Animal Spatial Cognition:

Comparative, Neural & Computational Approaches

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Behavioral and Neural Mechanisms of Homing and Migration in Birds

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Abstract

The extraordinary navigational ability of birds has fascinated natural historians for as long as animal behavior has been of interest. Successful navigation in birds is based first on an ability to determine directions in space (compass sense), relying on the sun, stars and earth's magnetic field. This compass sense promotes the development of an ability to determine relative location in space (map sense), which, depending on distance to a goal, exploits predictable variation in the spatial properties of visual landmarks, atmospheric odors and perhaps the earth's magnetic field. The hippocampus of birds is a brain region particularly well suited for implementing navigation based on the map-like representation of familiar landmarks. The experimental study of spatial cognition nurtures a revitalized comparative psychology that encourages the expression of species typical behavior accompanied by research into supporting neural mechanisms.

Chapter Outline & Navigation

I. Introduction

The extraordinary navigational ability of animals, which enables some species to carry out remarkably precise long-distance migrations and homing behavior, has fascinated natural historians for as long as animal behavior has been of interest. The observation of an arctic tern (*Sterna paradisaea*) carrying out a yearly migration between the arctic regions of the northern and southern hemisphere, a gray whale (*Eschrichtius robustus*) migrating between cold water feeding areas near Alaska and birthing sites around the Baja peninsula, a loggerhead sea turtle (*Caretta caretta*) migrating from feeding areas in the north Atlantic to egg deposition sites on the coastal beaches in tropical and sub-tropical North America, and a monarch butterfly (*Danaus plexippus*) making a one-way flight from temperate North America to their winter congregation site in central Mexico can seem mystifying (Figure 1). In fact, the seemingly routine ability of animals in general to accurately navigate space nurtures the speculation that the evolution of spatial cognitive abilities may have also served as pre-adaptation for other forms of cognition and associated brain mechanisms (e.g., O'Keefe, 1996). But how do animals navigate? The goal of this chapter is to review the behavioral mechanisms that are exploited by animals as they navigate large-scale, environmental space, as well present some findings related to brain mechanisms that support this ability. Because of their dramatic spatial behavior and extensive use as experimental subjects, we will concentrate our review on birds.

II. Compass Mechanisms

The ability to polarize space within some directional framework is essential if animals are to maintain movement in a constant direction with respect to the environment. Metaphorically, the challenge is similar to a human navigator needing to use a compass to identify directions in space and maintain a constant directional bearing while moving. Animal navigators possess biological compasses based on their sensitivity to the position of the sun projected on the horizon, or azimuth, stars and the earth's magnetic field. These compass mechanisms, although providing only directional information, form the basis from which richer, map-like representations of space can emerge.

Sun compass.

For diurnal animals with sensory access to the sky, the sun undoubtedly offers the richest source of information to define compass directions and orient movements in space whether it is a short-distance flight of a bee navigating between its hive and a food source or a diurnally migrating swallow making a journey of several thousand kms. The discovery and properties of the sun compass in birds were thoroughly investigated by numerous German researchers in the 1950s and ‘60s (Hoffmann, 1954; Kramer, 1952, 1959; Schmidt-Koenig 1958, 1961). Conceptually, the challenge the sun presents an animal that wants to maintain, for example, a southerly bearing is that the position of the sun in the sky changes during the course of the day. To continue moving south, a bird in the northern hemisphere would need to keep the easterly sun to its left in the morning, fly toward the southerly sun at midday and keep the westerly sun to its right in the evening. The changing azimuth of the sun across the day needs to be calibrated with respect to stable compass directions in space. Birds seem to carry out this conceptually challenging computation effortlessly. They do so by relying on their internal sense of time, which manifests itself in the form of endogenous circadian rhythms. Endogenous, biological circadian rhythms oscillate with a period of about 24 hours and are entrained or calibrated against the light-dark cycle of the environment. A point in time would correspond with a point in the cycle of the circadian rhythm. As such, reading off the circadian rhythm can be used to define time of day and therefore be used to read off a compass bearing from the sun's azimuth.

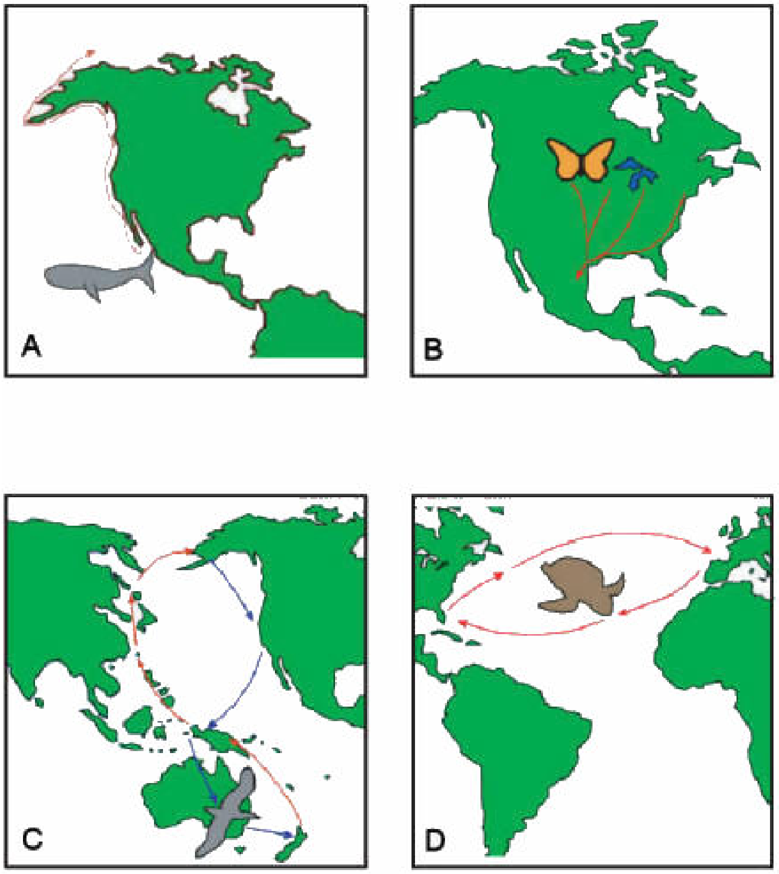

Figure 1. Global migratory paths of four exceptional navigators: A) gray whale (*Eschrichtius robustus*); B) monarch butterfly (*Danaus plexippus*); C) arctic tern (*Sterna paradisaea*); D) loggerhead sea turtle (*Caretta caretta*).

