

The Avian Hippocampus, Homing in Pigeons and the Memory Representation of Large-Scale Space¹

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SYNOPSIS. The extraordinary navigational ability of homing pigeons provides a unique spatial cognitive system to investigate how the brain is able to represent past experiences as memory. In this paper, we first summarize a large body of lesion data in an attempt to characterize the role of the avian hippocampal formation (HF) in homing. What emerges from this analysis is the critical importance of HF for the learning of map-like, spatial representations of environmental stimuli used for navigation. We then explore some interesting properties of the homing pigeon HF, using for discussion the notion that the homing pigeon HF likely displays some anatomical or physiological specialization(s), compared to the laboratory rat, that account for its participation in homing and the representation of large-scale, environmental space. Discussed are the internal connectivity among HF subdivisions, the occurrence of neurogenesis, the presence of rhythmic theta activity and the electrophysiological profile of HF neurons. Comparing the characteristics of the homing pigeon HF with the hippocampus of the laboratory rat, two opposing perspectives can be supported. On the one hand, one could emphasize the subtle differences in the properties of the homing pigeon HF as possible departure points for exploring how the homing pigeon HF may be adapted for homing and the representation of large-scale space. Alternatively, one could emphasize the similarities with the rat hippocampus and suggest that, if homing pigeons represent space in a way different from rats, then the neural specializations that would account for the difference must lie outside HF. Only future research will determine which of these two perspectives offers a better approximation of the truth.

INTRODUCTION

Investigations into the neural basis of animal orientation and navigation are confronted with an extraordinary array of spatial behavior mechanisms. These mechanisms can vary with respect to the sensory modality used, whether a mechanism operates exclusively in perceptual space, *i.e.*, in the space directly accessible by an animal's sensory systems, or whether memory-based information can expand the operational space of an animal beyond what it can perceive, and the way spatial information can be represented in the nervous system. Consequently, research into any one spatial system in one species can only provide a representative answer to the broad question of how animals navigate in space and how a nervous system can support navigational behavior. The representative system we will explore is the navigational behavior of homing pigeons, and specifically, the role of a particular brain region, the avian hippocampal formation (HF), in this behavior.

BEHAVIORAL MECHANISMS OF HOMING IN PIGEONS: ONE PERSPECTIVE

The legendary ability of a homing pigeon to return to its home loft, including the ability to approximate the direction home, from unfamiliar locations hun-

dreds of kms away is one of the most extraordinary examples of animal navigation known. Research into the behavioral mechanisms that guide homing pigeon navigation has been a cornerstone of ethological research for more than 50 years, beginning with the seminal work of Gustav Kramer (1952). However, it is worth acknowledging that there is less than unanimity among researchers in their conceptualizations of the spatial behavior mechanisms used in homing. Therefore, we first offer a brief summary of what we think are the most essential features of the various spatial behavior mechanisms that contribute to the homing performance of pigeons.

When displaced to an unfamiliar location, homing pigeons must first determine their direction of displacement with respect to home before an approximate homeward bearing can be computed. To do so, they employ what has been described as their so-called "*navigational map*." The navigational map is a memory-based, spatial representational mechanism that allows a pigeon to determine at least its direction and possibly distance of displacement relative to home even from locations never before visited.

Once determining the direction of displacement with respect to home, homing pigeons then rely on so-called "*compass mechanisms*" to take up an approximate homeward bearing. Compass mechanisms are spatial perceptual mechanisms that allow a pigeon to polarize or discriminate among directions in space in a manner metaphorically analogous to a compass (N, S, E, W). The sun (summarized in Schmidt-Koenig, 1979) and earth's magnetic field (*e.g.*, Walcott and

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Green, 1974) are potential sources of compass information. Successful homing when the navigational map is used for location (“where”) information requires the participation of compass mechanisms, and collectively they are referred to as the “*map and compass*” as initially conceptualized by Kramer (1952). By contrast, successful homing when familiar landmarks are used for location information depends on compass mechanisms to varying degrees (see below). By establishing a polarizing directional framework, compass mechanisms may also critically participate in the learning of a navigational map and landmark navigation.

Intuitively obvious, but difficult to investigate experimentally, is a second map-like spatial mechanism based on familiar landmarks. In regions where pigeons have had previous flight experience, they succeed in learning a map-like representation of familiar landmarks that they can use to return home. So-called “*familiar landmark navigation*,” which can resemble “*pilotage*,” is a memory based, spatial representational mechanism that allows a pigeon to determine at least its direction and possibly distance of displacement relative to home, like the navigational map. However, it is based on the use of previously experienced familiar environmental stimuli (landmarks). Such landmarks are not necessarily visual, but often are (Gagliardo *et al.*, 2001b).

