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MAGNETIC MAPS IN ANIMALS: A THEORY COMES OF AGE?

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ABSTRACT

The magnetic map hypothesis proposes that animals can use spatial gradients in the Earth's magnetic field to help determine geographic location. This ability would permit true navigation—reaching a goal from an entirely unfamiliar site with no goal-emulating cues to assist. It is a highly contentious hypothesis since the geomagnetic field fluctuates in time and spatial gradients may be disturbed by geological anomalies. Nevertheless, a substantial body of evidence offers support for the

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hypothesis. Much of the evidence has been indirect in nature, such as the identification of avian magnetoreceptor mechanisms with functional properties that are consistent with those of a putative map detector, or the patterns of orientation of animals exposed to temporal and/or spatial geomagnetic anomalies. However, the most important advances have been made in conducting direct tests of the magnetic map hypothesis by exposing experienced migrants to specific geomagnetic values representing simulated displacements. Appropriate shifts in the direction of orientation, which compensate for the simulated displacements, have been observed in newts, birds, sea turtles, and lobsters, and provide the strongest evidence to date for magnetic map navigation. Careful experimental design and interpretation of orientation data will be essential in the future to determine which components of the magnetic field are used to derive geographic position.

INTRODUCTION

WHEN William Gilbert published his magnetic philosophy in the 17th century (Gilbert 1600) and proposed that the Earth was a giant magnet, navigators and sailors hoped that the problems of locating latitude and, especially, longitude could be solved by using these newly described properties of the Earth (Pumfrey 2003). As we know today, the problem of determining latitude during overcast days could be resolved by using Gilbert's inclinometer, since magnetic inclination can be used as a rough measure of latitude (see below). The hope of using magnetic declination to identify longitude magnetically was dismissed, however, once people realized that declination is not constant, but steadily drifting (Pumfrey 2003).

While the hand-held Global Positioning System (GPS) unit has revolutionized the navigational performance of directionally challenged humans and solved the problem of determining global position, evidence is accumulating that many animals have their own remarkable positioning systems. Most people are familiar with the concept of deriving directional information from the geomagnetic field, as demonstrated by a compass needle swinging to point north. However, a compass does not provide information about our position on the globe or relative to a goal. To derive positional information, large-scale gradients of magnetic properties that form a predictable grid are necessary. Geomagnetic field strength and inclination form approximately parallel global gradients, which tend to vary predictably from a minimum in the vicinity of the magnetic equator to a maximum towards the poles (Figures 1 and 2).

The presence of large-scale magnetic gradients has led to the development of the magnetic map hypothesis (Yeagley 1947, 1951; Gould 1980, 1985; Moore 1980; Walcott 1980; Wallraff 1991; Phillips 1996). The model proposes that an animal learns the alignment,

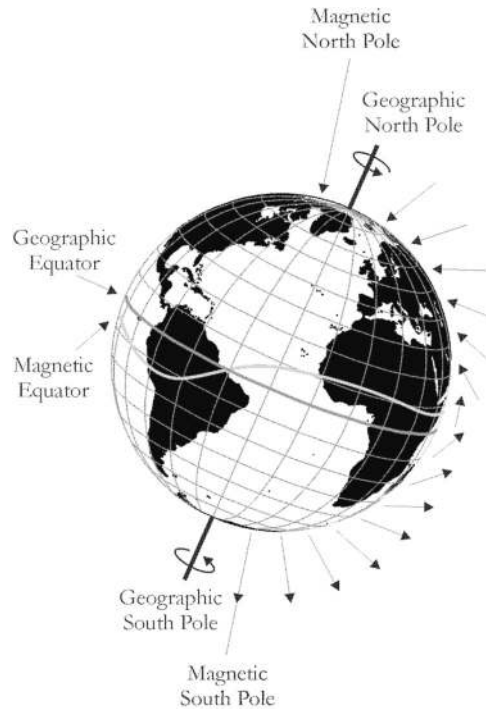


FIGURE 1. SCHEMATIC DRAWING OF THE EARTH AND ITS GEOMAGNETIC FIELD

The arrows show the course of the magnetic field lines. The lengths of the arrows are proportional to the total intensity of the geomagnetic field; their alignment relative to the Earth's surface indicates the inclination angle. The positions of the magnetic poles and the magnetic equator are calculated from the IGRF model for the year 2000.

