Animal Spatial Cognition:

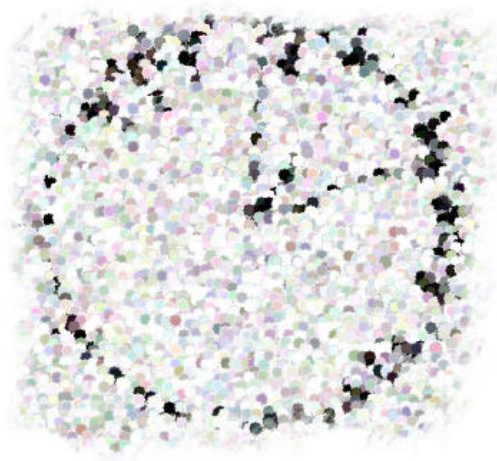## Comparative, Neural & Computational Approaches

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True Navigation: Sensory Bases of Gradient Maps

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Abstract

A variety of vertebrates and at least one invertebrate exhibit "true navigation", i.e., the ability to home over distances of tens to hundreds of kilometers without relying on familiar landmarks or information about the direction of displacement to the testing site. These remarkable feats of orientation are thought to involve positional ("map") information obtained from environmental gradient(s) of olfactory or magnetic cues that can be extrapolated beyond an individual's area of experience. We review the evidence for large-scale gradient maps, and contrast these with maps of spatial position used to orient in familiar surroundings (place maps, bearing maps, mosaic maps, etc.). The available evidence suggests that true navigation involves a patchwork of mechanisms, the use of which depends on the local environment (e.g., characteristics of local gradients), scale of movement, and individual age/experience.

Chapter Outline & Navigation

I. Introduction

True navigation is defined as the ability of an animal to return to its original location after displacement to a site in unfamiliar territory, without access to familiar landmarks, goal emanating cues, or information about the displacement route. This ability, which has been demonstrated in vertebrates (Rodda & Phillips, 1992) and one invertebrate (spiny lobster; Boles & Lohmann, 2003), requires both a sense of direction ("compass"), and a sense of geographic position ("map").

Vertebrates have multiple compass systems (sun, star, polarized light and magnetic compasses; Able, 1980; Emlen, 1975; Lohmann & Lohmann, 1996; Moore, 1987; Phillips, 1986b; Schmidt-Koenig, 1979; Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1995a; see also Bingman et al., this volume). Factors that determine which of these compass systems is used at any given time include weather conditions, time of day, and past experience. Each of these compass systems requires different sensory detection/processing mechanisms, e.g., a time compensation mechanism for the sun compass (Phillips & Waldvogel, 1988; Saint Paul, 1953; Schmidt-Koenig, 1990), an ability to relate the alignments of star patterns to the axis of celestial rotation for the star compass (Emlen, 1970; Sauer & Sauer, 1960; Weindler, Wiltschko, & Wiltschko, 1996; Wiltschko, Daum, Fergenbauer-Kimmel, & Wiltschko, 1987), and specialized sensory receptors capable of detecting the plane of polarized light and alignment of the geomagnetic field for the polarized light and magnetic compasses (Able & Able, 1993; Brines & Gould 1982; Phillips & Moore, 1992). Each compass system also incorporates to varying degrees both innate and learned components (Able & Able, 1997; Bletz, Weindler, Wiltschko, & Wiltschko, 1996; Gwinner & Wiltschko, 1978; Helbig, 1992, 1996). To avoid systematic errors in the direction of orientation when switching between compasses, each of these systems must be calibrated with respect to a common reference system. In birds, where the integration of compass information is best understood, the primary compass calibration reference appears to be derived from celestial cues, probably polarized patterns present at sunset and, possibly, also sunrise (Muheim, Moore, & Phillips, 2006a; Muheim, Phillips, & Akesson, 2006b).

Accurate navigation only requires that the map and compass are in register with one another, i.e., that the animal navigator is able to associate a geographic position specified by the map with a compass bearing that will enable it to return to the origin of a displacement or to some other predetermined destination. As noted above, however, birds appear to use a global reference system derived from celestial polarized light patterns to calibrate their compass and presumably, therefore, also their map systems.

The key feature of a navigational map is that it can be extrapolated to unfamiliar sites and used to orient homeward when there is no contact with familiar "landmarks" or reference points, or with goal-emanating cues. This definition of a navigational map applies to both olfactory and magnetic gradient maps (see below), but not olfactory mosaic maps (Able, 2000; Gould, 1982; Griffin, 1952; Wehner, 1998) or other forms of "piloting" or "place navigation" involving the use of familiar visual, olfactory or magnetic reference points. A "gradient" map requires an animal to learn the alignment and, possibly, steepness of one or more environmental gradients within its home range or territory, and to extrapolate these gradient(s) beyond its area of familiarity. Comparison of the value of such a map component at an unfamiliar site with that of the "home value" provides information about the animal's position along the gradient in relationship to home. Non-parallel gradients of two or more different map components would enable an animal to determine its position in two dimensions (bicoordinate position fixing).

The home value of each map component provides the reference necessary to determine the direction (and distance) of displacement along each extrapolated gradient. Since both magnetic and olfactory gradients change over time (Courtillot, Hulot, Alexandrescu, le Mouël, & Kirschvink, 1997; Ganzhorn, 1995; Skiles, 1985; Waldvogel, 1987; and see below), the home value(s) of an olfactory or magnetic map would have to be updated periodically. The animal, therefore, must have a means of distinguishing home from non-home locations ("home recognition" cues) that is independent of the cues used to derive geographic position ("map" cues). Manipulation of home recognition cues may produce dramatic changes in homing orientation and/or homing success that can easily be mistaken for an effect on cues underlying the map (see below).

II. Theoretical Considerations

A unified theory of spatial navigation requires integration of mechanisms used to guide movements within familiar configurations of landmarks (piloting, place maps, bearing maps, olfactory mosaic maps) with those used for homing from unfamiliar sites (bicoordinate navigation, gradient maps). However, attempts to develop a unified theory have generally failed to address the differences in the processing of sensory information required for these two types of response. For piloting or place navigation, spatial position in derived with respect to a configuration of familiar landmarks or reference points, with the critical values being the directions and, in some cases, distances to those reference points (Figure 1A), or related features such as the size and appearance of a visual landmark. A variant of this type of map, referred to as a "bearing map" (Jacobs & Schenk, 2003), defines locations in terms of their compass bearing (and distance?) from familiar reference points (Figure 1B). In contrast, for navigation using a gradient map, spatial position is derived from the difference between the local value of each map component and the home value of that component (Figure 1C and D).

Because large scale gradients of magnetic and olfactory cues are too weak for an animal to detect directly, the alignment (and possibly steepness) of such gradients have to be learned by obtaining multiple "point samples" at different sites that are in a known spatial relationship to one another (see Phillips & Deutschlander, 1987; Phillips, 1996). For such large scale gradients of magnetic (Phillips, 1996) or olfactory (Wallraff, 2004) cues, the origin or source of the gradient, and thus the direction and distance from that source, is undefined in the two dimensional world of the navigating animal.

Some types of cues may function in both local place maps and large-scale gradient maps. For example, local odor sources could be used in a "mosaic" olfactory map (comparable to a place map; Wallraff, 2004, see also Bingman et al., this volume). However, this type of map is limited in spatial scale by the detection range of discrete odor sources, and the spatial heterogeneity of odor distributions (Ganzhorn, 1995; Waldvogel, 1987). Over a larger spatial scale, other types of olfactory information (e.g., the ratio of odors from extended sources; Wallraff, 2004) have been proposed to function in a gradient map that can be extrapolated beyond an individual's area of familiarity.