Although there are still gaps in our knowledge of the behavioral mechanisms used by homing pigeons to navigate, the substantial understanding that has been achieved is impressive and permits exploration into the neural mechanisms that support the various behavioral abilities, but where to begin? For a neuroethological/behavioral neuroscience investigation into homing in pigeons, the first question that needs to be addressed is one of localization; in other words, the identification of specific brain regions that participate in some aspect of homing. Fortunately, prior to the beginning of neural basis research in homing pigeons, a vast literature had accumulated in mammals identifying one brain region, the hippocampus, as playing a critical role in memory-based, spatial behavior at least superficially resembling homing (see Eichenbaum *et al.*, 1990). Therefore, it was obvious that the avian hippocampal formation (HF; Fig. 1) was a good place to start to unravel the neural mechanisms that support homing. Using the behavioral scheme we outlined above, we will now offer a summary of what aspects of homing HF appears to participate in as revealed primarily by lesion studies.

HIPPOCAMPUS AND HOMING

Hippocampus and the navigational map

When adult experienced homing pigeons are subjected to HF lesion and then released from a distant, unfamiliar release site, they, perhaps surprisingly, display homeward orientation indistinguishable from intact control birds (Bingman *et al.*, 1988b). This consistent finding demonstrates that HF plays no neces-

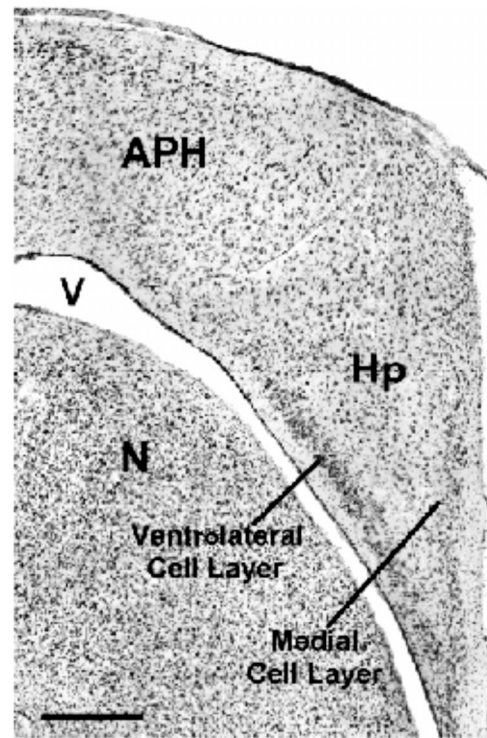


FIG. 1. Photomicrograph of a representative coronal section of the avian hippocampal formation consisting of a medial hippocampus (Hp) and dorsomedial parahippocampus (APH). The hippocampus is characterized by two distinct cell layers, collectively forming the so-called “V,” of large, densely packed cells. N: nidopallium (formerly neostriatum); V: ventricle; Calibration bar 0.5 mm.

sary role in the operation of an already learned navigational map, at least when that map is based on the distribution of atmospheric odors, which is typical of navigational maps learned across a large range of geographic regions (Benvenuti *et al.*, 1998; Papi, 1990).

By contrast, the relationship between navigational map learning or acquisition and HF is substantially more complex. Young homing pigeons learn their navigational map between 2 and 4 months of age. If during this time a young pigeon is given the opportunity to freely fly from its loft, HF lesion does not impair its ability to learn an olfactory navigational map (Ioalé *et al.*, 2000b). By contrast, if during the time of learning a young bird is held in an outdoor aviary, under conditions where intact birds do succeed in learning a navigational map (Walraff, 1966), HF lesion does impair navigational map learning (Bingman *et al.*, 1990). Under these two differing experience regimes, HF lesion impacts navigational map acquisition in one learning environment while not in the other.

Adding to the complexity of understanding the relationship between HF and navigational map learning is the recent finding that the HF of the left hemisphere may play a more important role than the right HF (Gagliardo *et al.*, 2001a). Intact control, right HF-lesioned and left HF-lesioned young pigeons were held in an outdoor aviary during the time of navigational map acquisition. After a three-month learning period,