and possibly the steepness, of one or more of these magnetic gradients as it moves within, and occasionally beyond, the home range. Once a gradient pattern has been learned, it may be extrapolated to unfamiliar areas far from home. By comparing the value of the component at the unfamiliar site with the home value, the animal could then derive its position along the gradient. If this procedure is carried out with two nonparallel gradients (one or both of which may be magnetic in character), the animal would be capable of bicoordinate position fixing. Bicoordinate position fixing is a prerequisite for “true navigation” (Griffin 1952), that is, the ability of an organism, displaced to an unfamiliar location, to orient homeward without reference to familiar landmarks, goal-emanating cues, or directional information obtained during the displacement. A map is used to determine position, and then a compass indicates the desired direction (Kramer 1961). The process of learning the map may be crucial, especially for accurate homing from short distances. On a local scale, the gradients can vary in both alignment and steepness; on both local and global scales, the gradient patterns change

dramatically as the geomagnetic field varies over time (Courtilot et al. 1997). Therefore, true navigation is likely to be observed only in experienced adult individuals, with inexperienced juveniles relying on alternative navigational strategies such as path integration or, in the case of long-distance migration, innate directional preferences (e.g., Wiltschko and Wiltschko 1985).

For a magnetic map to work, the animal must overcome several substantial challenges arising from the characteristics of the geomagnetic field (Phillips 1996; Phillips et al. 2006).

(1) Typical global gradients vary in total intensity by about 5–10 nT/km and in inclination by about 0.01°/km. The signal is extremely weak, especially for a short-scale migrant, which requires that the sensory mechanism(s) detecting spatial variation in the magnetic field must be extraordinarily sensitive (Phillips 1996). Furthermore, since magnetic gradients cannot be detected directly, the animal must make a series of “point samples” that are in a known spatial relationship to one another (Phillips and Deutschlander 1997). The animal must also be able to independently estimate geographic position within its

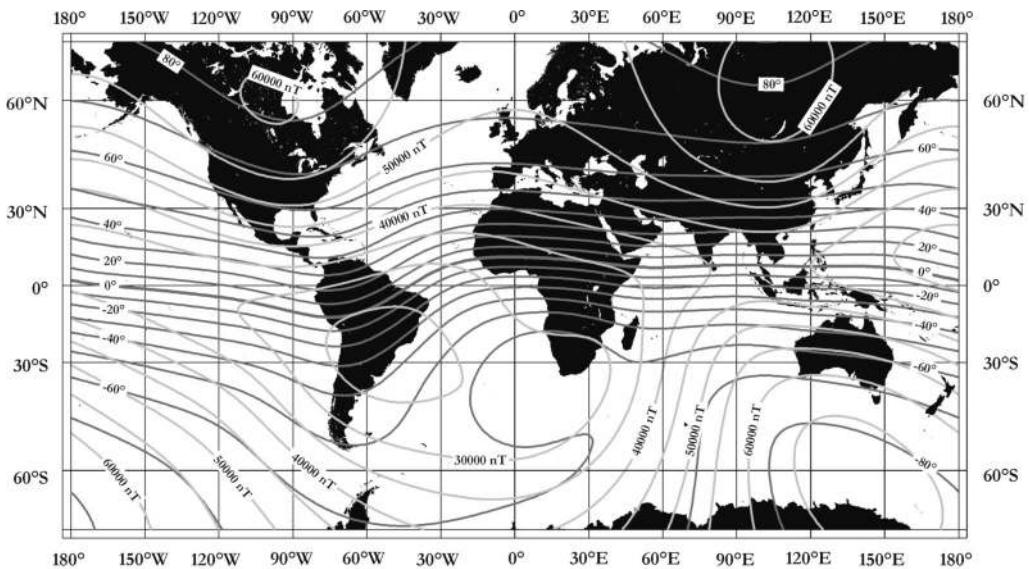


FIGURE 2. TOTAL INTENSITY AND INCLINATION OF THE EARTH'S MAGNETIC FIELD
 The total intensity is given in steps of 5000 nT, the inclination in steps of 10°. Values are according to the World Magnetic Model WMM 2000 (Macmillan and Quinn 2000). The map is drawn in a Mercator projection.

area of familiarity (e.g., a place map, bearing map) or determine its spatial position with a nonmap-based system (e.g., a path integration system, Wiltschko and Wiltschko 2000, 2003), in order to determine the spatial relationship among measurement sites. All this requires the capability to memorize these precise measurements from different sites within the spatial array.

