoor environment. *J Exp Biol* 205:1795–1805.
- Puelles L (2001) Thoughts on the development, structure and evolution of the mammalian and avian telencephalic pallium. *Phil Trans R Soc Lond B* 356:1583–1598.
- Quirk GJ, Muller RU, Kubie JL, Ranck Jr JB (1992) The positional firing properties of medial entorhinal neurons: description and comparison with hippocampal place cells. *J Neurosci* 12:1945–1963.
- Rodriguez F, Lopez JC, Vargas JP, Gomez Y, Broglio C, Salas C (2002) Conservation of spatial memory function in the pallial forebrain of reptiles and ray-finned fishes. *J Neurosci* 22:2894–2903.
- Rogers L J (1996) Behavioural, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. *Neurosci Biobehav Rev* 20:487–503.
- Rolls ET (1999) Spatial view cells and the representation of place in the primate hippocampus. *Hippocampus* 9:467–480.
- Roof RL, Havens MD (1992) Testosterone improves maze performance and induces development of a male hippocampus in females. *Brain Res* 572:310–313.
- Sharp P, Green C (1994) Spatial correlates of firing patterns of single cells in the subiculum of the freely-moving rat. *J Neurosci* 14:2339–2356.
- Sharp P (ed) (2001) *The Neural Basis of Navigation: Evidence from Single Cell Recording*. New York: Kluwer.
- Sherry DF, Vaccarino AL (1989) Hippocampus and memory for food caches in black-capped chickadees. *Behav Neurosci* 103:308–318.
- Sherry DF, Jacobs LF, Gaulin SJ (1992) Spatial memory and adaptive specialization of the hippocampus. *Trends Neurosci* 15:298–303.
- Sherry DF, Vaccarino AL, Buckenham K, Herz RS (1989) The hippocampal complex of food-storing birds. *Brain Behav Evol* 34:308–317.
- Siegel JJ, Nitz D, Bingman VP (2000) Hippocampal theta rhythm in awake, freely moving homing pigeons. *Hippocampus* 10:627–631.
- Siegel JJ, Nitz D, Bingman VP (2002a) Electrophysiological profile of avian hippocampal unit activity: a basis for regional subdivisions. *J Comp Neurol* 445:256–268.
- Siegel JJ, Hough II GE, Nitz D, Bingman VP (2002b) Space-specific single-unit activity in the homing pigeon hippocampus: a first order analysis. Program No. 477.11, 2002. Abstract viewer/itinerary planner. Washington DC: Soc. Neurosci., CD-ROM.
- Smith ML, Milner B (1981) The role of the right hippocampus in the recall of spatial location. *Neuropsychologia* 19:781–793.
- Strasser R, Bingman VP (1997) Goal recognition and hippocampal formation in the homing pigeon (*Columba livia*). *Behav Neurosci* 111:1245–1256.
- Strasser R, Bingman VP (1999) The effects of hippocampal lesions in homing pigeons on a one-trial food association task. *J Comp Physiol A* 185:583–590.
- Vanderwolf CH (1969) Hippocampal electrical activity and voluntary movement in the rat. *Electroencephalogr Clin Neurophysiol* 26:407–418.
- Wagner H, Takahashi T, Konishi M (1987) Representation of interaural time difference in the central nucleus of the barn owl's inferior colliculus. *J Neurosci* 7:3105–3116.
- Wood ER, Dudchenko PA, Eichenbaum H (1999) The global record of memory in hippocampal neuronal activity. *Nature* 397:613–616.

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