How do we know that the temporal calibration of the sun compass recruits endogenous circadian rhythms as the time giver? This was elegantly demonstrated in birds (homing pigeons and starlings) by placing experimental subjects in an environment where the light-dark cycle was shifted; for example, the lights in the room would come on at midnight and go off at noon basically advancing the day of the birds six hours relative to the light-dark cycle of the natural environment. Birds kept in these conditions for a week or so would experience a shift in their circadian rhythms; a rhythm would recalibrate to the changed light-dark cycle such that the circadian rhythm's morning would correspond or entrain to lights coming on, which would be midnight with respect to the natural environment. Imagine now a migratory bird or homing pigeon that would typically orient south held in the shifted light-dark cycle for a week. The bird would then be tested for its orientation, either by letting it fly (see Figure 2 and 3) or in a cage, during the natural morning when the sun is in the east. However, for our experimental bird the reading of its circadian rhythm would indicate that it is noon (remember its circadian rhythm has been shifted), and you would actually observe the bird orient not in the desired southerly direction but east (Figure 3)! Why? The midday sun is in the south, and according to the bird's internal rhythm, it is noon and it should fly toward the sun. But the sun is really in the east during the environmental morning; therefore movement toward the sun is actually an easterly movement and the wrong direction. It is this type of clock- or phase-shift experiment that has demonstrated that birds, and other animal groups including monarch butterflies (Mouritsen & Frost, 2002), use their internal sense of time to calibrate the movement of the sun in the sky. This enables them to use the sun as a stable reference to define compass directions in space.

To end our discussion of the sun compass, it should be mentioned that in addition to the disc of the sun, birds can also orient to patterns of skylight polarization derived from the sun. They can do so because the properties of skylight polarization change predictably with the changing position of the sun (e.g., Able, 1982). Bird visual sensitivity to ultraviolet light, like that of bees, may be important in detecting skylight polarization

Star compass.

The sun is not the only celestial body that can be exploited to define directions in space. Although nocturnal migrant birds can and do use the position of the setting sun to orient their nighttime migrations (Moore, 1987), they can also rely on the stars. But it is not just any star or cluster of stars that can be used to guide migration. It is the stars around the axis point of the night's sky apparent rotation that are preferentially relied on (Emlen, 1967). In the Northern Hemisphere, these would be circumpolar stars like those found in the constellations of the Big Dipper and Cassiopeia. However, this star compass has properties different from the sun compass. For example, orientation to the stars is not time compensated; phase shifting migrant birds do not alter their migratory orientation to the stars as they would sun compass orientation. It is also notable that whereas birds can be trained to use the sun compass to orient to a food source or other goal unrelated to migration or homing, orientation by the stars has only been demonstrated in the context of migration.

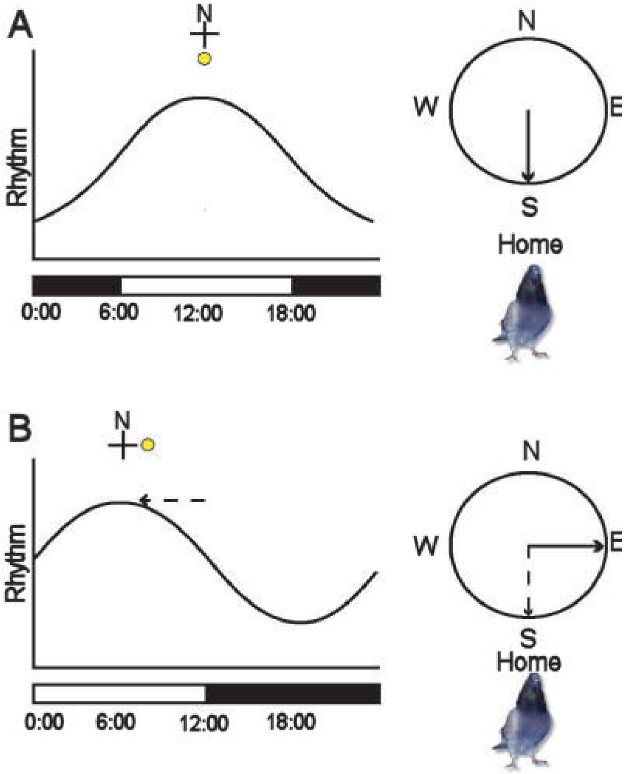

Figure 3. Effect of a phase-shift in the light-dark cycle on the sun compass orientation of homing pigeons. A.) Under natural conditions, the properties of a circadian rhythm would peak during midday and be associated with the sun in the south. A pigeon needing to fly south would then orient toward the sun at midday. B.) After being held for one week in a room where the light-dark cycle has been advanced by six hours, the peak in the circadian rhythm associated with midday would now occur during the natural morning. When released now during the natural morning, the pigeon's subjective noon, the same bird needing to fly south would again fly toward the sun, which would be east! Because of the change in the circadian rhythm, the peak in the circadian rhythm previously associated with midday and the sun in the south would now actually correspond to environmental morning and the sun in the east.

Geomagnetic compass.

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Figure 2. Video illustration of a homing pigeon experimental release that could be used to determine the properties of the sun compass.