(2) Local gradients in the magnetic field at both the home and release sites often differ in direction and/or steepness from the regional gradient because of irregularities in the underlying rock layers (spatial anomalies, see discussion on pigeon homing below). This can introduce large errors in position defining. As a consequence, a gradient map may not be useful at some sites.

(3) Interactions between the Earth's magnetosphere and solar wind cause daily fluctuations in total intensity of about 30–100 nT and in inclination of about 0.33° (Wiltschko and Wiltschko 1995a). This regular temporal variation could introduce significant errors in fine-scale map estimates. For animals that use the magnetic field for a short-distance (high-resolution) map, 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 minimal, may be necessary to minimize this source of error (Rodda 1984; Phillips 1996; Diego-Rasilla et al. 2005). Animals could recognize magnetic storms by the rapid, large, and unpredictable fluctuations in the magnetic field and avoid taking map measurements during such times (Phillips 1996).

(4) Secular variation over longer periods of months to years (see section on adult sea turtles below) would also cause some difficulties since the magnetic values for a particular location could change enough over an individual's lifetime to cause considerable errors in position determination. Long-term temporal variation might be factored out by regular measurements of the magnetic field at one specific location. Strategies to minimize the effects of temporal variation could include taking measurements immediately before and after displacements (cf. Phillips et al. 2006).

FUNCTIONAL PROPERTIES OF THE PUTATIVE MAGNETORECEPTOR

The requirement for a magnetoreceptor sufficiently sensitive to accurately measure small differences (as little as 2–3 nT, corresponding to less than 1 km) (Schmidt-Koenig and Walcott 1978) in geomagnetic components provides an opportunity to look for evidence of the magnetic field's involvement in the map. The two predominant theoretical mechanisms believed to mediate sensitivity to the geomagnetic field involve either excited states of macromolecules (Schulten and Windemuth 1986; Ritz et al. 2000) or biogenic magnetite (Kirschvink and Walker 1985; Winklhofer et al. 2001). Both mechanisms appear to be involved in deriving directional (i.e., compass) information (for review see Wiltschko and Wiltschko 1995a), but only a receptor utilizing single-domain or superparamagnetic magnetite particles is thought to be sensitive enough to measure the small changes in geomagnetic field components that would be required by a map detector (Yorke 1981; Fleissner et al. 2003).

Large single-domain magnetite particles have a magnetic moment that is constrained by shape anisotropy to lie along the long axis of the particle in either of the two opposite directions, effectively producing a small, permanent magnet. The magnetic moment of smaller superparamagnetic particles is free to rotate in the presence of an external magnetic field, independent of the particle alignment. A magnetite-based receptor could respond to minute changes in the direction and/or intensity of the magnetic field by coupling single-domain particles to a suitable transduction mechanism (e.g., a sensory hair or stretch receptor) that results in a change in membrane conductance (Kirschvink and Gould 1981; Yorke 1985; Edmonds 1992; Walker et al. 2002). Alternatively, clusters of superparamagnetic particles can be deformed by earth-strength magnetic fields, which results in activation of mechano-sensitive membrane receptor channels (Winklhofer et al. 2001; Fleissner et al. 2003). Deposits of single-domain magnetite have been found in a variety of higher animals that exhibit magnetic

sensitivity, including fish, newts, birds, and mammals (Kirschvink et al. 1985; Brassart et al. 1999). Furthermore, innervated superparamagnetic magnetite has been found in the upper beak of the homing pigeon (Hanzlik et al. 2000; Winklhofer et al. 2001).

Biogenic magnetite may play many different roles in the physiology of an organism that may or may not involve providing a source of map information. Consequently, the mere presence of magnetite does not indicate the presence of a magnetic map. However, experimental manipulations, which should affect the magnetic properties and/or structural integrity of a magnetite-based receptor and are found to have predictable effects on an organism's homing orientation (particularly if associated with the map step of homing), would provide indirect evidence for magnetic map navigation. Both single-domain and superparamagnetic magnetite magnetoreceptors can be predictably affected by pulse remagnetization, which involves applying a single, brief directional magnetic pulse. In the case of single-domain particles, treatment with a magnetic pulse of greater intensity than the coercivity of single-domain particles of magnetite (Kalmijn and Blake-More 1978) causes particles, in which the magnetic moment is aligned antiparallel to the pulse, to be remagnetized in the opposite direction. This should reverse (or at least alter) the directional response of the receptor and cause a change in the orientation direction of the organism. A strong magnetic pulse applied to clusters of superparamagnetic magnetite will result in the formation of agglomerations of clusters and impairment of the magnetoreceptor for a few days (Winklhofer et al. 2001).