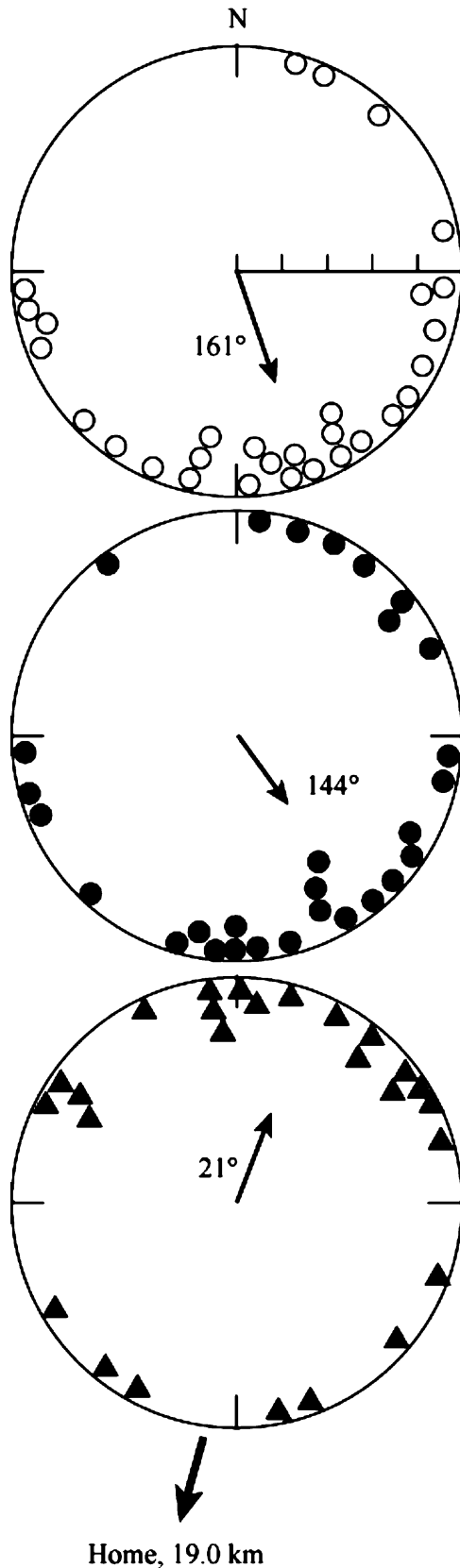


FIG. 2. Vanishing bearings of intact control (top, open circles), right hippocampal-lesioned (middle, filled circles) and left-hippocampal-lesioned (bottom, filled triangles) young homing pigeons when released for the first time from a distant, unfamiliar release

the birds were given a series of experimental releases to determine what effect the lesions had on navigational map learning. Data from one of the releases are presented in Figure 2. As expected, control lesioned birds successfully flew off in an approximate home direction demonstrating that they had learned a navigational map. Pigeons with lesions to the right HF also flew off in an approximate home direction demonstrating that the left HF was sufficient to support navigational map learning. By contrast, pigeons with left HF lesions, like bilaterally HF-lesioned pigeons, failed to fly off in the home direction indicating that they had not learned a navigational map. These findings suggest that the left, but not right, HF plays a critical role in the learning processes that regulate a pigeon's acquisition of a navigational map while held in an outdoor aviary. This robust lateralization finding highlights the need to more thoroughly explore how the left and right HF may make different contributions to the memory representation of space.

Hippocampus and compass mechanisms

The inability of young, HF lesioned pigeons to fly off in the home direction during experimental releases, when confined in an aviary during learning, is a consequence of their failure to learn a navigational map. However, logically the poor homeward orientation could have been a consequence of the young birds not being able to use the compass mechanisms, which are used in conjunction with the navigational map and needed for homeward orientation. Because compass mechanisms are likely more ancient evolutionarily and emerge in development earlier than map-like navigational mechanisms, they are of particular interest with respect to what role, if any, HF may play in their operation. Demonstration of sun compass orientation has traditionally relied on clock- or phase-shift manipulations of the light-dark cycle to predictably alter the relationship between an animal's internal circadian rhythm(s) and the apparent movement of the sun across the sky (summarized in Schmidt-Koenig, 1979). The critical point is that if a homing pigeon is relying on its sun compass for orientation, then a predictable shift in its orientation should occur following a phase-shift of the light-dark cycle. And indeed, HF lesioned pigeons show an appropriate shift in their orientation after a phase-shift manipulation demonstrating that the HF plays no necessary role in the operation of the homing pigeon sun compass (Bingman *et al.*, 1996; Ioalé *et al.*, 2000a).

However, an operational sun compass independent

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 site. Each data point within a circle represents the vanishing bearing of one homing pigeon. The arrow in each circle represents the group mean vector, the length of which can be read from the scale in the top diagram. The longer the mean vector (maximum of 1.0 equal to the radius of a circle), the more clustered are the individual vanishing bearings around the group mean direction. North is at the top of each circle. Adapted from Gagliardo *et al.* (2001a).

of a functional HF does not mean that the HF is unimportant under conditions when sun compass information would be used to provide a directional reference to learn about the distribution of stimuli in space. Exploitation of sun compass directional information is implied in many models of navigational map and landmark navigation learning. In a particularly interesting paper, Bingman and Jones (1994) found that HF lesions thoroughly interfere with the ability of pigeons to use their sun compass to locate the directional position of a food reward in an experimental arena. This suggests that the inability of young, HF lesioned homing pigeons to learn a navigational map when held in an outdoor aviary, or the inability of similarly lesioned young and adult homing pigeons to learn map-like representations of familiar landmarks (see below), is a consequence of the critical role HF plays when the sun compass is used as a directional reference to determine the location of stimuli in space.