The sensitivity of birds to visual orientation stimuli is not surprising given that they have well developed visual systems, and the idea of a sun and star compass was quickly embraced by researchers. This was not the case for the now well established behavioral ability of birds to orient by the earth's magnetic field. The problem with celestial cues is that there are times, in some places frequently, when the sky is obscured by clouds. Lengthy periods of time without access to celestial orientation cues could substantially compromise survival and reproduction if birds could not rely on some alternative compass mechanism. In areas familiar to a bird, known landmarks could serve as orientation cues. But what about a migrant flying high over completely unfamiliar terrain? A sensitivity to the earth's magnetic field, the central nervous representation of which still remains poorly understood, is the solution that natural selection has provided birds for the challenge of compass orientation without access to celestial cues. The experimental demonstration of geomagnetic orientation is apparent when either migrant birds or homing pigeons experience a shift in the ambient magnetic field lines under conditions when they would rely on non-visual cues for orientation. Simply, the birds shift their orientation in parallel with the altered magnetic field. One curious property of their magnetic compass is that it is not the kind of compass that people use while hiking; a so-called polarity compass. Rather, the bird geomagnetic compass is a so-called inclination compass by which north and south are defined by the angle the ambient magnetic field lines make with some vertical reference like gravity (Wiltschko & Wiltschko, 1972).

Ontogeny: The importance of experience.

This book is about spatial cognition, and the compass mechanisms described above would not usually be considered in discussions of animal cognition. At first glance they have an innate, reflexive quality that might be of more interest to an ethologist than a traditional comparative psychologist; however, as we will present below, spatial behaviors readily identified as relying on "cognitive" representations are grounded in these compass mechanisms under field conditions. But labeling these compass mechanisms as innate, even if they played no role in higher order spatial cognition, would be an oversimplification. Young birds must experience the sun's arc across the sky if they are to use it as a compass cue (Wiltschko & Wiltschko, 1981). Even seeing the movement of the sun during only one part of the day, for example the afternoon, enables young birds to make meaningful inferences about the sun's position at unfamiliar times of day, in this case the morning (Budzynski, Dyer, & Bingman, 2000). Birds must continually adjust to the changing solar ephemeris due to the shortening and lengthening of the day, a challenge compounded in migrants because of their geographical displacements.

For nocturnal migrants that use the stars to orient, similar experience is required. Failure to see the night sky during their first summer renders young birds unable to use the stars to guide their first migration. However, even experience with a night sky rotating around a false axis, like a planetarium sky rotating around Betelgeuse in Orion, or a completely artificial rotating night sky is sufficient to enable young birds to adopt the point of rotation as a migratory reference. In the northern hemisphere, young experimental birds during their first migration will orient away from the point of rotation, or "south," thus displaying meaningful migratory behavior (Emlen, 1970).

The type of deprivation experiment that easily identifies a crucial role for experience in shaping how birds use the sun and stars as a compass has not been carried out with respect to the earth's magnetic field. However, geomagnetic orientation is responsive to experience, and this is most apparent when conflicting information about the direction of migration is provided by the different compass mechanisms.

Compass mechanisms: Interactions among the different cues.

Some have described the orientation mechanisms of birds as "redundant." However, the term redundant, suggesting that the different sources of compass information provide identical information, is clearly inappropriate. There is nothing redundant about the earth's magnetic field when the sun or stars are obscured by clouds. Similarly, there is nothing redundant about the sun or stars for birds near the magnetic equator where the inclination of the earth's magnetic field would render geomagnetic orientation ambiguous. Multiple sources of compass information are clearly adaptive. But multiple sources also raise the question of whether orientation mechanisms are organized hierarchically; is one source of information preferentially used over the others, and might orientation to one cue be calibrated against another?

The answer to this question is not straightforward. For young birds learning about environmental orientation cues during their first summer, both North American and European species seem to preferentially rely on celestial cues, in particular the sun and patterns of skylight polarization, as a geographic reference to define north. Young birds will in fact use celestial cues to determine their migratory orientation with respect to the ambient magnetic field (Bingman, 1983). The use of celestial cues to calibrate orientation to the earth's magnetic field is adaptive because whereas the point of celestial rotation provides a temporally and spatially stable reference to define geographic compass directions, variation in the earth's magnetic field in space and time render it less reliable.

In experienced adult migrants, the relationship between geomagnetic and celestial orientation mechanisms depends on geographic location. In Europe, magnetic field information is preferentially used to calibrate orientation to celestial cues indicating an ontogenetic shift in the hierarchy among the orientation mechanisms (Wiltschko & Wiltschko, 1975). By contrast, in North America, at least at more northern latitudes, celestial information continues to be preferentially used to calibrate orientation to the ambient magnetic field (Able & Able, 1990; Cochran, Mouritsen, & Wikelski, 2004). These findings raise the question of why North American and European experienced migrants should behave differently? A likely answer is related to the relative stability of sun and geomagnetic information as birds migrate in time and space (Bingman, Budzynski, & Voggenhuber, 2003). As a bird migrates south in North America, changes in the angular distance between geomagnetic north and geographic north (declination) and changes in the compass direction of the setting sun are similar. There would be no advantage to shift away from the developmental pattern of preferentially relying on celestial cues. By contrast, as a bird migrates south in Europe, the angular distance between geomagnetic north and geographic north remains essentially constant while the direction of the setting sun changes as the migratory season progresses. Therefore, for European migrants, it would be adaptive to adopt the earth's magnetic as the preferential orientation cue once migration begins because of its stability as a directional reference.

III. Map-like or Navigational Mechanisms

Compass mechanisms enable birds to define directions in space to guide oriented movement. However, a compass does not inform an organism of *where* it is in space. That birds have a map sense of where, in addition to a sense of direction, is readily attested to by their remarkable ability to return to the same breeding and wintering sites year after year, and their ability to do so even after dramatic experimental displacements; the most notable example of which is the homing ability of pigeons. However, not all goal navigation necessarily requires a map sense of where.

Getting there without knowing where.

Many typically diurnal songbirds will carry out their first migration at night alone in the absence of any stable social network. Yet the vast majority of these birds will reach their species typical over-wintering area often thousands of kms away. It is difficult to imagine that such birds have acquired map-like knowledge of their migratory route in the absence of any previous experience, so how do they succeed? The answer is a remarkable example of genetic programming (Berthold, 2003). Although the development of celestial sun and star compass mechanisms requires experience, the initial orientation angle a bird makes with respect to those cues seems to be innate. Once a bird is able to define directional space using the sun, stars or earth's magnetic field, how they orient on their first migration, although amenable to change, is innately represented in the nervous system. This innate directional preference can start a naïve migrant moving at least in the direction of its population specific over-wintering site. In fact, the genetic programming can be so sophisticated as to include appropriate changes in direction, for example, when some European species shift their orientation from southwest to south as they approach Africa (Wiltschko & Gwinner, 1974).