The orientation of experienced adult migratory birds (Wiltschko et al. 1994; Beason et al. 1995) and pigeons (Wiltschko and Wiltschko 1995b; Beason et al. 1997) is influenced by pulse remagnetization treatment. Interestingly, effects of pulse remagnetization on homing pigeons were only evident at release sites located 80 km or more from the home loft, which provides evidence for the use of a magnetic map only for long-distance homing. Young inexperienced silvereyes, that have not yet made their first migration, are not affected by pulse remagnetization. In contrast, experi-

enced birds, that have migrated at least once before, are affected by the same treatment (Munro et al. 1997a,b). In neither case is pulse remagnetization likely to affect the magnetic compass, since the same compass systems appear to be used by pigeons for homing from sites at different distances from the loft, and by naive young and experienced adult migratory birds (Wiltschko and Wiltschko 1985). Similarly, any nonspecific effects of pulse remagnetization (i.e., effects on behavior or physiology unrelated to magnetic sensing) would be expected to be independent of age and/or distance of displacement.

Neurophysiological recordings from the ophthalmic branch of the trigeminal nerve of the bobolink (Beason and Semm 1987; Semm and Beason 1990) revealed responses to changes in the rotation of the vertical or horizontal component of the geomagnetic field and to changes of intensity of as little as 50–200 nT (the geomagnetic field is approximately 50,000 nT). The trigeminal nerve innervates the ethmoidal region, where single-domain/superparamagnetic magnetite has been identified in numerous vertebrates including bobolinks (Beason and Nichols 1984; Kirschvink and Walker 1985; Hanzlik et al. 2000). Beason and Semm (1996) showed that blocking the trigeminal nerve with a local anaesthetic eliminated the effects of pulse remagnetization normally observed in this species. Evidently, their magnetic compass sense was unaffected by the treatment since they continue to be well oriented in the correct migratory direction in the absence of other compass (e.g., celestial) cues. All of these lines of evidence are consistent with the hypothesis that migratory birds use a magnetite-based receptor to derive map information, however, the approach is oblique, and alternative explanations remain.

INDIRECT EVIDENCE FOR THE MAGNETIC MAP HYPOTHESIS

PIGEON HOMING DURING MAGNETIC STORMS AND AT MAGNETIC ANOMALIES

Early interest in the possibility that animals might indeed be able to use a magnetic map was stimulated by observations that the performance of homing pigeons correlated with both temporal and spatial disruptions in the

geomagnetic field. These studies have been reviewed in detail by Walcott (1991) and so will only be described briefly.

Several studies analyzed the results from pigeon races and found significant correlations between homing speed and/or success, and the number of sunspots that cause substantial variation in the geomagnetic field (magnetic storms) on the day before the race (Yeagley 1951; Schreiber and Rossi 1976, 1978). Subsequent studies showed correlations between the initial orientation of pigeons and changes in the K index (a measure of sunspot-induced variation in the geomagnetic field) observed 12–24 hours prior to release (Keeton et al. 1974; Kowalski et al. 1988). These correlations were eliminated when small bar magnets were attached to the pigeons (Larkin and Keeton 1976); one effect of which would be to grossly distort the geomagnetic field around the pigeon, thus preventing it from using a magnetic map. In addition, the geomagnetic field exhibits a small daily variation cycle caused by the impact of the solar wind on the side of the Earth facing the sun. Studies by Wiltschko et al. (1986) and Becker (1991) indicate that the orientation of pigeons is sometimes shifted at noon (when the daily variation is at a maximum) compared to the morning and afternoon, and this shift also disappears when small bar magnets are attached to the pigeons.

These effects of very small changes in the magnetic field are significant, as they indicate that the lower limits of sensitivity of pigeons to variation in the geomagnetic field are of the order required for magnetic map navigation. Moreover, the effect of such naturally occurring changes on the directional response of the birds' magnetic compass would be insignificant (generally less than 1°). Although these findings are suggestive, they provide only circumstantial evidence for the magnetic map hypothesis. Indeed, a close examination of the data raises difficulties for the hypothesis (Walcott 1991): small changes in the magnetic field should cause predictable errors in position fixing, resulting in specific directional errors that depend on the relative positions of the release site and the loft. Instead, the directional errors tended to be the same on a particular day, even when

pigeons were released from different points relative to the loft.