Spatial variation in the magnetic field has also been suggested to provide map information over different spatial scales (Phillips, 1996; Walker et al., 1997). Over distances > 50-75 km (depending on the locality), regional gradients in magnetic field components such as inclination, total intensity and, possibly, declination could be used to provide unicoordinate or bicoordinate map information. At the other extreme, local
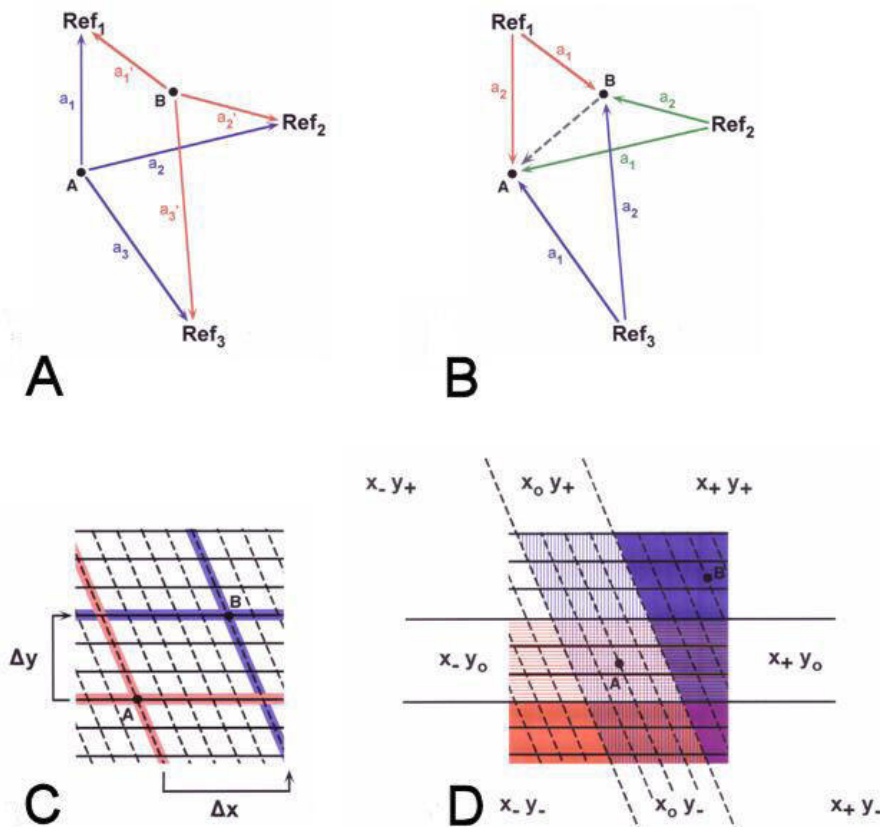
Figure 1. Maps of spatial position. A) Place map, B) Bearing map, C) Bicoordinate gradient map, D) Simple gradient map. 'a_n' indicates a measure of relative spatial relationship to the organism at a given site (in A) or a compass bearing from a familiar reference site (in B). "x" and "y" are the values of two non-orthogonal environmental gradients.
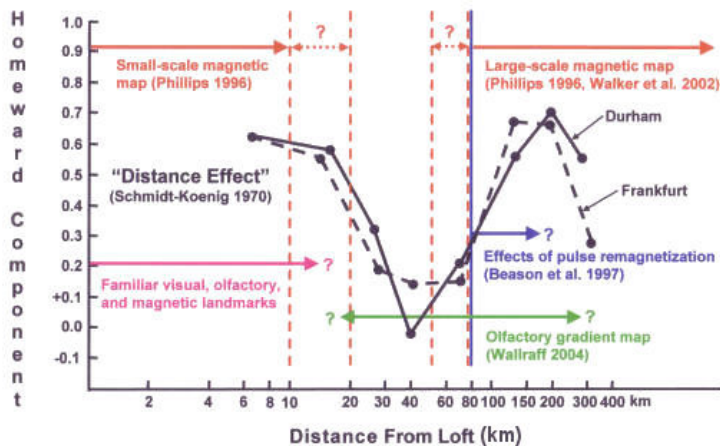

Figure 2. Effects of distance on the accuracy of pigeon homing (data from Schmidt-Koenig, 1970). Solid black symbols show homeward component calculated from the pooled vanishing bearings of birds released at four sites around a loft in Durham, NC USA (solid black line) and a loft in Frankfurt, Germany (dashed black line). Horizontal arrows show predicted range of magnetic gradient maps (red), olfactory gradient maps (green), familiar landmarks (purple), and range of distances at which pulse remagnetization was found to affect pigeon homing (blue). Vertical lines show boundaries of predicted ranges of magnetic gradient maps (red) and of range at which effects of pulse remagnetization were observed (blue). Question marks indicate where boundaries are not specified (green), dependent on experience (purple), or data are not available (blue).

gradients extending over distances of < 5-10 km, which often differ from the regional gradient in both direction and steepness, may provide the basis for a small scale gradient map. Recognizable local "anomalies" in the magnetic field may also provide reference points (possibly in combination with visual or olfactory cues) for a place or bearing map (Ganzhorn, 1990; Walker, Dennis, & Kirschvink, 2002). At intermediate distances (from 10-20 km to 50-70 km), local and regional variation tend to be similar in magnitude, so both higher and lower magnetic field values are likely to be encountered in all directions. At these distances, the magnetic field is unlikely to provide a reliable source of map information (Phillips, 1996). Given the spatial heterogeneity of potential map cues, animals that differ in mode of locomotion and range of movement are likely to use different types of maps to determine spatial position. Moreover, the same species may rely on different sources of map information for short and long distance movements. Interestingly, Schmidt-Koenig (1966; 1970) found that homing pigeons at a loft in the United States and one in Germany showed markedly poorer homing orientation from sites at intermediate distances from the loft (30-70 km) in comparison to sites both closer and further away (Figure 2), suggesting that different (and, at these sites, non-overlapping) navigational mechanisms may be used for short and long-distance homing (see also Matthews, 1963).

Gradient maps may also differ in complexity (and, consequently, in underlying neural architecture) in different animals. At one extreme, a bicoordinate map may provide estimates of actual position that vary continuously in both direction and distance from the animal's "home" or final destination (bicoordinate position fixing; Figure 1C). At the other extreme, a relatively simple stimulus/response system that triggers a limited number of discrete behaviors ("orient to the southwest if the values of both map coordinates are greater than the home values"; i.e., X_+Y_+ in Figure 1D) may suffice to produce accurate homing under some conditions (K. Lohmann, personal communication). A simple gradient map like that shown in Figure 1D may be functionally indistinguishable from a course-grained bearing map in which compass bearings are associated with large areas or sectors around an individual's home. Finally, sites that an animal initially localizes by means of one type of map (e.g., a magnetic or olfactory gradient map; Figure 1C) may subsequently be incorporated into a grid of familiar reference points (i. e., place map; Figure 1A), and/or assigned a particular directional relationship to home or other final destination (bearing map; dashed arrow in Figure 1B; see Jacobs & Schenk, 2003). Subsequent recognition of such sites may involve a unique "signature" of cues from the same, or a different, sensory modality, including local olfactory, visual, or magnetic cues (Burt, Holland, & Guilford, 1997; Ganzhorn, 1990; Walker et al., 2002). Like home/non-home recognition cues, the role of cues in providing unique labels or signatures of familiar sites ("site labeling" cues) may be difficult to distinguish from that of cues used to initially establish

the spatial position of that site ("map cues").

III. Sensory Basis of the Navigational Map

Both olfactory and magnetic cues have been proposed as potential sources of gradient map information (Guilford et al., 1998; Hays et al., 2003). Olfactory effects on homing have been relatively easy to document, although the question of whether olfactory cues are involved in the map is more controversial. Magnetic field effects on homing have been more difficult to demonstrate reliably. However, there is a growing body of evidence for the magnetic field's involvement in the map component of homing, due largely to the development of experimental systems that have made it possible to study map-based homing (true navigation) under controlled laboratory conditions (Boles & Lohmann, 2002; Fischer, Freake, Borland, & Phillips, 2001; Fischer, Munro, & Phillips, 2003; Lohmann, Lohmann, Ehrhart, Bagley, & Swing, 2004; Phillips, Adler, & Borland, 1995; Phillips, Freake, Fischer, & Borland, 2002b).