Although HF lesioned pigeons show an appropriate shift in orientation following a phase-shift of the light-dark cycle, demonstrating intact sun compass orientation, their behavior is still curiously different from intact controls: their shift in orientation is generally greater (Bingman *et al.*, 1996; Ioalé *et al.*, 2000a). This is not an impairment, just a difference. The origins of this consistently larger shift of HF lesioned pigeons remains obscure (Ioalé *et al.*, 2000a), however, we continue to believe it has something to do with possible HF participation in the re-entrainment of a bird's endogenous circadian rhythm(s) to a rapidly changing light-dark cycle. However, Wiltschko and Wiltschko (2001) have offered as an alternative hypothesis that the larger shift in the orientation of the HF lesioned birds is a consequence of HF lesions interfering with the magnetic compass of homing pigeons. Might HF play a critical role in geomagnetic orientation? Two experiments have been carried out to explore this possibility. First, HF lesioned Savannah sparrows (*Passerculus sandwichensis*) were tested for their ability to orient their migratory activity by the earth's magnetic field (Bingman *et al.*, 1999). Although the HF lesioned birds were not as active as the intact controls, their activity was still well oriented in the migratory direction. Second, experienced homing pigeons with HF lesions (their navigational map was unimpaired) were released from several release-site locations under overcast conditions; conditions when homing pigeons are known to rely on the earth's magnetic field for orientation (Walcott and Green, 1974). Similar to the Savannah sparrows, the HF lesioned pigeons oriented in a manner indistinguishable from controls (Ioalé *et al.*, 2000a). The results from these two experiments indicate that HF plays no necessary role in the operation of the homing pigeon geomagnetic compass. However, neither of these experiments involved an experimental manipulation of the ambient magnetic field, and thus one should at least remain sensitive to the possibility that HF may play some role in geomagnetic orientation. Perhaps like the sun com-

pass, HF may be important if and when the geomagnetic field would be used to learn about the spatial distribution of stimuli in the environment.

In summary, HF does not appear to be necessary for compass orientation by the sun or earth's magnetic field, but in the case of the sun compass, HF becomes critical when compass information is used to learn the directional location of stimuli in space.

Hippocampus and familiar landmark navigation

Although experimentally elusive, enough data has now accumulated to demonstrate that as homing pigeons gain familiarity with an area, they succeed in learning something about the landmarks that characterize the familiar area to be able to use those landmarks for navigation in a manner dissociable from the navigational map (Gagliardo *et al.*, 1999, 2001b; Hartwick *et al.*, 1977). In fact, it is landmark navigation, both its learning and operation, that is most impacted by HF lesions and presumably where HF critically participates in homing pigeon navigation. As a brief summary, HF lesions impair the ability of young homing pigeons to learn to navigate in the vicinity of the home loft (Strasser *et al.*, 1998), result in adult, experienced pigeons taking more time and more circuitous routes to reach the loft (Bingman *et al.*, 1988a; Bingman and Mench, 1990), and impair the ability of experienced pigeons, with their navigational map rendered inoperative, to determine a homeward bearing when exposed to familiar landmarks from a novel perspective (Bingman *et al.*, 1989). As a separate confirmation, when homing pigeons navigate home over familiar terrain, heightened expression of the immediate early gene protein ZENK can be observed in HF (Shimizu *et al.*, 2004). Collectively, these findings highlight the strong connection between HF and familiar landmark navigation. However, the relationship between HF and familiar landmark navigation is more complex than it first appears.

The classic demonstration of familiar landmark navigation is to first train a group of birds from one or more locations with repeated releases. The trained group, together with a group of pigeons naïve to the training sites, are then brought to one of the training sites and released with their navigational map rendered inoperative. Typically, an anosmic procedure is employed to eliminate the navigational map (Gagliardo *et al.*, 1999, 2001b; Hartwick *et al.*, 1977). Under these conditions, the naïve pigeons typically fail to orient in a homeward direction (no navigational map), and the time they take to return home is slow. By contrast, the trained birds display strikingly precise homeward orientation and return home quickly. The successful navigation on the part of the trained birds, despite not being able to rely on their navigational map, is assumed to be based on familiar landmark navigation acquired during the training flights.

Given the close relationship between HF and landmark navigation, it would obviously be expected that HF lesions should impair the familiar landmark navi-

gational learning described above. Surprisingly, however, it does not. When HF lesioned pigeons are given similar training and then released from a familiar location with their navigational map rendered inoperative, they fly off in the homeward direction in a manner indistinguishable from intact controls (Bingman *et al.*, 1988*b*; they do take somewhat longer to return home). However, this apparent contradiction can be resolved if one considers differences in landmark spatial representations that can support familiar landmark navigation.