In addition to temporal variation in the geomagnetic field, the global magnetic gradients are affected locally by variation in the iron content of the underlying rock, resulting in local gradients that differ to some degree from the global gradient. In extreme cases, "magnetic anomalies" associated with iron ore deposits are formed, which should substantially impair magnetic map navigation in such areas (Lednor 1982). Numerous studies have demonstrated that pigeons released at magnetic anomalies are disoriented, and scatter is greatest at the strongest anomalies (Walcott 1978; Frei 1982; Kiepenheuer 1982, 1986; Wagner 1983). Since the initial orientation of the pigeons was altered predictably by clock-shifting (which alters directional information obtained from the time-compensated sun compass), and performance improved with subsequent releases at the same anomaly, it would suggest that the anomalies were exerting an effect on the map rather than on the compass component of homing. These findings provided what was considered at the time some of the best evidence for the magnetic map hypothesis. Nevertheless, skepticism arose as it became clear that not all pigeons are disoriented at magnetic anomalies. Walcott (1992) showed that pigeons from one loft were disoriented when released at anomalies, while pigeons from another nearby loft were well oriented at the same anomalies. The same pattern was observed when siblings were separated after hatching and raised in two different lofts, indicating a strong effect for loft location. More recently, these and other related findings (Wiltschko et al. 1989) have led to the conclusion that the navigational system of pigeons is extremely flexible and that characteristics of the home loft and surrounding area and/or the rearing/training procedure can have an appreciable effect on the types of cues utilized by pigeons for homing. It is possible, therefore, that magnetic map cues may be used for homing by pigeons raised at some sites but not at others. Characteristics of the release site may also determine which sensory cues pigeons use for navigation (Ganzhorn 1990). The pigeon experiments illustrate the need for direct ex-

perimental tests where potential map cues may be controlled and manipulated to compare their effects on the map and compass.

MAGNETIC INCLINATION AS PART OF A MAGNETIC MAP IN ALLIGATORS?

A possible role of geomagnetic inclination in navigation was indicated by differences in homing behavior exhibited by alligators, *Alligator mississippiensis*, after substantial (11–34 km) displacements from their home lakes (Rodda 1984). Nonyearling alligators (that presumably have sufficient experience to develop a map) were able to orient in the homeward direction despite circuitous displacements. In addition, “errors” in their homeward bearings were correlated with small deviations of inclination angle and/or horizontal intensity from the value observed during the preceding night. The geomagnetic field exhibits daily fluctuations in intensity and inclination, with minimal fluctuations during the night. Therefore, the nighttime value may provide a baseline measurement of the field parameters. Notably, the correlation was only significant for the deviations observed at the precise time each animal was tested—values measured 20 minutes before or 30 minutes after the tests did not correlate with the direction the animals moved (Rodda 1984). As discussed earlier, small changes in geomagnetic field parameters may result in large changes in estimates of geographic position for short-distance navigators (Phillips 1987). Thus, in this study, nonyearling alligators appear to base their estimate of geographic position on the magnetic field value observed at the moment of release, and when this value differed from the true value (established by baseline measurements during the preceding night), errors in position-fixing ensued. The data suggest that alligators may be sensitive to changes in magnetic inclination of as little as $0.01\text{--}0.02^\circ$ (roughly 1–2 km).

MAGNETIC MAPS IN SEA TURTLES?

Geomagnetic Cues as Boundary Markers in Sea Turtle Hatchlings

Evidence for changes in orientation direction resulting from small changes in geomag-

netic inclination and intensity was obtained in experiments with hatchling sea turtles carried out by Ken Lohmann and colleagues. Young loggerhead sea turtles, *Caretta caretta*, spend their first several years of life in the open ocean following a circular migratory path that is largely dependent on passive transport by the currents of the North Atlantic gyre (for a review, see Cain et al. 2005). When exposed to values of geomagnetic inclination found at the northern and southern latitudinal limits of the gyre, the hatchlings chose directional headings that direct them back to the center (Lohmann and Lohmann 1994). This is likely critical to the survival of the young sea turtles, since to stray outside the gyre would risk being swept into regions of fatally cold water or even an entirely different current system. When exposed to values found near the middle or far beyond the boundaries of the gyre, the hatchlings oriented randomly (perhaps because extreme inclination values are normally never experienced by this population of sea turtles, while mid-gyre inclination values would indicate no immediate threat). Likewise, when exposed to values of magnetic intensity found near the eastern or western longitudinal boundaries, the hatchlings chose bearings back toward the center (Lohmann and Lohmann 1996a). Finally, both inclination and intensity were altered together to simulate three different bi-coordinate locations found near the western, northeastern, and southern edges (Lohmann et al. 2001). The resulting orientation patterns were again highly consistent with movements intended to keep the hatchlings within the gyre.