More generally, attempts to understand the sensory basis of navigational gradient map(s) have been hampered by an overly simplistic view of animal navigation which has largely ignored components of navigation systems other than the map and compass. As a consequence, investigators often fail to consider alternative hypotheses that involve, e.g., effects on cues used for home vs. non-home recognition, and for recognition or "labeling" of familiar sites. By discussing such alternatives, we hope to stimulate future studies that will clarify the complex interactions of different types of sensory information that underlie animal navigation and, specifically, the navigational map or maps.

3.1 Olfactory Map

A variety of vertebrates have been shown to recognize and orient towards odors associated with discrete food sources, nesting sites, or breeding areas over distances from a few hundred meters to a kilometer or more (e.g., Clark & Shah, 1992; Joly & Miaud, 1989, 1993; Nevitt, Reid, & Trathan, 2004). In birds, discrete odor sources have also been hypothesized to play a role in providing map information over longer distances, forming a "mosaic" map of olfactory space. In a mosaic olfactory map, discrete odor sources function in the same manner as the reference sites (landmarks) in a place map. Like distant visual landmarks, it has been hypothesized that the location of discrete odor sources can be determined without the individual actually visiting the site where the odors originate by associating particular odors or combinations of odors with winds blowing from different directions (but see below). Even in birds, however, the range over which a mosaic olfactory map can operate is likely to be limited to at most a few tens of kilometers (Bingman et al., this volume; Ganzhorn, 1995; Waldvogel, 1987). For animals confined to the substrate, olfactory cues are likely to function over considerably shorter distances, perhaps only a few hundred meters (Joly & Miaud, 1989, 1993). This is especially true in forested habitats where turbulence in the understory eliminates any consistent relationship between overhead wind direction and the direction of air currents at ground level (e.g., Baldocchi, 1989; Hutchison & Hicks, 1985). At the other extreme, Wallraff (2004) proposed that birds may use an olfactory gradient map based on the spatially varying ratio of certain atmospheric chemicals that can be extrapolated to unfamiliar areas over distances of hundreds or even thousands of kilometers.

Figure 3. Effects of exposure to bottled air and "nonsense odors" during displacement to unfamiliar release sites on the homeward orientation of pigeons. Vanishing bearings from four release sites plotted as deviations from the mean vector bearing of controls at each site. MVB=mean vanishing bearing (J.B. Phillips, J. Ganzhorn & K Schmidt-Koenig, unpublished data)

A variety of techniques have been used to investigate whether olfactory cues are involved in the map component of navigation using pigeons as a model organism, including: (1) olfactory deprivation (plugging the nostrils, anesthesia or chemical ablation of the olfactory mucosa, sectioning of the olfactory nerve, exposure to filtered or bottled air during displacement to a release site, and masking of natural odors with strong odorants), and (2) altering the relationship between wind direction and natural or artificial odors to which birds are exposed in their home loft, in some cases with exposure to the same or different odors at an unfamiliar release site prior to release.

Olfactory deprivation either during displacement to a release site and/or during the homeward journey has been shown to cause increased scatter in initial homing orientation and/or decreased homing success in a large number of experiments (e.g., Grant, Anderson, & Twitty, 1968; Sinsch, 1990a, 1990b; Wallraff, 1990, 2004; Wallraff, Kiepenheuer, Neumann, & Streng, 1995). However, these effects are not universal in pigeons or other animals (e.g., Ganzhorn, 1990, 1992; Sinsch, 1990b; Wiltschko, Schöps, & Kowalski, 1989). For example, in homing pigeons the effects of olfactory deprivation have been shown to vary with loft location and/or early experience, and with characteristics of individual release sites (Ganzhorn, 1990, 1992; Wiltschko et al., 1989). More importantly, experiments showing effects of olfactory deprivation on homing have often failed to rule out alternative explanations involving effects on sensory systems other than olfaction (Mora, Davidson, Wild, & Walker, 2004), and/or olfactory effects on component(s) of the bird's navigational system other than the map (e.g., Ganzhorn, 1990; Phillip & Waldvogel, 1988; Wiltschko, 1996; and see below).

Two alternative explanations for effects of olfactory deprivation on homing warrant particular attention. In birds, a specialized magnetoreception system associated with the trigeminal nerve has been implicated in the map component of homing (e.g., Beason & Semm, 1987, 1996; Beason, Wiltschko, & Wiltschko, 1997; Munro et al., 1997a; Munro, Munro, Phillips, & Wiltschko, 1997b; Walker et al., 1997; and see below). In conditioning experiments with pigeons, Mora et al. (2004) found that anesthesia of the olfactory mucosa, a technique used to produce olfactory deprivation in behavioral studies of pigeon homing (see Wallraff, 2004), also blocks trigeminal nerve mediated responses to magnetic stimuli. Consequently, studies of homing orientation using this technique may inadvertently deprive birds of magnetic, as well as olfactory, information. Secondly, deprivation of olfactory information may deprive birds of the ability to distinguish home from non-home, or to recognize the olfactory signature of familiar sites (see earlier discussion). The possibility of such effects is suggested by preliminary experiments with homing pigeons (Phillips, Ganzhorn, & Schmidt-Koenig, unpublished data). Previous experiments have shown that preventing access to olfactory cues during displacement to an unfamiliar release site can, under some conditions, affect the homing orientation of pigeons (e.g., Papi, 1990; Wallraff, 2004; Wiltschko et al., 1989). In an attempt to distinguish map-related and non-map-related effects of olfactory deprivation, experienced homing pigeons were subjected to one of three treatments during displacement to four release sites arrayed symmetrically around the home loft. Controls were exposed to natural odors during displacement. One experimental group
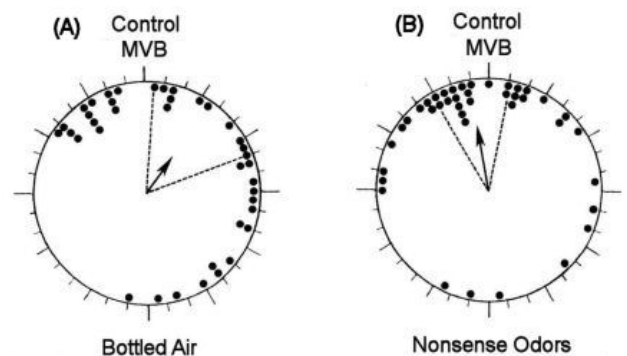
was exposed to synthetic bottled air during transport that eliminated access to natural odors ("bottled air" group). A second experimental group was also exposed to synthetic bottled air during displacement, but a series of artificial odors (peppermint, spearmint, orange, clove, etc.) was introduced into the air stream ("nonsense odor" group). A new odor was introduced every five minutes during the displacement to prevent habituation. The same sequence of artificial odors was presented to the birds during transport to each of the release sites, so that even if one of the nonsense odors occurred naturally in a particular direction from the home loft, exposure to this odor would not produce consistent homeward orientation when departure directions were pooled from all four release sites.