One can conceptualize one type of representational mechanism as what we call “*site-specific compass orientation*.” In this case, with repeated training from the same locations with an intact navigational map, homing pigeons come to associate certain landscape features (landmarks) with the compass direction flown (as instructed by the intact navigational map) to return home. When subsequently released from one of the familiar locations now with an inoperative navigational map, the pigeons recall the compass (sun) direction flown home based on the learned association with the familiar landscape features, and use the sun compass to orient homeward. This representational mechanism, based on the learned landscape-compass direction association, contrasts with another type of landmark representational mechanism referred to as “*pilotage*.” For pilotage, homing pigeons would learn to navigate by directly exploiting the spatial relationship among familiar landscape features without referring to any compass mechanism. There is a critical behavioral difference between the two types of representational mechanisms. Site-specific compass orientation is effective when a pigeon is released from or very near a training location. Its effectiveness as a navigational strategy diminishes as the perspective from which a bird perceives the familiar landscape features increasingly differs from the training perspective because of the increasing angular error between the trained compass direction taken and the true compass direction home. What the pigeons learn in this case is something like a compass route home, and any displacement from that route (starting point) will lead to error. By contrast, what likely occurs in pilotage is that the birds learn something about the distribution of familiar landscape features relative to the home loft; perhaps represented in a way resembling a map. Critically, if this map-like quality does characterize the pilotage mechanism we are describing, then this kind of representation should allow pigeons to recognize when an error in their homeward flight is occurring, and allow for at least partial correction for any perceived error. Based on the still influential cognitive map theory of HF function developed from mammalian data (O’Keefe and Nadel, 1978), one might expect HF to play a critical role in pilotage while being unimportant from site-specific compass orientation.

Experimentally how can one dissociate familiar landmark navigation guided by site-specific compass orientation from pilotage? The best strategy involves

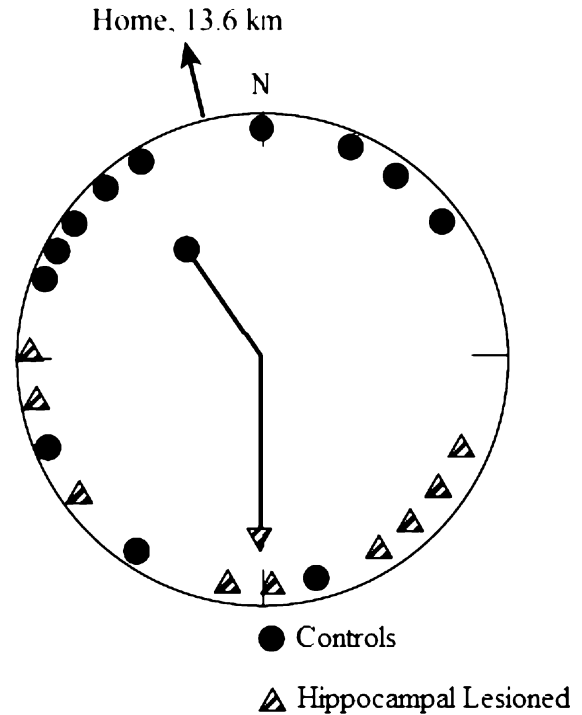


FIG. 3. Vanishing bearings of intact control (filled circles) and hippocampal lesioned (striped triangles) homing pigeons when released from a familiar training site south-southeast of home. All birds were rendered anosmic and phase-shifted 6 hours fast. The mean vector for each group is displayed in the middle of the diagram. The length of a line in the middle of the figure corresponds to a group mean vector length, with a line equal to the radius of the circle equivalent to a maximum mean vector length of 1.0, which occurs when all vanishing bearings are in the same direction. Adapted from Gagliardo *et al.* (1999).

a phase-shift of the light dark cycle. Because site-specific compass orientation is ultimately based on sun compass orientation (on sunny days), the phase-shift should lead to appropriately shifted orientation away from home when this navigational mechanism is employed. By contrast, when pilotage is used for navigation, the phase-shift should not influence homeward orientation because it is compass independent.

Summarized in Figure 3 are the results of one experimental release, taken from the data of Gagliardo *et al.* (1999), in which a group of intact control pigeons and a group of HF lesioned pigeons were released from a familiar training site after having their navigational maps rendered inoperative by anosmia, and being subjected to a 6 hr fast phase-shift of the light-dark cycle. As noted above (Bingman *et al.*, 1988*b*), in the absence of the phase-shift both groups would have oriented in the homeward direction. In this experiment, however, the intact control birds oriented close to the homeward direction while displaying a slight counter-clockwise shift. Because the intact pigeons failed to show the typically large shift in orientation associated with sun compass use following a phase-shift of this type, we interpret these findings as demonstrating that the birds learned a landmark rep-

resentation that could support pilotage-like navigational behavior. The slight shift relative to home indicates they also learned a site-specific compass orientation response, which also influenced their behavior, but not substantially. By contrast, the HF lesioned pigeons showed a typically large, counter-clockwise shift in orientation demonstrating that their behavior was entirely guided by a learned, site-specific orientation (sun compass) response. Consistent with the argument developed above, the intact control birds also homed faster than the HF lesioned birds suggesting that a pilotage-like strategy allows pigeons to more readily make homeward directed course adjustments after the introduction of some displacement error.

In summary, HF lesions appear to compromise the ability of pigeons to learn a landmark representation that can guide pilotage-like navigational behavior, but they have no apparent impact on the learning of landmark based, site-specific compass orientation. So, does the HF critically participate in landmark navigation? The answer is indeed yes, but a qualified yes. Collectively, the data suggest that HF participates critically in landmark navigation, but only when landmarks are represented in what can be best described as a map-like fashion. Navigational learning when landmarks can be associated with simple compass responses, *i.e.*, route-like spatial behavior, does not require the participation of HF.