It is tempting to conclude that these experiments provide evidence for magnetic map navigation by sea turtles. However, Lohmann and colleagues (Lohmann and Lohmann 1996a,b; Lohmann et al. 2001) are careful to note that these studies involve newly hatched individuals with no previous experience of the geomagnetic inclination and intensity patterns. Magnetic navigation requires an ability to derive geographic position relative to a specific goal or target. One possibility is that the entire North Atlantic gyre is one big goal/target (Ken Lohmann, personal

communication); sea turtles have evolved an ability to navigate back to the gyre, and this ability is present even in hatchlings. Given the relatively rapid changes in the geomagnetic field (Courtilot et al. 1997, and see below), however, it is highly unlikely that hatchlings could be born genetically imprinted with a complete magnetic map of inclination and intensity gradients covering the entire range of the population. A simpler mechanism that would help to prevent young turtles from straying beyond the gyre would be to adopt a fixed compass bearing (or a specific shift in orientation direction) when they encounter magnetic field values normally associated with the species's range boundaries ("range boundary hypothesis"). Based on these findings, it is not necessary to assume, nor indeed likely, that hatchling sea turtles possess a magnetic map. Nevertheless, the hatchlings' responses do provide evidence for sensitivity to small changes in both geomagnetic inclination and intensity, with critical values being genetically imprinted as "signposts" to indicate the boundaries of their range. The responses also suggest that loggerhead sea turtles possess the sensory apparatus required to detect the natural spatial variation in magnetic parameters, raising the possibility that they develop a magnetic map for use later in life based on the experience gained while travelling within the gyre as juveniles.

Other concerns have been raised concerning the methodology and interpretation of the sea turtle hatchling experiments: Courtilot et al. (1997) point out the difficulties that are likely to be caused by secular variation in the geomagnetic field. Over the last two hundred years, significant changes in the geomagnetic field have occurred. For example, the inclination values at the northern and southern edges of the gyre have changed by 13° and 15° respectively, and the locations of the intensity values currently associated with the eastern and western edges of the gyre have shifted by up to 2000 km. Also, the orthogonal bicoordinate grid of intensity and inclination currently observed in the south Atlantic did not exist 200 years ago when isolines were more or less parallel. In order for the range boundary hypothesis to be adaptive, sea turtle hatchlings must be born with

the crucial signpost values genetically imprinted, yet these values change significantly over the course of a few tens to hundreds of generations. One possibility is that strong selection causes rapid evolution that maintains signpost values within a viable range (Ken Lohmann, personal communication); rapid evolution of an innate directional preference has been seen in the acquisition of new migratory routes over just a few generations in birds (Helbig 1991a,b, 1996; Berthold et al. 1992). The effects of secular variation may also be minimized if hatchlings respond to a certain amount or proportion of change in the magnetic field relative to the natal beach, rather than to a specific magnetic field value(s) (Ken Lohmann, personal communication). In addition to experiments with hatchlings acclimated to different "natal" values, information on the stability of such relative measures of spatial variation in the magnetic field over evolutionary time scales is needed to evaluate this possibility (Ken Lohmann, personal communication). Even so, the case for magnetic map navigation by sea turtles has been greatly strengthened by a more direct line of evidence: juvenile green sea turtles, *Chelonia mydas*, captured on feeding grounds off the coast of Florida and tested in magnetic fields found approximately 300 km north or south of the capture location, oriented themselves in the appropriate general direction that would return them to the capture site (Lohmann et al. 2004). This is significant since juvenile green sea turtles would have had several years to acquire map information, perhaps sufficient to allow quite accurate position finding, rather than merely indicating the boundary of a general area (range boundary hypothesis).

Magnetic Map in Adult Sea Turtles?