But what about distance, how does a naïve migrant know how far it should fly? The solution to this challenge seems to be time (Figure 4). The genetic program that appears to guide a young bird's first migration includes how long it should be active migrating (Berthold & Querner, 1981). This was elegantly demonstrated by studying different populations of European black caps (*Sylvia atricapilla*). Identically hand raised young black caps from a long-distance migratory northern population and a short-distance southerly population were tested in cages for the amount of nocturnal activity displayed during their first fall migration. Young birds from the northern population displayed substantially more migratory activity for a longer period of time during the fall compared to the southern population. Interesting from a genetic perspective, crosses of the northern and southern populations produced young that displayed intermediate levels of migratory activity. The genetic program that guides a young bird's first migration seems to control distance by controlling the amount of time a bird engages in migration.

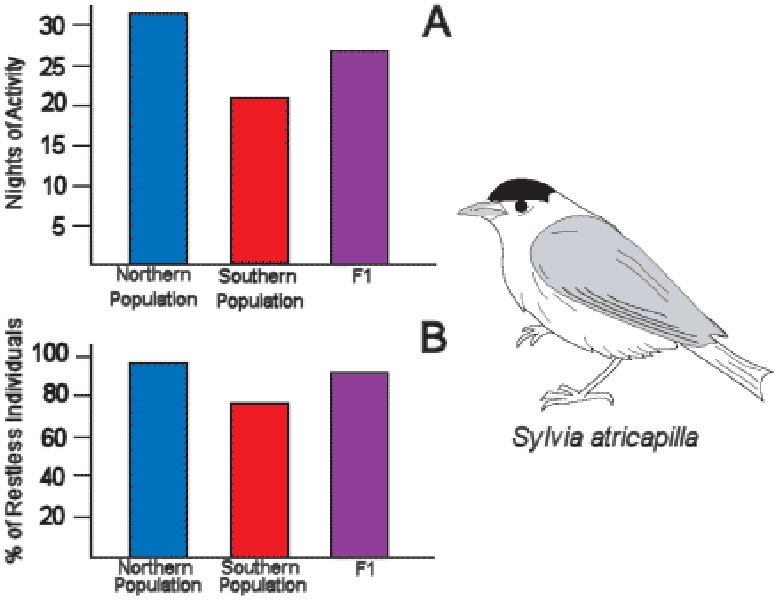

Figure 4. Hand-raised black caps from a northern population that naturally migrate farther (blue) display more nights with nocturnal migratory activity (A) and a greater percentage of migratory active individuals (B) than black caps from a more southern population (red). Crosses between northern and southern population individuals produce F1 birds (purple) that display intermediate levels of migratory behavior.

In summary, a young bird on its first migration succeeds in navigating to its population specific over-wintering site without a map sense of where. A genetic program that defines which direction and how long to fly seems sufficient to get them close, and in the literature this type of navigation is often referred to as "vector navigation."

Getting there and knowing where.

As programmed as a young bird's first migration may be, experience provides them with opportunities for a far richer representation of space that enables a map-like sense of almost global proportions. This map sense can be used by birds to navigate to specific goal locations following displacements to unfamiliar places sometimes thousands of kms away. Layson albatrosses (*Phoebastria immutabilis*), white-crowned sparrows (*Zonotrichia leucophrys*), European starlings (*Sturnus vulgaris*) and routinely homing pigeons (*Columba livia*) are examples of species that have been used in displacement experiments, successfully demonstrating the ability to goal navigate over unfamiliar terrain.

For a bird to have a map-like representation of space, it needs to take advantage of some spatial variation in the quality of environmental stimuli. For a map of a familiar (experienced) environment, this variation may be the spatial relationship among landmarks; such landmarks would typically be visual (Biro, Meade, & Guilford, 2005; Gagliardo, Odetti, & Ioalé, 2001; Lipp, Vyssotski, Wolfer, Renaudineau, Savini, Tröster, & Dell'Omo, 2004) but potentially of other sensory modalities as well. In fact, the spatial relationship among the familiar landmarks and goal locations is likely represented in a directional framework defined by the sun or some other compass mechanism described above (Bingman & Jones, 1994). An important point is that a bird would not be able to extrapolate a map of familiar landmarks beyond the range of sensory contact with the landmarks. But the map sense of birds extends well beyond the boundaries of the sensory range of their experienced space.

The challenge of a map that

extends beyond the range of experienced space is that when a bird is displaced beyond the boundaries of familiarity it must infer its location relative to a goal location. As conceptualized by Wallraff (1974), a bird's map of unfamiliar space could be based on the qualities of two environmental stimuli that vary *predictably* in space in a gradient like fashion (Figure 5). The gradient axes of the two stimuli must also intersect, not necessarily orthogonally, to create a bi-coordinate grid-like system. Using the homing pigeon as an example, let's assume that with respect to the home loft the quality of stimulus x increases to the north and decreases to the south, the quality of stimulus y decreases to the east and increases to the west. A pigeon learns the predictable properties of this variation during flights over familiar areas. More importantly, what a pigeon learns has the properties of an algorithm such that it can infer how the qualities of the stimuli change *beyond* its area of familiarity. When a pigeon is now displaced to the southeast beyond the range of familiarity, it will detect a decrease, compared to the home loft, in the quality of stimulus x and infer its relative displacement northward. It will also detect a decrease in the quality of stimulus y and infer its relative displacement westward. The pigeon could then essentially locate its position on the gradient map to compute a vector or at least direction home to be read off one of its compasses.