Figure 3A & B shows the vanishing bearings ("initial orientation") of the two experimental treatments plotted as deviations from the mean vector bearing of controls tested at the same release site. Plotting the bearings in this way eliminates any effect of site-specific deviations from the home direction. The distribution of vanishing bearing from bottled air birds differed significantly from that of controls (Figure 3A). In contrast, the distribution of vanishing bearings from nonsense odor birds was indistinguishable from that of controls (Figure 3B). While by no means conclusive [Footnote 1], these findings illustrate the importance of carrying out experiments to determine whether exposure to unfamiliar odors that provide no information about the position of the release site relative to the home loft mimics the effect of exposure to natural odors [Footnote 2]. If so, this would suggest that olfactory cues play a role in a component(s) of the animal's navigation system other than the map. For example, exposure to non-home odors could activate the birds' navigational system, causing the birds to access stored map and compass information and/or to acquire non-olfactory information necessary for homing. The crucial point here is that despite the large number of experiments showing effects of olfactory deprivation on homing (for reviews see Papi, 1990; Wallraff, 2004), critical controls have not been carried out to determine whether these effects are due to the involvement of olfactory cues in the map [Footnote 3]. The same criticism can be leveled at experiments comparing the orientation of groups of pigeons exposed to natural odors at a "false" release site and then rendered anosmic before being transported to a site in the opposite direction from the home loft for testing (e.g., Benvenuti & Wallraff, 1985; Kiepenheuer, 1985).

In addition to olfactory deprivation, a number of experiments with homing pigeons using techniques that alter the relationship between wind direction and either natural or artificial odors have produced findings consistent with the olfactory map hypothesis. However, like the olfactory deprivation experiments, most, if not all, of these experimental findings are open to alternative interpretations. Here we focus on one type of such experiments, the so-called "deflector loft" experiments. In these experiments, three lofts were constructed with sides of wire mesh and vertical louvers that allowed air to pass through unimpeded. Two of the lofts were equipped with large "deflector panels" attached to the sides that rotated incoming winds in either a clockwise (CW) or counterclockwise (CCW) direction (Figure 4). We focus on the deflector loft experiments for several reasons: (1) birds are exposed to natural, rather than artificial, odors, (2) shifts in wind direction are produced passively, thus avoiding potential artifacts associated with fans (noise, infrasound, turbulence, electromagnetic fields, etc), (3) the predicted effects of the deflector lofts are unambiguous, i.e., if pigeons learn the distribution of odor sources by associating the presence of specific odors with winds arriving from particular directions, then rotation of wind direction in the deflector lofts must produce a corresponding shift in the birds' olfactory map and, therefore, in the direction of homing orientation (Phillips & Waldvogel, 1982), and (4) the deflector loft effect has been replicated by laboratories in Italy, Germany and the United States (e.g., Baldaccini, Benvenuti, Fiaschi, & Papi, 1975; Ioalè, Papi, Fiaschi, & Baldaccini, 1978; Kiepenheuer, 1978; Waldvogel, Benvenuti, Keeton, & Papi, 1978).
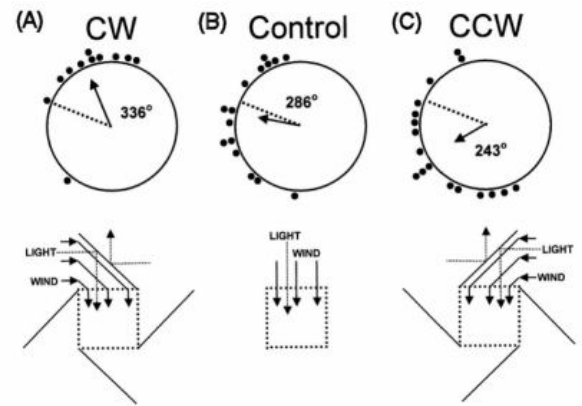

Figure 4. Initial orientation of homing pigeons after housing in deflector and control lofts (data from Waldvogel & Phillips, 1982). A) Initial orientation of pigeons housed in deflector loft that produced a clockwise (CW) rotation of wind direction and reflected light cues (see inset). B) Initial orientation of pigeons housed in control loft without deflector panels. C) Initial orientation of pigeons housed in deflector loft that produced a counterclockwise (CCW) rotation of wind direction and reflected light cues (inset).

Although the deflector loft experiments are frequently cited as support for the olfactory map hypothesis (Wallraff, 2004), several findings call this conclusion into question.

(1) Kiepenheuer (1979) prevented deflector loft birds from detecting olfactory cues by anesthetizing the olfactory mucosa or plugging the nostrils prior to displacement to an unfamiliar release site. Despite their inability to detect natural odors, the birds exhibited shifted orientation indistinguishable from that of pigeons that had been housed in the deflector lofts but were able to detect natural odors. These findings indicate that the deflection of initial orientation of deflector loft birds is not a response to olfactory cues.

(2) Kiepenheuer (1982) removed the vertical louvers from the sides of the deflector lofts (leaving only wire mesh and the deflector panels), resulting in a "whirlwind" pattern of wind flow within the lofts that eliminated any consistent relationship between prevailing wind direction and the wind direction experienced by birds at different locations within the loft. Again the deflection of initial orientation was unaffected, suggesting that associating odors with wind direction does not play a role in the deflector loft effect.

(3) Phillips & Waldvogel (1982) showed that the deflected initial orientation of pigeons held in deflector lofts for five to seven days ("short-term" residents) was a response to light cues reflected from the deflector panels, rather than wind-born cues. The deflected orientation of "permanent resident" birds was also shown to be a response to the altered pattern of light cues visible to the birds in the deflector lofts, rather than wind-borne odors (Phillips & Waldvogel, 1991). Phillips & Waldvogel (1982, 1988) presented evidence that the deflector loft effect results from rotation of a polarized-light-based reference system used to calibrate the sun compass and, possibly also, the magnetic compass of pigeons. Subsequent experiments with migratory birds have demonstrated the use of polarized light cues to calibrate the sun compass (Phillips & Moore, 1992) and magnetic compass (Muheim, Moore, & Phillips, 2006a; Muheim, et al., 2006b).

(4) Waldvogel and Phillips (1982) found that the shift in the initial orientation of permanent resident deflector loft birds was present when birds were released under sunny skies, but not under overcast skies. Since pigeons are unlikely to rely on different source(s) of map information under sunny and overcast conditions, these findings provide further evidence that the deflector loft effect is linked to the use of the sun compass, rather than an olfactory map.

The results of these four experiments demonstrate: a) that the deflector loft effect is caused by rotation of light, rather than olfactory, cues, and b) that wind-borne cues perceived in the home loft do not play a role in the navigational system of pigeons, at least under the conditions used in these experiments. Despite the consistency of the findings outlined above, the results of a fifth type of deflector loft experiment has been widely cited as evidence for an olfactory map.

In pigeons, olfactory input projects to the ipsalateral hemisphere and from there, via the anterior commissure, to the contralateral hemisphere. Foa, Bagnoli, and Giongo (1986) sectioned the anterior commissure of homing pigeons, restricting olfactory input from each nostril to one hemisphere. After recovery, "split brain" birds were housed alternately in the CW and CCW deflector lofts. While housed in the CW loft, the birds' right nostrils were plugged, so olfactory information reached only the left hemispheres. While housed in the CCW loft, the birds' left nostrils were plugged, so olfactory information reached only the right hemispheres. When the birds were released at an unfamiliar site with their right nostrils plugged, their initial orientation was deflected CW. When the birds were released with their left nostrils plugged, their initial orientation was deflected CCW. These findings are consistent with the birds having established independent CW- and CCW- rotated olfactory maps on the two sides of the brain (Foà et al., 1986), and appear to contradict those of the four experiments described above.

However, like the effects of olfactory deprivation, there are a number of alternative explanations for the results of the "split brain" experiments. Here we discuss one such possibility. As discussed earlier, olfactory cues may play a role in a component of the pigeon's navigational system other than the map, such as distinguishing home from non-home (Figure 3). We propose that calibration of the pigeon's sun compass (which is altered by light cues in the deflector lofts; see earlier discussion), and access to this stored calibration information, is triggered by exposure to home and non-home odors (respectively). According to this scenario, the effects of plugging the right or left nostril in the split brain experiments are a consequence of storing and accessing differently calibrated sun compass systems on the two sides of the brain. In contrast to an effect on the olfactory map (as proposed by Foà et al., 1986), this explanation reconciles the split brain experiments with the earlier deflector loft results.