In theory, adult sea turtles would be ideal for testing the magnetic map hypothesis in mature, experienced migrants since they clearly perform remarkable navigational feats, such as finding the nesting beaches of Ascension Island 2200 km from feeding grounds off the coast of Brazil. Unfortunately, mature turtles are extremely large (adults of green and loggerhead sea turtles reach masses of 150–

180 kg, while leatherback sea turtles may exceed 1000 kg), and populations are highly threatened, rendering it difficult or impractical to perform critical tests using artificially altered magnetic fields. There have recently been a number of studies using satellite telemetry to test whether adult sea turtles can compensate for substantial oceanic displacements, however, and attempts have been made in some studies to eliminate potential cues, including the geomagnetic field after long-distance displacements. Particular interest has focused on adult green turtles, that migrate roughly every two to three years from feeding grounds along the Brazilian coast to lay eggs at their natal beaches on Ascension Island. Papi et al. (2000) showed that adult green turtles were able to successfully migrate from Ascension Island to their Brazilian feeding grounds despite the presence of magnets attached to their carapace. But, this experiment only shows that geomagnetic cues are not essential for finding the relatively large target represented by the feeding grounds. This would only require the sea turtles to maintain a generally westerly heading (and in all likelihood could be accomplished using either a magnetic compass or, in the case of Papi et al.'s experiments, a nonmagnetic compass such as a sun compass), and says little about the potential importance of geomagnetic cues for pinpointing small isolated islands. Luschi et al. (2001) and Hays et al. (2003) investigated this more demanding navigational task by tracking female adults displaced after egg-laying on the nesting beaches of Ascension Island. They found that adult females displaced 60–450 km from the island generally exhibited rather irregular paths and variable homing success, however, individuals displaced to the northwest showed the highest homing success and tended to have straighter paths. A number of individuals displaced in other directions only found the island after their circuitous paths brought them to a point northwest of the island, after which they adopted a more-or-less direct southeasterly path to the nesting beaches. Because prevailing winds in this part of the Atlantic Ocean blow southeast to northwest, the authors suggest that wind-born cues were likely the pri-

mary cue used by the sea turtles to find the island, and they conclude that the sea turtles were not able to use geomagnetic cues in a map sense since direct paths to the island were only observed from one direction. However, an analysis of historic drift of the geomagnetic field values of Ascension Island suggests an alternative explanation that is consistent with the possibility of magnetic navigation. Over the last 50 years, secular variation has caused the magnetic coordinates of the island to shift toward the northwest (Figure 3). Thus, an adult sea turtle returning to the island using a magnetic map memorized a few years earlier (assuming there was no correction for secular variation) would tend to arrive at a point northwest of the island and then start searching for the island from this direction. Assuming that the sea turtles take a reading of the magnetic field before they leave the island as hatchlings and use this magnetic map information when returning for the first time about 25 years later as adults, they would reach an area northwest of the island. Only sea turtles able to locate the island from the northwest, by exhibiting an innate compass heading to the southeast (see below) or by using short-range orientation cues (e.g., wind borne olfactory cues) learned as hatchlings, would successfully reproduce. The indirect paths exhibited by sea turtles prior to reaching the location to the northwest of the island's actual location may simply reflect a lack of motivation (e.g., females typically spend several days offshore between nesting bouts) (Ken Lohmann, personal communication) and/or the competing demands of activities other than migration (e.g., feeding, temperature regulation).

If sea turtles use magnetic map information to actively home to a location to the northwest of Ascension Island, the question remains: why do they not correct for the regular change in the map coordinates caused by secular variation, especially in the case of adult females that could update map information during their visits to the nesting beaches? A possible explanation stems from the possibility that the magnetic map used for large-scale movements is relatively inaccurate. As discussed previously, the map's accuracy may be limited by local variation in the