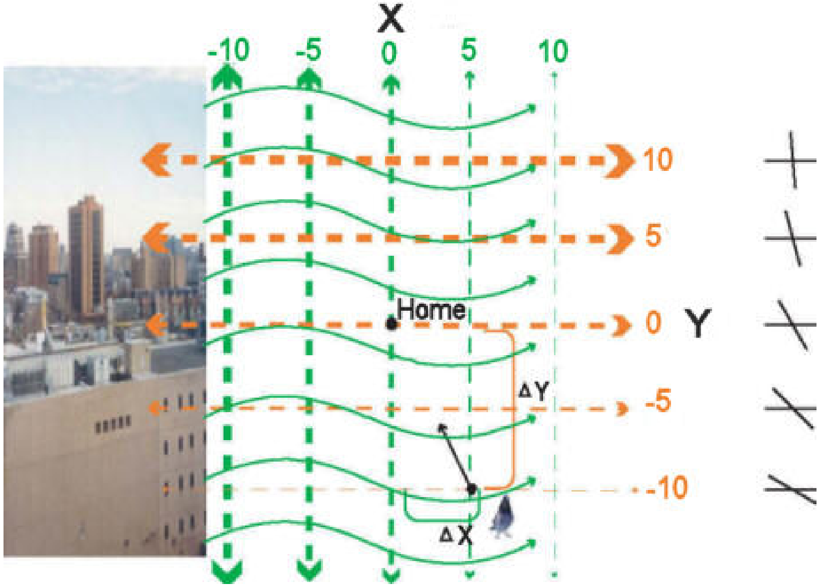

Figure 5. Conceptualization of Wallraff's gradient model of a navigational map. In this hypothetical example, variation in geomagnetic field inclination (far right black lines) increases to the north (Y axis, orange dashes of increasing thickness bracketed by arrows). By contrast, a source of atmospheric odors (city to the left) creates an odor gradient that decreases to the east (X axis, green dashes of decreasing thickness bracketed by arrows). A homing pigeon transported to a location southeast of home would measure its relative displacement by determining the difference between the local atmospheric odor intensity and geomagnetic field inclination with the home values (relative values ranging from +10 to -10). Once the direction of displacement is determined, a homeward vector, or at least direction, can be computed.

Wallraff's elegant model can explain goal navigation from unfamiliar locations, but is it right? The first challenge is to identify environmental stimuli that have the requisite qualities of predictably varying in space. It is not surprising that properties of the earth's magnetic field other than those used to define compass directions have been popular candidate stimuli. On a coarse global scale, a number of geomagnetic parameters, e.g., geomagnetic inclination, vary predictably in space. Therefore, assuming a sensory system capable of detecting often very small differences, two of these geomagnetic parameters with intersecting gradient axes could be used to construct a map. Unfortunately, for homing in pigeons on a scale of tens to a few hundred kms geomagnetic variation can be very noisy and only poorly predicts relative location. Also, there is practically no experimental evidence that favors the presence of a geomagnetic map in homing pigeons (Wallraff, 1999). However, recent work with migrant birds in Australia (Fischer, Munro, & Phillips, 2003), and theoretical considerations (Bingman & Cheng, 2005), are consistent with the possibility of coarse scaled, geomagnetic map information operational at much larger distances from a goal.

If not the earth's magnetic field, then what? Surprisingly, the answer seems, at least in part, related to spatial variation in the distribution of atmospheric odors (Wallraff, 2001). Numerous experiments carried out in homing pigeons have demonstrated that olfactory deprivation sabotages homing ability from distant, unfamiliar locations while sparing homing from sites where familiar landmarks can be used as an alternate source of navigational information. More impressive, false olfactory information, in other words releasing pigeons from one unfamiliar location while being exposed to odors from another location, leads to predictable changes in the direction flown by pigeons upon release. The orientation of the "fooled" pigeons is consistent with them being released from the site recognized by the odors and *not* their actual location.

Could variation in the spatial distribution of atmospheric odors make up one or both of the gradients in Wallraff's model? Developmental studies have demonstrated that even homing pigeons held in an outdoor aviary without the opportunity to fly can learn an olfactory navigational map. Under these conditions, it is difficult to imagine how a gradient map can be learned without a bird experiencing quantitative differences in stimulus quality while actively moving through space. Birds held in an outdoor aviary learn an olfactory navigational map by associating different odor qualities with winds from different directions. Rather than learn a gradient map, they learn what has been described as a "mosaic map," in which patches of different atmospheric odor qualities are associated with different compass directions (Papi, Fiore, Fiaschi, Benvenuti, & Baldaccini, 1972). Note again that a compass mechanism, like the sun compass, would be used to represent how odors vary in space. When subsequently released from a distant, unfamiliar location, a pigeon would sample the odor profile at the release site, recall the wind direction associated with that odor profile experienced at the loft and then, using its sun or magnetic compass, fly off in a direction opposite from the associated wind direction. Interestingly, such a mechanism would render what are ostensibly unfamiliar locations "familiar." The odor profile of unfamiliar sites would be "familiar" to the pigeons because of the odor profile having been transported to the loft by winds. Odor profile would take on the quality of a landmark that could be experienced remotely because of wind.

So does such a mosaic map of atmospheric odors completely solve the problem of navigation after displacement to a distant, unfamiliar location? Probably not. The primary obstacle is that successful navigation can occur over hundreds of kilometers beyond a range conceivable for wind borne odors to be reliably brought to one site like a pigeon loft. How would a pigeon discriminate between an odor profile from the north 50 kms away compared to one from the north 500 kms away? It may well be that a mosaic map is operational over relatively short distances (50-100 kms) and a gradient-like map is operational over longer distances. But is there any evidence that pigeons can learn two types of dissociable navigational maps? We will discuss the role of the hippocampal formation in avian spatial behavior in more detail below, but it is noteworthy that young homing pigeons with hippocampal lesions are unable to learn an olfactory navigational map when held in an outdoor aviary; a presumptive mosaic map (Bingman, Ioalé, Casini, & Bagnoli, 1990). By contrast, young homing pigeons with hippocampal lesions can learn an olfactory navigational map if given the opportunity to fly freely from the loft under conditions when the gradient quality in odor profile could be sampled as the birds move through space (Ioalé, Gagliardo, & Bingman, 2000). The different effects of hippocampal lesions on navigational map learning under conditions of varying experience are consistent with the two map idea. One would be a hippocampal dependent mosaic map operational over relatively short distances, the other a hippocampal independent gradient map operational over much larger distances.