Evidence that the deflector loft effect is not due to wind-borne odors appears to be contradicted by other "wind redirection" experiments with homing pigeons (reviewed by Papi, 1990; Wallraff, 2004). However, here again, alternative hypotheses involving both olfactory and non-olfactory cues have been largely ignored. For example, the effects observed in these experiments could be caused by: a) light cues reflected from glass or Plexiglas panels (Phillips & Waldvogel, 1988), b) aversive stimuli associated with electric fans (electromagnetic fields, air turbulence, infrasound, etc.), or c) pigeons using distinctive odors to "label" wind direction [Footnote 4].

In summary, the literature does not provide compelling evidence for the involvement of olfactory cues in a long-distance gradient map. In birds like homing pigeons, there remains the possibility that olfactory cues play a role in a short-distance "mosaic" map, comparable to a place or bearing map (Ganzhorn, 1990, 1992). However, the findings of the deflector loft experiments make it unlikely that either type of olfactory map involves natural wind borne odors reaching pigeons in their home loft. As in the examples discussed earlier, other experiments that have provided evidence consistent with an olfactory mosaic map require additional controls to rule out alternative explanations involving effects on both olfactory and non-olfactory cues. Particular attention should be paid to the possibility that specific odors encountered during displacement to, or upon arrival at, a release site may provide one type of "site labeling" cues that help identify previously visited localities or regions (Ganzhorn, 1990) and/or distinguish home from non-home (Figure 3), rather that providing remote (i.e., wind-borne) information about the location of distant odor sources (see earlier discussion). Clearly, a better understanding of the role of olfactory cues in both map and non-map components of animal navigation systems is crucial to interpreting the effects of a variety of experimental treatments, including ablations of brain regions involved in processing both spatial and olfactory information (e.g., Gagliardo, Ioalé, & Bingman, 1999; Gagliardo, Ioalé, Odetti, Kahn, & Bingman, 2004; Gagliardo, Mazzotto, & Bingman, 1997; Bingman, Gagliardo, & Ioalè, 1996; Ioalé, Gagliardo, & Bingman, 2000).

3.2 Magnetic Map

On a global scale, magnetic field intensity currently varies from a minimum of 20,000-25,000 nT at the magnetic equator to a maximum of 60,000-65,000 nT at the poles, and magnetic inclination varies from 0° (horizontal) at the magnetic equator to 90° (vertical) at the poles. Yeagley (1947, 1951) was the first to investigate the possibility that spatial variation in the magnetic field could provide homing pigeons with a source of north-south position (see also Gould, 1985; Moore, 1980; Walcott, 1991). However, there are a number of potential problems with the use of a magnetic map, especially for organisms that must resolve differences in spatial position on the order of a kilometer or less (Phillips, 1996).

(1) Magnetic field gradients are extremely weak, i.e., variation in total intensity averages only ~5-10 nT/km (~0.01% of the total field intensity) and in inclination only ~0.010^o/km. The weakness of the magnetic gradients has several important implications for the design of animal navigation systems: a) the sensory mechanism(s) responsible for detection of spatial variation in the magnetic field must be extraordinarily sensitive (Phillips, 1996), b) magnetic gradients can not be detected directly, but instead must be derived from a series of "point samples" [i.e., isolated measurements that contain no information about the alignment of the gradient(s) at the measurement site but are in a known spatial relationship to one another (Phillips & Deutschlander, 1997)], c) the organism must have an independent means of estimating geographic position within its area of familiarity (e.g., a place map, or bearing map), or a non-map-based system for determining its spatial position (e.g., a path integration system; Wiltschko & Wiltschko, 2000, 2003), in order to determine the spatial relationship among measurement sites, d) the organism must be able to store precise measurements of magnetic field component(s) in memory to compare the values obtained at different sites within the spatial array, and e) because an organism must sample multiple sites to build up a knowledge of spatial variation in the magnetic field, use of a gradient magnetic map will be dependent on experience. That is, there should be an ontogenetic progression from reliance on familiar configurations of landmarks (a place or bearing map) and/or path integration, to reliance on a full blown gradient map (Wiltschko & Wiltschko, 2000, 2003).

(2) Due to difference in the iron content of the underlying rock layers, local gradients in the magnetic field often differ in direction and/or steepness from the regional gradient. These local irregularities in the magnetic field will introduce large errors in map estimates if extrapolation of the local gradients is used to estimate geographic position after long distance displacement. As discussed earlier, a gradient map may be used at some (but not all) sites for short distance movements within the range of the local gradients (< 5-10 km). A gradient magnetic map may also be used for movements over long distances (>50-75 km) where the regional gradient predominates. For such a large-scale map, the spatial variation that occurs at distances of less than ~ 50-75 km (i.e., variation due to local gradients) would constitute noise. Consequently, such a large-scale magnetic map could only be used to locate an area 50-75 km in diameter, rather than a specific site within this area (Phillips, 1996; Walker et al., 2002). At intermediate distances from 10-20 km to 50-75 km, where the contribution of local and regional spatial variation is similar in magnitude, there is unlikely to be a spatial signal that could used to provide a meaningful estimate of geographic position. Therefore, the geomagnetic field is likely to be used either for a short-distance, high-resolution map or for a long-distance, low-resolution map, but not for a map that functions at intermediate distances (Figure 2). Consequently, animals that navigate over long distances may be forced to rely on different sources of map information and/or different types of spatial information (place or bearing vs. gradient maps) for different scales of movement.

3) Regular temporal variation in the magnetic field that tends to be greatest during the day light hours could introduce significant errors in fine scale map estimates. For animals that use the magnetic field for a short distance (high resolution) map, therefore, strategies such as averaging multiple measurements over extended periods of time and/or taking measurements at night when temporal variation in the magnetic field is reduced may be necessary to minimize this source of error (Phillips, 1996; Rodda, 1984).

(4) Magnetic storms produce large and unpredictable fluctuations in the magnetic field that could introduce large errors in estimates of map position,

especially in animals using a short-distance, high resolution map. One way to minimize such errors would be to use characteristics of magnetic storm activity, e.g., rapid fluctuations in the geomagnetic field that occur during magnetic storms, to avoid taking map measurements when the field is unstable (Phillips, 1996; Phillips & Deutschlander, 1997).

(5) Finally, long term variation in the magnetic field could introduce systematic errors when significant periods of time separate displacement into unfamiliar territory and the return back to the origin of that displacement, e.g., intervals of several years that occur in some species between juvenile dispersal from a natal site, and the return migration of adults to the natal site to breed (Courtillot et al., 1997). Strategies such as taking measurements immediately before and after displacements (or during the nights immediately before and after displacement) to minimize the effects of temporal variation, and/or factoring out the regular component of such variation based on measurements obtained during intervals between bouts of movement would be necessary to prevent map coordinates from "drifting" over time due to such long term changes.

Despite these very real difficulties, there is a growing body of evidence for the use of a magnetic map for both short-distance and long-distance homing. "Route-deprivation" studies [Footnote 5] of homing orientation by newts (Phillips et al., 1995), juvenile alligators (Rodda, 1984), sea turtles (Lohmann et al., 2004), homing pigeons (Walcott & Schmidt-Koenig, 1973) and spiny lobsters (Boles & Lohmann, 2003) show that these animals are able to use map information obtained at the testing site to determine geographic ("map") position. Newts provide an especially interesting case. As discussed previously, in woodland habitats where newts occur, turbulence in the understory eliminates any consistent relationship between prevailing wind direction and the direction of air currents at ground level (Baldocchi, 1989; Hutschison & Hicks, 1985), thus eliminating any possibility that newts use wind-borne odors to learn the distribution of distant odor sources. The magnetic field, therefore, appears to be the only potential source of gradient map information available to newts, and other similar organisms, that live in this type of habitat. Nevertheless, showing magnetic field effects on homing orientation is not sufficient to establish the use of a magnetic map. Magnetic compass (as opposed to map) cues have been shown to play a role in two important aspects of homing. (1) Young inexperienced individuals may rely on the magnetic compass to determine displacement direction (i.e., path integration; Wiltschko & Wiltschko, 2000, 2003) before they acquire sufficient experience to learn the distribution of map cues. (2) Magnetic compass information may be used for the compass component of homing, e.g., when cloud cover restricts access to celestial compass cues (Diego-Rasilla, Luengo, & Phillips, 2005; Ioalè, 1984).