Implications of the hippocampal lesion effects on homing

The experimental findings described above reveal that the relationship between HF and homing is not simple, and highlights the complexity of both the various spatial behavioral mechanisms that can support homing and the relative role of HF in those behavioral mechanisms. Noteworthy, however, are what the findings reveal about homing mechanisms and the role of HF in spatial behavior. From a behavioral perspective, the HF data emphasize that the concepts of navigational map and landmark navigation need to take into account that there is not just one kind of navigational map or one mechanism by which landmarks can be represented in spatial memory. HF lesions impact navigational map learning under some conditions but not others. HF lesions impact the memory representation of landmarks in some ways but not others.

From the perspective of understanding how the brain, and HF in particular, represents spatial information that can be used to guide goal-directed navigation, the homing pigeon data are of potentially crucial significance. The navigational behavior of homing pigeons is based on a range of spatial behavior mechanisms adapted to the characteristics of their environment and spatial ecology, as well as being influenced by their evolutionary history. HF participation in a number of spatial behavior mechanisms associated with homing is presumably associated with some degree of anatomical or physiological specialization in HF information processing compared to both related

and unrelated species with different spatial ecology and behavior. Any species (or race of pigeon) different from homing pigeons in, for example, sensory capability and preferred sensory modality, locomotor style, circadian pattern of activity, foraging behavior and range (artificial selection for expanded range in homing pigeons), and open-field movement patterns would create selective pressure for differences in how HF participates in the representation of space. As an extreme contrast, there is certainly a dramatic difference in the spatial ecology and behavior of homing pigeons and the extensively studied laboratory rat that are likely reflected in HF organizational differences. Uncovering any HF specialization(s) that may be critical for the representation of large-scale, environmental space in homing pigeons could substantially enhance our understanding of how the brain is able to create a physical memory trace of past experiences and how species-specific variation in the characteristics of HF can influence the properties of memory.

HIPPOCAMPUS AND THE ANATOMICAL AND PHYSIOLOGICAL REPRESENTATION OF SPACE

We begin this part of the paper with the assumption that the relationship between HF and spatial navigation in homing pigeons is, in part, structured to support the extraordinary navigational ability of this species. To frame this comparative discussion in as contrasting a way as possible, we use as backdrop the question of how might the organization of the homing pigeon HF differ from that of the common laboratory rat, promoting the ability of homing pigeons to successfully navigate to their home loft over sometimes extraordinary distances? However, we recognize that differences between homing pigeon and rat HF could also reflect their divergent evolutionary history and forebrain organization, which are not necessarily adaptations to their respective spatial ecology and behavior.

Anatomy

The mammalian HF is an elegant anatomical structure made up of cytoarchitecturally distinct subdivisions. One of the most striking characteristics of the mammalian HF is a prevailing feed-forward processing network, the so-called tri-synaptic circuit, which passes serially through several of the mammalian HF subdivisions (Amaral and Witter, 1995). Might the presumed differences in the way a homing pigeon represents space compared to a rat be reflected in a different type of HF internal pathway organization? Using a combination of anatomical pathway tracing substances (Kahn *et al.*, 2003) and electrophysiological stimulation/recording techniques (Hough *et al.*, 2002), we have explored connections among the various subdivisions of the avian HF as revealed by nissl stain (Fig. 1) and neurochemical markers (Erichsen *et al.*, 1991). The results of this work are complex, but what is clear is that a similarly organized feed-forward-like network can be seen in the avian HF. As summarized in Figure 4, at any given anterior-posterior level, re-

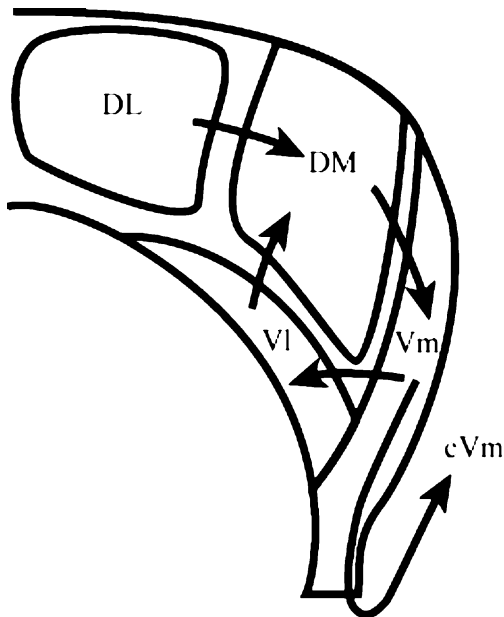


FIG. 4. Schematic representation of a prominent feed-forward network through a representative coronal section of the avian hippocampal formation (see Fig. 1). DL: dorsolateral; DM: dorsomedial; Vm: ventromedial cell layer; cVm: contralateral ventromedial cell layer; VI: ventrolateral cell layer. Note that the projection from VI may not terminate in the same region of DM that projects to Vm.