It must be admitted that the proposal of an olfactory navigational map has not been unanimously embraced by researchers in the field. A frequent criticism has been the intuitive difficulty in accepting that the spatial variation in atmospheric odors is stable and predictable enough in space and time to support a gradient or mosaic map of the types described above. This criticism has now been successfully answered by research actually measuring spatial variation in trace atmospheric substances over distances homing pigeons routinely return from. If one looks not at one substance but the relationship among the concentrations of numerous substances, the spatial variation of that *relational* quality is stable and predictable enough to support a gradient map and explain how homing pigeons can identify the direction home from hundreds of kms away (Wallraff, 2004).

We are comfortable with the idea that homing pigeons can rely on atmospheric odors to construct a navigational map, and that they do so in different global regions with substantial differences in climate. There is evidence that other species of birds can use a similar navigational mechanism over relatively short distances (50-100 kms). But it seems impossible to explain migrations of thousands of kms based on a map of atmospheric odors. What type of environmental stimulus could serve as an element in a gradient map of this scale? Although not necessarily satisfying given the general lack of empirical support, and despite Wallraff's admonishment (Wallraff, 1999), there is a persistent temptation to think that at some point the answer will be related to some variation(s) in the earth's magnetic field (Bingman & Cheng, 2005). However, one should be open to any theoretically possible solution as the sensory and cognitive abilities of birds continue to offer surprises.

IV. The Neural Representation of Space in Birds: The Avian Hippocampus

Under natural conditions, birds display an enormous range of spatial behavior mechanisms including different compass mechanisms, vector navigation, navigation by familiar landmarks, and mosaic and gradient maps of atmospheric odors. But there is no reason to think we have fully uncovered all the ways birds represent space or their sensory basis. The different behavioral mechanisms would be supported by different neural representational mechanisms, which would to a lesser or greater extent be supported by different brain regions. To date, it is the hippocampal formation (HF) that has been most extensively studied in the context of avian spatial behavior, and not surprisingly, its importance appears restricted to only a subset of the behavioral mechanisms described above. Although playing some role in navigational map learning under conditions of confinement in homing pigeons, the available data indicate that the prevailing role of HF in the spatial behavior of birds is in the map-like representation of familiar landmarks used to guide goal navigation over familiar terrain.

Lesion and immediate early gene studies.

The very first study examining the effects of HF lesions on the homing behavior of experienced pigeons was accompanied by the disappointment of beautiful homeward orientation from a distant, unfamiliar location and the mystery that the lesioned birds never showed up at the loft (Bingman, Bagnoli, Ioalé, & Casini, 1984). How could one explain an intact navigational map but failed homing? The hypothesis put forth was that as a pigeon approaches its home loft it becomes increasingly reliant on familiar landmarks to guide the final phases of the homing flight, and it is navigation by familiar landmarks that engages HF. The importance of HF for familiar landmark navigation has subsequently been demonstrated in numerous field and laboratory studies, but we will only highlight two to illustrate the complexity of this relationship.

Intact and HF lesioned homing pigeons were trained from two familiar locations and then tested to reveal the kind of landmark-based strategy they learned to return from the familiar sites (Gagliardo, Ioalé, & Bingman, 1999). When tested, the pigeons were rendered anosmic. Blocking the ability to smell would eliminate the ability of the birds to rely on their olfactory navigational map to return home, thus forcing them to rely exclusively on their representation of familiar landmarks. They also had their internal clocks phase-shifted. Conceptually, homing pigeons could use familiar landmarks as an independent map and guidance system, using the landmarks to guide their flight home by serially locating their position in space and noting their movement with respect to the landmarks. Alternatively, they could simply use the landmarks at the familiar release site to recall the compass direction flown from that site during training, and then use their sun compass to take up the homeward bearing. Phase-shifting would dissociate these two strategies. Navigating home by gauging movement with respect to the familiar landmarks alone would not be influenced by the phase-shift manipulation. By contrast, recalling the compass direction home and then orienting by the sun would result in a shift in orientation away from the homeward direction.

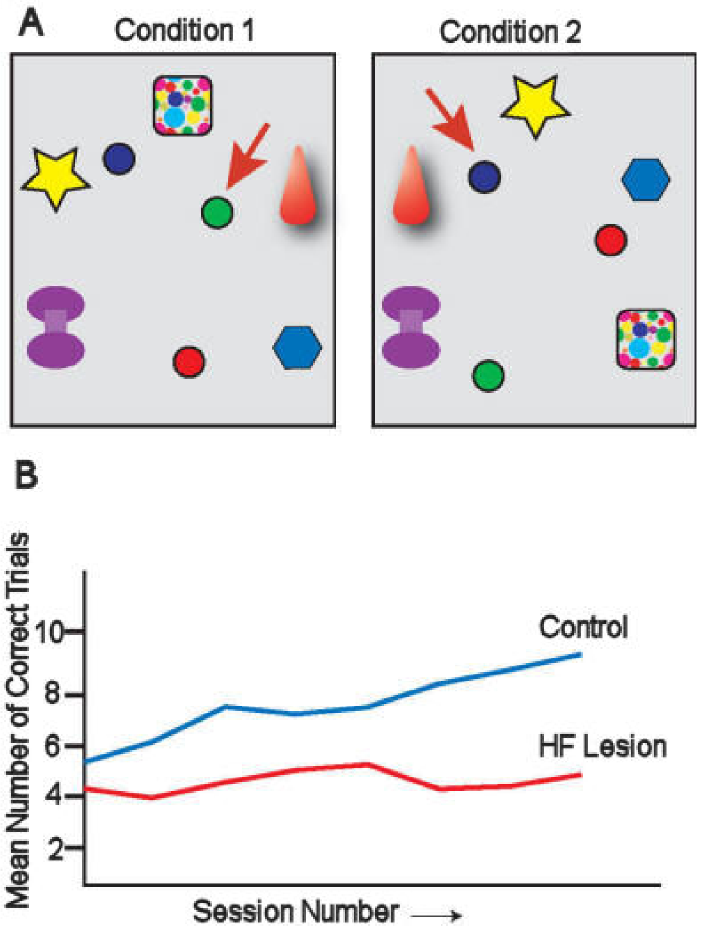

Figure 6. A.) Two five-landmark array environments that differed in the spatial (topological) relationship of the landmarks (e.g., the purple spool was counter-clockwise of the star in one environment and counter-clockwise of the red pyramid in the other). The green bowl contained food in one environment (arrow); the blue bowl in the other (arrow). The red bowl never contained food. B.) Control pigeons (blue line) successfully learned to discriminate the two landmark arrays to choose the correct food bowl. At the end of training they were getting close to 90% of all trials correct. Although the HF lesioned birds (red line) learned to preferentially choose the green and blue food bowls and not the red, they never learned to associate the green and blue bowls with the correct landmark array.