Two lines of evidence indicate that, in addition to providing compass information, the magnetic field is an important source of map information: (1) amphibians and birds have two distinct magnetoreception mechanisms, one that provides compass information and one that plays a specialized role in the map component of homing, and (2) under some conditions, experienced adult amphibians, reptiles and birds respond to small magnetic field changes as if they have been displaced to a new location ("simulated magnetic displacements").

IV. Dual Magnetic Systems

Magnetic compass orientation in amphibians and birds has been shown to be sensitive to the presence and wavelength of light (Deutschlander, Borland, & Phillips, 1999; Muheim, Bäckman, & Åkesson, 2002; Phillips & Borland, 1992a, 1992b; Wiltschko, Munro, Ford, & Wiltschko, 1993; Wiltschko & Wiltschko, 1995b, 1998, 1999, 2001), consistent with theoretical models of the mechanism of magnetoreception that implicates a photoexcited radical pair reaction occurring in a specialized photoreceptor (Ritz, Adem, & Schulten, 2000). Both frogs and salamanders trained to exhibit shoreward orientation under natural light oriented in the trained direction when tested under full spectrum light, but exhibited 90º shifted orientation under wavelengths of light $\geq$ 500 nm (Freake & Phillips, 2005; Phillips & Borland, 1992a, 1992b). Control experiments in which newts were trained under wavelengths $\geq$ 500 nm and tested under either full spectrum or long-wavelength light indicate that the 90º shift results from a direction effect of light on the underlying magnetoreception mechanism (Phillips & Borland, 1992a, 1992b). In newts, the 90º shift is the result of an antagonistic interaction between short-wavelength ($\leq$ 450 nm) and long-wavelength ($\geq$ 500 nm) inputs mediated by extraocular photoreceptors located in or near the pineal organ (Deutschlander et al., 1999; Phillips & Borland, 1992a, 1992b). Magnetic compass orientation in birds shows a complex dependence on the wavelength and intensity of light (Wiltschko & Wiltschko, 2001). Unlike amphibians, the light-dependent magnetic compass is mediated by photoreceptors in the retina. As found in a number of visual mechanisms in birds (e.g., Clayton & Krebbs, 1994), the light-dependent magnetic compass is strongly lateralized, involving only the right retina (Wiltschko, Traudt, Güntürkün, Prior, & Wiltschko, 2002b; Wiltschko, Munro, Ford, & Wiltschko, 2003). Recent experiments showing effects of low-level radio frequency radiation on magnetic compass orientation in birds (Ritz, Thalau, Phillips, Wiltschko, & Wiltschko, 2004) are consistent with the energy state transitions predicted to occur in a mechanism involving a photo-excited radical pair reaction (Ritz et al., 2000).

In addition to the light-dependent magnetic compass, both amphibians and birds have a second, non-light-dependent mechanism utilizing a permanent magnetic material that is most likely biogenic magnetite (Munro et al., 1997a, 1997b; Phillips, Borland, Freake, Brassart, & Kirschvink, 2002a; Wiltschko, Munro, Wiltschko, & Kirschvink, 2002a). In birds, the magnetite-based receptor appears to be associated with the trigeminal nerve system (Beason & Semm, 1987; Fleissner et al., 2003). A similar system has been characterized in salmonid fish, although its role in behavior remains to be established (Walker et al., 1997). The magnetite-based receptor in birds and amphibians is not involved in magnetic compass orientation, but instead is brought "on line" when these animals navigate using map-based cues (Beason & Semm, 1996; Beason et al., 1997; Munro et al., 1997a, 1997b; Phillips, 1986a; Phillips & Borland, 1994; Phillips et al., 2002a). In birds, evidence for a magnetite-based receptor's involvement in the navigational map has come from pulse remagnetization experiments, in which animals are exposed to a rapid, high intensity magnetic pulse that is strong enough to remagnetize single domain magnetite particles, but with no lasting effects on a photoreceptor-based mechanism involving a radical pair mechanism. Munro et al.(1997a, 1997b) found that pulse remagnetization altered the migratory orientation of experienced adult birds that navigate using both map and compass information, but not that of naïve, young birds that undertake their first migration using only compass information (Perdeck, 1958). Similarly, pulse remagnetization was found to affect the initial orientation of homing pigeons, but only at sites $\geq$ 80 km from the home loft (Beason et al., 1997; see Figure 2). The absence of an effect on pigeons released at shorter distances is consistent with the use of a large scale, low resolution magnetic map.

V. Responses to Simulated Magnetic Displacement

Experiments with newts (Fischer et al., 2001; Phillips et al., 2002b), sea turtles (Lohmann et al., 2004) and migratory birds (Fischer et al., 2003) have been carried out to investigate the magnetic field's role in providing gradient map information. In these experiments, subjects were exposed to different values of one or more magnetic field components similar to those found at locations north and south of the testing site ("simulated magnetic displacements"). Both newts and sea turtles exhibited opposite directions of orientation corresponding to the relative positions of the simulated magnetic map coordinates.

In initial experiments with newts, the inclination of the magnetic field was changed by $\pm$ 2° Figure 5a,e). In subsequent experiments, smaller changes in the magnetic field inclination were used to "titrate" the home value. Consistent with the magnetic map hypothesis, reversal of the newts' homing

orientation bracketed the home value of magnetic inclination (Figure 5b,d) and newts exposed to the home value of inclination failed to show a consistent direction of orientation (Figure 5c). To rule out the possibility that the changes in magnetic inclination affected the magnetic compass, newts exhibiting shoreward magnetic compass orientation, which does not require map information, were exposed to ± 2° changes in inclination (Fischer et al., 2001). There was no effect on shoreward magnetic compass orientation, indicating that the magnetic compass was unaffected.

Simulated magnetic displacement studies of Tasmanian silvereyes also point to a possible role of the magnetic field in providing map information, although the findings are less clear than those observed in newts and sea turtles. During the fall migration, Fischer et al. (2003) captured adult silvereyes *en route* from Tasmania northward along the southeast coast of Australia. In initial baseline tests, carried out in the ambient field of Armidale, NSW, silvereyes oriented in a seasonally appropriate north-northeasterly direction. The silvereyes were then divided into two groups and exposed to values of magnetic field intensity and inclination that would normally be encountered to the south (simulated south displacement; SimS) and to the north (simulated north displacement; SimN) of the testing site. The northern values correspond to locations either within (intensity), or to the north of (inclination), the silvereye's winter range. The orientation of the two groups of birds was then tested on alternate days to obtain five to six directional responses from each bird. Birds exposed to the SimS displacement continued to show northeasterly magnetic orientation similar to their control responses, while birds exposed to the SimN displacement failed to show a significant direction of orientation and differed significantly from their control responses, as well as from the responses of the birds exposed to the SimS condition (Fisher et al., 2003).