flective of at least some topographic organization, a dorsolateral HF region, which receives input from a variety of other telencephalic sensory processing regions (Casini *et al.*, 1986), sends a projection to a more dorsomedial HF region. This region then projects onto a layer of densely packed, large cells oriented ventral to dorsal along the midline, the medial arm of the so-called "V." This medial cell layer then sends a projection to the same HF region contralaterally, via the hippocampal commissure, and an ipsilateral projection to the layer of densely packed, large cells oriented along the ventricular wall; the so-called lateral arm of the V. Neurons in the lateral arm of the V then send a projection back to the dorsomedial HF, but perhaps to a sub-region different from the source of the projection to the medial arm of the V.

The pathway connectivity scheme highlighted above is only a skeleton of a much more complex anatomical organization (see Kahn *et al.*, 2003). Indeed, there are other connections that we have found that were not included in the summary, including at least one that is not contained within any anterior-posterior level (not topographic). However, the existence of a discernable feed-forward network in the avian HF suggests first that this type of organization is an ancient (conserved) feature of HF organization, and second, that any difference between rats and homing pigeons in the HF representation of space cannot be explained by a qualitative difference in the internal connectivity among HF subdivisions.



FIG. 5. Photomicrograph of the avian HF capturing what appears to be robust migration of suspected neuroblasts along a network of radiating glia, which emerges from the ventricle wall (bottom). Noteworthy are the cells (neuroblasts?) that have been caught on migration away from the ventricle wall (arrows). Staining was, surprisingly, made with the anterograde pathway tracing substance biotinylated dextran amine (BDA) injected into dorsomedial hippocampus away from the region of labeling.

Neurogenesis

It has been known for quite sometime that the avian telencephalon continues to display neurogenesis well into adulthood (Goldman and Nottebohm, 1983). One region of the avian brain known to display neurogenesis is HF, as best described in a species of food-storing bird (Barnea and Nottebohm, 1994). Neurogenesis is also characteristic of the homing pigeon HF (Kahn *et al.*, 2001). Figure 5 is a photomicrograph that captures what we interpret to be robust migration of neuroblasts into HF along a centrifugal network of radial glia emerging from the ependymal layer bordering the ventricle. We should emphasize that specific glia and neuronal labels were not used in this preparation.

Neurogenesis was for a long time considered a unique property of non-mammalian forebrains, and thus might offer a physiological mechanism for how the homing pigeon HF and rat HF may not represent space in the same way. Recently, however, neurogenesis has been unequivocally demonstrated in the mammalian HF (*e.g.*, Gould *et al.*, 1999), and therefore, neurogenesis can no longer be viewed as a logical source of a difference between the homing pigeon and rat HF.

Electrophysiology

In our opinion, some of the most important findings in the recent history of behavioral neuroscience have been the discovery of two prominent physiological features of the mammalian HF. One is the occurrence of a robust rhythmic field potential (derived from syn-

chronized, spontaneous activity in a population of neurons) in the 4 to 12 Hz range referred to as theta rhythm (Green and Arduini, 1954). In rats, this rhythm is particularly prominent during locomotion, and it has been speculated by some to reflect active exploration of the environment in the context of learning about space. The other is the occurrence of HF neurons that are preferentially active when a rat is in a particular location in a familiar environment: so-called “place cells” (Muller *et al.*, 1987; O’Keefe and Dostrovsky, 1971; Wilson and McNaughton, 1993). Place cells are thought to reflect, at least in part, how assemblies of neurons in the rat HF represent space. The occurrence of place cells and theta rhythm in the rat HF, and their obvious sensitivity to spatial aspects of the environment, suggest that generally similar features should also characterize the homing pigeon HF. However, differences, even if subtle, are also expected as a consequence of how the homing pigeon HF has been (presumptively) adaptively shaped by evolution to participate in the representation of space ranging for tens and even hundreds of kms.

Summarized in Figure 6A are two electrophysiological recordings of spontaneous field potential activity: one in a freely moving homing pigeon, the other in a freely moving rat. Two things are noteworthy. First, the homing pigeon HF regularly displays rhythmic field potential activity in the theta range (4–7 Hz; Siegel *et al.*, 2000). In this sense, the homing pigeon and rat HF are similar. However, the frequency of the homing pigeon theta is slower than typical for rat theta, which is usually around 8 Hz. Also, homing pigeon theta is less closely correlated with actual movement. Pigeon theta is often recorded when an animal is not moving, and often does not occur while an animal is moving.

Summarized in Figure 6B is the characteristic electrophysiological profile of one type of neuron encountered in the HF of freely moving homing pigeons (Siegel *et al.*, 2002). What is noteworthy about this particular unit type is that it resembles some place cells found in the mammalian HF. The resemblance includes a relatively slow firing rate, but when active, a tendency to fire bursts of 1 to 4 action potentials with 5–15 msec inter-spike intervals at an inter-burst rate of 4 Hz. This last finding suggests some possible relationship between the activity of this unit type and theta. Although not shown, we have a number of anecdotal observations suggesting that the activity of this type of neuron is modulated by some spatial quality of a pigeon’s behavior, but not in a way identical to the rat place cell.