The results of this study demonstrate how subtle the differences can be in the navigational strategies used by control and HF lesioned pigeons. Control pigeons oriented in a direction approximating the true direction home, and therefore, were for the most part uninfluenced by the phase-shift manipulation. They used the unspecified array of familiar landmarks in a map and guidance-like fashion. By contrast, the HF lesioned pigeons displayed a shift in orientation away from the home direction indicating that they relied on their sun compass once determining their location relative to home, presumably by recognizing landmarks at the training site and then recalling the compass direction home flown during training. It is clear that the map-like spatial memory representation learned by the control pigeons was much richer in terms of spatial information available and the potential for inferring route corrections in the event of displacement. This ability requires recruitment of the HF. Simply learning to associate a compass direction with a cluster of familiar landmarks, instructed by the olfactory navigational map available during the training phase of the study, does not require an intact HF.

It is appealing to label the spatial learning of the control pigeons in the previous study as reflecting map-like or spatial relational learning; what has been called a cognitive map (O'Keefe & Nadel, 1978). However, under field conditions it is prohibitively difficult to determine if landmarks are actually being used and how they are represented (but see Guilford, Roberts, Biro, & Rezek, 2004; Lipp et al, 2004); the landmarks can't be manipulated. In a companion study (Figure 6), control and HF lesioned pigeons were trained to discriminate between two landmark arrays, which varied with respect to the spatial relationship among the landmarks, to determine which one of three possible goal locations contained food (White, Strasser, & Bingman, 2002). The landmarks used in the two arrays were identical, just their spatial relationship with respect to each other varied between the two conditions. Control pigeons were successful in discriminating between the landmark arrays. In striking contrast, the HF lesioned pigeons gave no indication of learning that the spatial relationship among the landmarks was different in the two conditions. This laboratory study, together with the previously described field study, offer compelling evidence that the avian HF is crucial for successfully representing landmarks in a map-like, relational manner; a map that can then be used to guide to navigation among goal locations.

The usefulness of lesion techniques for the study of brain-behavior relations is indisputable. However, it is desirable that conclusions drawn from lesion studies be supported by less invasive experimental procedures. One such procedure relies on the activation of so-called immediate early genes that are thought to be often recruited when some type of neuronal re-organization in support of learning occurs. For both homing pigeons learning to navigate by familiar landmarks (Shimizu, Bowers, Budzynski, Kahn, & Bingman, 2004) and a species of songbird remembering the locations of cached seeds to be recovered later (Smulders & DeVoogd, 2000), increased activation of an immediate early gene has been observed in HF. Both the lesion and immediate early gene data converge on the conclusion that the avian HF is critical for landmark-based, map-like representations of space.

Unit recording studies.

The realization that the avian HF is crucial when map-like representations are recruited to navigate and recognize salient locations in space raises the challenging question of how space may be represented at the level of the response properties of HF neurons (units). As background to this question are the well described "place cells" found in the rodent hippocampus (O'Keefe & Nadel, 1978). Place cells are neurons that routinely display large increases in activity when a laboratory rat is at a restricted location in an experimental environment. The place cell has shaped discussion of hippocampal function since its discovery more than 30 years ago and necessarily looms as a standard by which HF unit response properties in other species are measured. However, given the substantial differences in spatial ecology and evolutionary history between rats and birds like homing pigeons, it is likely that the spatial response properties of HF neurons would differ between the two groups in some adaptive fashion.

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Figure 7. Video illustration of a homing pigeon, navigating an analogue 8-arm radial maze (Hough & Bingman, 2004), with HF implanted electrodes connected to a recording cable.

In fact, recordings of HF neurons carried out in freely moving homing pigeons navigating a laboratory environment (Figure 7) have yet to reveal place cells so easily encountered in rats. Rather, what have been found are neurons of two types that are relevant to the challenges of navigating and recognizing locations in space (Hough & Bingman, 2004; Siegel, Nitz, & Bingman, 2005, 2006). One type of neuron is characterized by a tendency to display increased levels of activity (action potential firing rate) when a pigeon is at or near a goal location—a type of neuron we have referred to as a "*location*" cell. Although perhaps superficially resembling place cells, these pigeon HF location cells differ from rat place cells with respect to a number of response property characteristics. The second type of neuron is characterized by a tendency to display increased levels of activity when a pigeon is moving through corridors that leads to and from goal location—what we have referred to as a "*path*" cell. The types of response properties described are consistent with the speculation that homing pigeon HF neurons participate in relating the position of goal locations with the computation of navigational trajectories that lead to those locations. But perhaps the biggest surprise is that neurons with different response properties tend to lateralize to the HF on different sides of the brain.

A lateralized HF: Adaptation for navigating avian space?

The functional lateralization of the vertebrate forebrain was once thought to be a uniquely human characteristic. However, it has now been clearly demonstrated that the avian forebrain is similarly lateralized with the different hemispheres preferentially recruited in the control and expression of different behavior (Güntürkün, 1997). This has been convincingly shown in the domain of spatial behavior in a number of bird species such as chicks, homing pigeons and songbirds. More recently, the asymmetrical contribution of the HFs of the two forebrain hemispheres in guiding spatial behavior has been revealed. In one lesion study carried out in homing pigeons (Kahn & Bingman, 2004), birds were trained to locate a food goal by relying on landmark cues locally distributed in the experimental environment, which the birds could move through (Figure 8). They could also rely on distal cues such as light fixtures and markings on the walls and ceiling in the room where the experimental environment was located. Pigeons with left and right HF lesions both learned the task without difficulty. However, the spatial representation that guided their behavior, as revealed by probe trials that set information from the local landmarks in conflict with the distal room cues, was notably different. Pigeons with left HF lesions overwhelmingly relied on the distal room cues to locate the goal and behaved as if the local landmarks did not exist. By contrast, pigeons with right HF lesions used the distal room cues less and were more reliant on the local landmarks to locate the goal. The results suggest that the right HF may be more important for the representation of goal locations reliant on global/distal properties of an environment. It is interesting to note that pigeons with right HF lesions can also use the sun compass to learn the location of a goal or an olfactory navigational map; both of these spatial abilities are impaired in pigeons with left HF lesions.