Fischer et al. (2003) discussed several possible explanations for the failure of birds in the SimN condition to exhibit a consistent direction of orientation. However, a recent reanalysis of these data suggests that rather than a failure to orient (or a failure of individual birds to agree on a single direction of orientation), birds in the SimN condition may have exhibited a two stage response. Figure 6 shows the orientation of birds in the SimS and SimN conditions during the first three days (Figure 6, left diagrams) and the second 2-3 days (Figure 6, right diagrams) of testing. There was no difference in the orientation of birds in the SimS condition during these two time periods (Figure 6, bottom diagrams; p>0.10, Hotelling's two-sample test). However, birds in the SimN condition oriented to the east during the first three nights (Figure 6, top left diagram; p<0.05, Hotelling's one-sample test), and then exhibited a significant shift in the direction of orientation (p<0.05, Hotelling's two-sample test), resulting in a directional tendency (p<0.10) opposite that of the birds in the SimS birds (Figure 6, bottom right diagram).
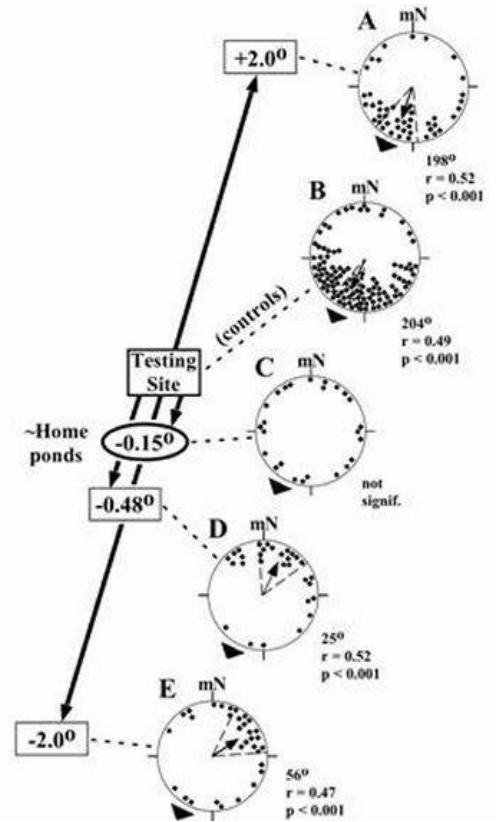

Figure 5. Effects of small changes in magnetic inclination on homing orientation of Eastern red-spotted newts (data from Fischer et al., 2001; Phillips et al., 2002b). Magnetic bearings pooled from newts tested in one of four horizontal alignments of the magnetic field (magnetic North = north, east, west or south). Values at the left indicate the changes in inclination to which the newts were exposed relative to the ambient value at the testing site (controls). Changes in inclination were made with little or no change in the total intensity. Newts were collected from ponds located ~42 km south-southwest of the testing site (home direction = 207°). Magnetic inclination at the "home ponds" was approximately 0.17° less than the inclination at the testing site. mN = magnetic north.

Mouritsen (2003) proposed that migratory birds use a unicoordinate map to determine north-south position, and rely on major topographic features (rather than a second map coordinate) to determine their east-west position. In southeastern Australia, silvereyes migrate along a narrow corridor parallel to the coastline that runs roughly north-northeast/south-southwest. Consistent with Mouritsen's suggestion, the tendency of birds in the SimN condition to fly to the east would have enabled them to locate the coastline and, therefore, to determine their east-west position. The subsequent tendency of the birds to orient in a southerly direction, i.e., opposite that of birds in the SimS condition, is consistent with the birds interpreting their geographic position as being to the north of their winter range. In other words, these findings suggest that the birds may be able to derive their north-south position from the geomagnetic field.

Consistent with a map effect, more recent experiments using somewhat larger magnetic field changes have found an affect of the SimN (but not SimS)
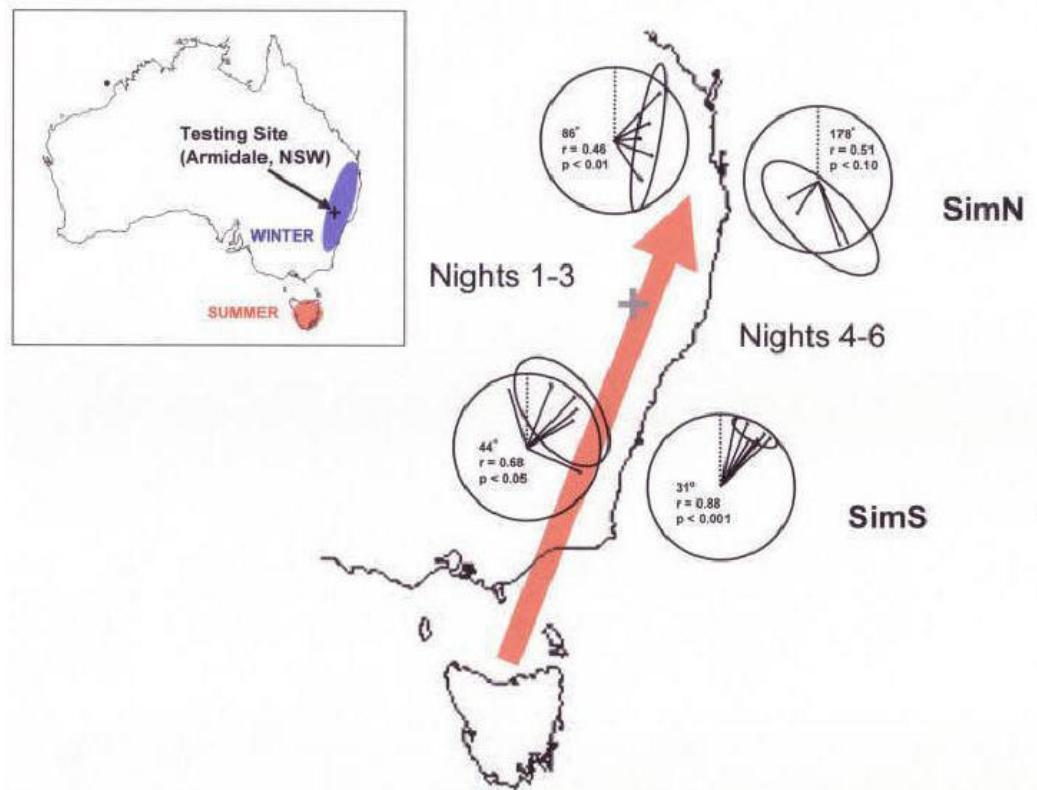

Figure 6. Migratory orientation of Tasmanian silvereyes after exposure to simulated north (SimN) and south (SimS) magnetic displacements. Black outline shows the coast of Tasmania (bottom of figure) and of southeastern Australia. Lower circular diagrams show the orientation of birds exposed to magnetic field values normally encountered to the south near the start of the Fall migration (simulated south displacement, or SimS). Upper circular diagrams show the orientation of birds exposed to magnetic field values normally encountered at the northern edge of, or to the north of, the winter range (simulated north displacement or SimN). Left circular diagrams of each pair show data from nights 1-3 of testing. Right circular diagrams show data from nights 4-5 (SimS) or 4-6 (SimN) of testing. Lines originating from the center of each diagram are mean vectors calculated for individual birds from its nightly bearings. Ellipses are 95% confidence intervals for each distribution. Statistics (mean vector bearing, mean vector length, and probability level) are for the Hotelling's test (Batschelet, 1981) used to test for departure from a random distribution. Gray cross shows the approximate location of the testing site. Inset: Map of Australia showing breeding range of this population in Tasmania (red) and the approximate winter range along the southeastern coast of Australia (blue). Testing site (Armidale, NSW) is indicated by a black cross.

condition on the orientation of experienced adult birds, but not that of naïve young birds captured on the breeding grounds shortly after fledging and prior to their first migration (Deutschlander et al., in preparation). Birds migrating for the first time rely on a "vector strategy" that combines compass information with a temporal program (Berthold, 1990, 1991; Perdeck, 1958), rather than true navigation that requires both a map and compass. Other than the use of map information, the physiological state of young inexperienced and experienced adult migrants appears to be quite similar (increased fat reserves, nocturnal restlessness, etc.). Consequently, these findings suggest that, rather than an effect on the compass, the response of experienced birds in the SimN condition is due to an effect on the map.