The electrophysiological research in homing pigeons is still in its infancy. However, the limited data available can be viewed from two very different perspectives. The apparent subtle differences in the electrophysiological profile of the homing pigeon HF compared to the rat, *e.g.*, the slower theta and the apparent absence of robust, rat-like place cells, offers an intriguing beginning to explore how the HF of homing pi-

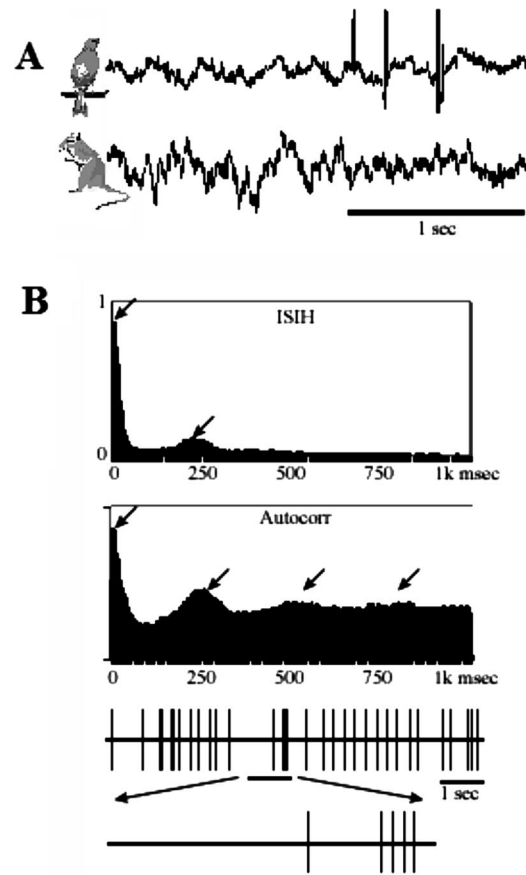


FIG. 6. Characteristic, spontaneous field potential activity (EEG) recorded from a pigeon and rat (A, top) and representative example of the electrophysiological activity profile of one type of neuron found in the avian hippocampal formation (B, bottom). A: Hippocampal theta rhythm (spontaneous field potential activity) recorded from a pigeon (4 Hz) and a rat (8 Hz) (adapted from Siegel *et al.*, 2000). Curious is that 4 Hz characterizes both hippocampal theta and the activity of the neuron type described in B. B: An inter-spike interval histogram, autocorrelogram and 10 sec of spike train activity from one representative type of HF neuron. The neuron tended to fire bursts of 1 to 4 spikes (action potentials) at an inter-burst frequency of about 4 Hz (adapted from Siegel *et al.*, 2002).

geons may differ from rat hippocampus, perhaps reflecting its participation in the representation of large-scale space. As this research progresses, we will be able to better characterize the spatial qualities that are critical in determining the activity of HF neurons in homing pigeon. This alone could substantially advance our understanding of how the homing pigeon HF is able to structure memory for large-scale space. We continue to believe that electrophysiological research into the homing pigeon HF will reveal some enormously interesting spatial coding features not found in rats; features that could explain the relationship between homing pigeons and the representation of large-scale space.

Alternatively, one could look at the anatomical, neurogenesis and electrophysiological data and say that, at least so far, no substantial differences have been found in the organization of the rat and homing pigeon

HF. If this perspective is a better approximation of the truth, then one would be left with trying to explain how the brain of the homing pigeon permits the representation of large-scale space so different from the world of a laboratory rat. Where might one find the neural adaptations that make homing pigeons, and other birds, superb navigators? An answer to this still rhetorical question might be found in other regions of the brain of birds and mammals; regions that have hypertrophied during the course of avian and mammalian evolution. Mammals have experienced a substantial enlargement of the neocortex (isocortex) during their evolution. Less well known, birds have experienced a similar, evolutionary independent enlargement of the anterior forebrain including a region known as “*the wulst*.” The avian anterior forebrain and mammalian neocortex, although developing from the same portion of the developing telencephalon, are very different from each other in anatomical organization (Medina and Reiner, 2000). However, both participate in sensory processing and both are the source of sensory input into HF. Might the presumed difference in spatial representational ability between homing pigeons and rats, and birds and mammals in general, be a reflection of the properties of the forebrain processing of sensory input into HF rather than the differences in HF? (It should be noted that differences in the properties of sensory inputs are not mutually exclusive of differences in HF.)

Speculation is easy at this stage in our electrophysiological investigations into how the HF of homing pigeons is able to structure memory representations of large-scale, environmental space. However, we hope we have shared our excitement for this work and our belief that pursuit of this research could substantially advance not only our understanding of how the HF participates in the representation of large-scale space, but how the brain is able to preserve past experiences as a neural representation we call memory.

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