The different sensitivity of the right and left HF to different aspects of space as revealed by the lesion studies is paralleled by unit recording data (Siegel et al., 2006). The occurrence of location and path cells described above do not distribute symmetrically in the HFs of the two hemispheres. Location cells are more likely to be found in the right HF while path cells are almost exclusively found in the left HF. The spatial response profile of neurons in the left and right HF also differ in other respects, the most notable of which is the greater temporal stability or reliability in the spatial variation in the firing rate of left HF cells. Neurons in the left HF likely participate more in representing aspects of space that are stable in time.

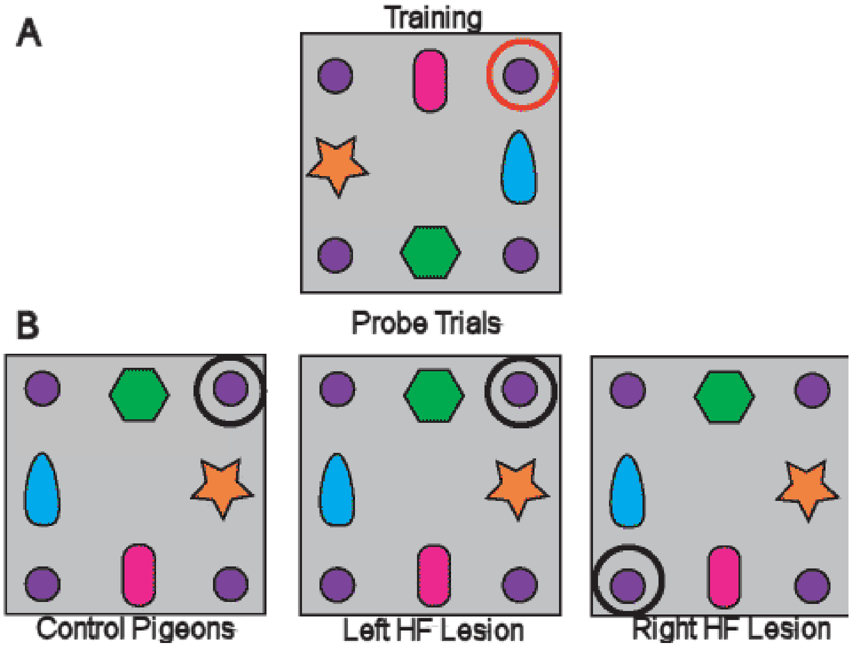

Figure 8. In a lesion study carried out in homing pigeons (Kahn & Bingman, 2004), birds were trained to locate a food goal by relying on landmark cues locally distributed in the experimental environment the birds could move through. Figure A shows the goal location in training while figure B shows the birds selection of the goal location in probe trials.

Reconciling the lesion and unit recording data.

Surveying the lesion and unit recording data reveals a complex picture of HF function and its apparent defining characteristic of lateralization. This lateralized quality is interesting because the human HF is also lateralized while there is little indication of it in the rat. When the dust settles, lateralization, and particularly HF lateralization in the context of spatial behavior, may be a defining adaptive feature of the avian HF organization that explains in part the extraordinary ability of birds to navigate space (Bingman, Hough, Kahn, & Siegel, 2003). But what is really lateralized? As a working model, we view the right HF as preferentially participating in the representation of goal or "event" locations (location cells) defined by global spatial features of the environment (lesion data). By contrast, the left HF preferentially participates in navigating the environment and computing trajectories among goal locations (path cells) relying on map-like representations of landmarks learned with the aid of directional cues like the sun compass. However, it must be emphasized that the proposed functional asymmetry is in some sense an experimental artifact. In intact pigeons, the two HFs work cooperatively and collectively in supporting behavior; goal navigation requires an ability to determine a path trajectory or route as well as recognize the location of a goal once close. A very large hippocampal commissure offers testimony that the two HFs function as an integrated unit in the control of spatial behavior. Indeed, navigating by familiar landmarks in the field as described previously is disrupted by either left or right HF lesions (Gagliardo, Odetti, Ioalé, Bingman, Tuttle, & Vallortigara, 2002). Neurons in the left and right HF may be preferentially sensitive to different aspects of space, but both are required to support the challenge of navigating by a map-like representation of familiar landmarks.

V. Fitting into a General Comparative Psychology of Spatial Cognition

Traditionally, the study of comparative psychology has relied on controlled experimental settings in an intellectual environment setting shaped by learning theory. Although undeniably successful as a science, this research may have necessarily diminished the detection of species differences as subjects were tested in laboratory environments that often failed to promote the expression of species typical behavior and the cognitive mechanisms that support them. The research described in this chapter is inspired by a complementary approach to comparative psychology that draws on the lessons of ethology. It can be taken as axiomatic that during the course of evolution a species' ecology and natural history have substantially shaped the relationship among brain organization, behavior and the underlying cognitive processes that support behavior. The unique suite of spatial behavior mechanisms that birds rely on to navigate space, from a magnetic compass and vector navigation that require little experience to become operational, to open-ended, HF mediated familiar landmark navigation, can all be viewed as adaptive responses to the challenges of their spatial ecology. From this perspective it is easy to understand why the homologous HF of rats and homing pigeons can differ in the qualities of space represented. More subtle HF differences can be expected even among different species of birds or any taxonomic group. In our view, a growth area in comparative psychology is a revitalized interest in an experimental philosophy that encourages the expression of species typical behavior accompanied by research into supporting neural mechanisms. The comparative study of spatial cognition is an example of how successful this approach can be.

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