Can the findings of the simulated magnetic displacements be explained by an effect on a component of animals' navigation system other than the map? In these experiments, subjects were exposed to a single magnetic field (equivalent to a "point sample" discussed earlier) and, thus, were unlikely to interpret the altered magnetic field as a familiar magnetic "landmark" or reference point; use of magnetic landmarks would require recognition of unique spatially varying features of local magnetic topography (i.e., directions and rates of change in one or more magnetic field components; Walker et al., 2002). Moreover, subjects in the simulated magnetic displacement experiments were exposed to different magnetic field conditions at the same site, so other potential map cues such as odors were held unchanged. Consequently, the findings of these experiments cannot be explained by assuming that the altered magnetic fields caused the experimental subjects to attend to non-magnetic (e.g., olfactory) map cues. The most likely explanation for the findings of the magnetic displacement experiments, therefore, is an effect on a magnetic gradient map.

VI. Unicoordinate vs. Bicoordinate Map

A major unresolved issue is whether short-distance migrants like newts, and/or long distance migrants like sea turtles and many species of birds, have unicoordinate or bicoordinate maps. Simulated magnetic displacement experiments with newts, sea turtles and migratory birds have provided evidence for the use of the magnetic field to derive a map coordinate that provides information about geographic position along roughly the north-south axis. Regional gradients in magnetic field components such as inclination and intensity run more-or-less north-south and, thus, are well suited to provide information about geographic position along this axis. It remains to be determined whether these animals are able to determine their geographic position along a second, non-parallel (east-west) axis.

If these animals are able to use a second map coordinate, what might this coordinate be? In many parts of the world, large-scale variation in magnetic declination (the angle between magnetic and geographic north) varies along a gradient that is roughly orthogonal to the gradients of intensity and inclination and, thus, provides a possible second map coordinate. Birds have been proposed to derive geographic North as a reference for calibration of their compass systems by averaging the positions of the band of maximum skylight polarization at sunrise and sunset (Muheim, et al., 2006b; Phillips & Waldvogel, 1982, 1988). It remains to be determined whether measurements of magnetic declination using such a reference system would be accurate enough for a large-scale map. Nevertheless, for long-distance migrants like silvereyes, a second map coordinate derived from magnetic declination remains a possibility. For example, silvereyes migrating from Tasmania northward along the coast of eastern Australia travel in a corridor approximately 200 km wide. Magnetic declination changes by about two degrees over this distance. Since the gradient of magnetic declination is roughly perpendicular to the gradients of intensity and inclination, silvereyes provide an excellent model system in which to investigate the possibility of a bicoordinate magnetic map. Use of a bicoordinate magnetic map is not ruled out by the experiments described earlier in which silvereyes appeared use an alternative

strategy ("fly east until you encounter the coastline") to determine east-west position (Figure 6). The birds in these experiments were housed and tested indoors without access to celestial cues and, thus, could not have used a reference system based on celestial polarized patterns to obtain measurements of magnetic declination (see earlier discussion).

Bicoordinate navigation is even more problematic for animals that require short distance, high resolution map information (i.e., for movements over distance <5-10 km). At such short distances, it is unlikely that magnetic declination could to be used to derive a second map coordinate, since the required accuracy would be roughly 100 times greater than that required by, e.g., a migratory bird, and the forest canopy would limit the access of newts and other inhabitants of the forest floor to celestial cues such as polarized light patterns that could be used to derive a geographic reference (Muheim, et al., 2006b). An alternative possibility is that local variation in the magnetic field results in non-parallel gradients of components such as inclination and intensity that do not require an independent directional reference. However, local gradients suitable for bicoordinate navigation are likely to be present at some sites, but not at others (Phillips, 1996). If so, a bicoordinate magnetic map cannot provide a universal solution to the problem of navigation over small spatial scales. An interesting question is whether newts, and other organisms that require short-range, high resolution map information, are found at higher population densities in areas where local magnetic field gradients are suitable for bicoordinate navigation (S.C. Borland, personal communication).

VII. Conclusions

We have argued for a fundamental distinction between local "place" maps (and related maps that involve familiar reference sites, including bearing maps), and larger scale gradient maps that can be extrapolated beyond an individual's area of familiarity. Not only are these two categories of maps likely to involve different types of sensory information, but also different processing mechanisms and, consequently, different populations of neurons in the central nervous system. Contrary to a number of recent authors (Bingman et al., this volume; Jacobs & Schenk, 2003; Wallraff, 2004), we also conclude that there is no compelling evidence for the involvement of olfactory cues in a large-scale gradient map. In contrast, a compelling case is emerging for the use of magnetic cues to derive at least one map coordinate. Both amphibians and birds have a magnetoreception mechanism distinct from the magnetic compass that appears to play a specialized role in the map component of homing. Simulated magnetic displacement experiments have provided evidence that amphibians, reptiles and birds (see also recent findings from spiny lobsters; Boles & Lohmann, 2003) will, at least under some conditions, interpret small changes in the magnetic field as changes in geographic position. Nevertheless, magnetic navigation does not provide a universal solution to the problem of map-based homing, i.e., the magnetic field does not provide useful map information at all sites or at all spatial scales.

The emerging picture from studies of animal navigation systems is one of a patchwork of mechanisms that vary in utility depending on local environment (e.g., the characteristics of local gradients), range of movement, and individual age/experience. Map information involving multiple sensory modalities may be involved, including both olfactory and magnetic cues, as well as both map-based and route-based mechanisms for deriving spatial position at unfamiliar locations. Furthermore, both map-based and route-based sources of spatial information are likely to be replaced by large scale place or bearing maps as increased familiarity produces qualitative changes in the processing and neural representation of spatial information (Jacobs & Schenk, 2003. Further work is needed to determine the range over which different navigational mechanisms operate (e.g., Beason et al., 1997; Schmidt-Koenig, 1966, 1970), whether gradient maps provide unicoordinate or bicoordinate information, and the extent to which olfactory cues are involved in providing map information as opposed to distinguishing home from non-home, triggering acquisition and recall of stored map and compass reference information, and recognizing familiar sites.

[1] Original data from this experiment are no longer available due to the closing of the Schmidt-Koenig laboratory at the University of Tübingen.

[2] Given recent evidence for spatial, temporal, and experiential heterogeneity of the spatial cues used by pigeons for homing (e.g., Beason et al. 1997; Ganzhorn 1990, Wiltschko et al., 1989), nonsense odor experiments should be carried out using birds of different ages and levels of experience (see Footnote 3), exposed to different types of training, and tested at a variety of distances and directions from the home loft.

[3] In another series of "nonsense odor" experiments, young inexperienced birds were exposed to the control, bottled air, and non-sense odor treatments combined with anesthetization of the olfactory mucosa at the release site. In these experiments, only the bottled air group showed significant homeward orientation when bearings were pooled from four sites arrayed symmetrically around the release site. Neither controls nor non-sense odor birds exhibited significant homeward orientation. For young, inexperienced birds, therefore, the sudden loss of olfactory input just prior to release, rather than the absence of olfactory cues *per se*, appears to have been the cause of disorientation, again suggesting that non-spatial aspects of olfactory input can have dramatic effects on homing.

[4] An example of an odor-labeled wind compass would be the use of odors associated with the "sea-breeze" to identify the onshore/offshore directions in a maritime environment.

[5] In "route-deprivation" experiments, animals are deprived of potential sources of compass information (magnetic, olfactory, visual, kinesthetic) during displacement to the testing site to rule out the use of path integration (also known as "route reversal") to determine the home direction.

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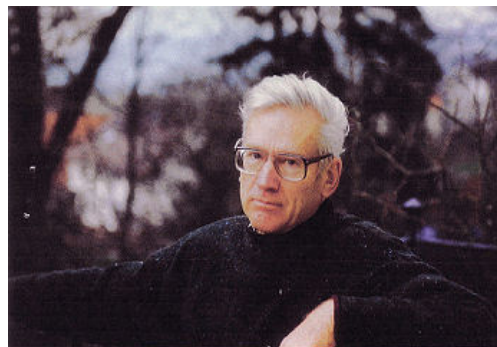
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