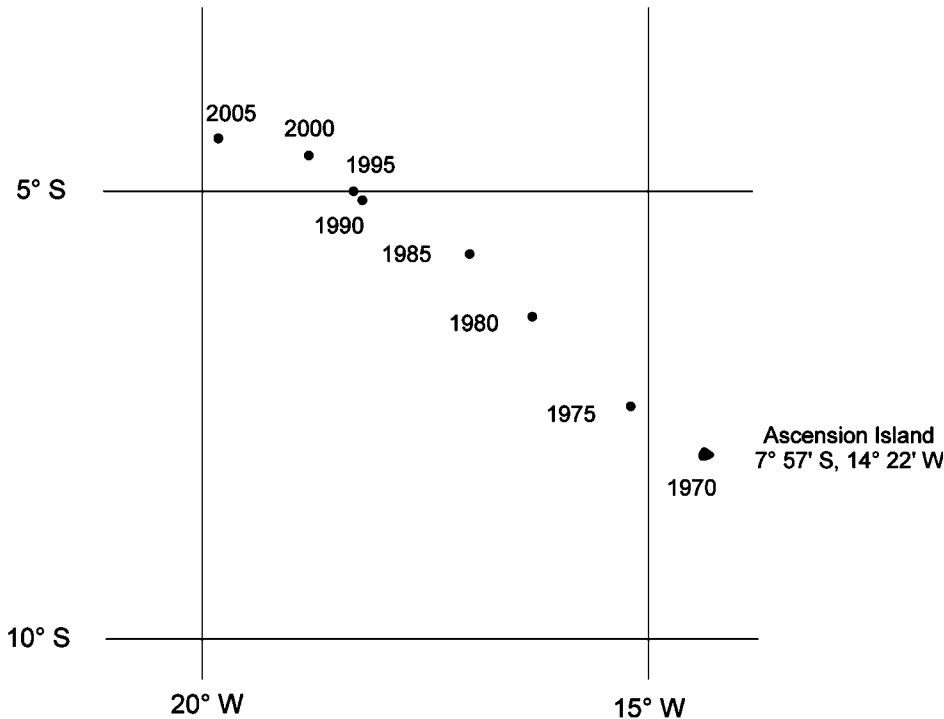


FIGURE 3. SECULAR CHANGES OF THE GEOMAGNETIC FIELD AT ASCENSION ISLAND

The reference values are taken at Ascension Island from the available magnetic field model for 1970 (DGRF 70). To illustrate the positions with the same magnetic field values as Ascension Island 1970 (total intensity of 28230 nT and inclination of -32°), the best matching geographical positions were searched using the magnetic field models from the years 1945–2005.

magnetic field and/or by the resolution of the sensory mechanism(s) used by the turtle to measure spatial variation in the magnetic field. In either case, a turtle homing to Ascension Island may miss its target or, said another way, may only be able to home to an area that is larger than the range over which short-distance cues (such as odors, foraging pelagic birds, wave patterns, among others) are available to guide the final approach to the island. Under these circumstances, it may be advantageous to: a) home to a location/area that is predictably to one side of the intended target and have an innate compass preference that biases the subsequent search (i.e., to the southeast in the case of sea turtles homing to Ascension Island); and/or b) home to a location on the side of the intended target where short-range cues are more easily detected (e.g., the downwind side of Ascension Island). A strategy of biasing the

search/approach direction to the intended target may be especially critical if the timing of arrival at nesting beaches is important. If sea turtles corrected for long-term changes in the map coordinates of Ascension Island and homed directly to its estimated position, but with some probability of error, then the likelihood that the subsequent (random) search will initially carry the turtle away from the Island, rather than toward it, is quite high. Therefore, even if the average investment of time and energy does not differ appreciably between the “consistent error/biased search” and “unpredictable error/random search” strategies, the decreased variability in the timing of arrival (and/or in search costs) may make the former strategy advantageous. As long as secular change produces a consistent direction of drift in the map-based estimate of the island’s position (as has been the case for at least the last 50 years) (Figure 3), a sim-

ple implementation of the consistent error/biased search strategy would be for hatchling sea turtles to imprint the map coordinates as they leave the natal beach, use the uncorrected coordinates to direct their return migrations as adults, and then conduct a directed search along a compass heading opposite that of the apparent drift in the island's location. This version of the hypothesis can be readily tested. Because the amount of drift in the map-derived location of Ascension Island relative to its true position will depend on the time that has elapsed since a turtle imprinted the map coordinates of the natal beach, older individuals should begin the final (southeasterly) approach from progressively greater distances to the northwest of Ascension Island.

MAGNETIC CUES AS TRIGGER FOR BEHAVIORAL AND PHYSIOLOGICAL CHANGES IN BIRDS

There is ample evidence that birds use a magnetic compass to determine their migratory direction, but only a few studies have examined whether birds also use geomagnetic parameters as triggers for behavioral or physiological changes during migration. Beck and Wiltschko (1988) tested the orientation of handraised juvenile pied flycatchers, *Ficedula hypoleuca*, and tested indoors in three different magnetic field conditions. One group of birds was exposed to a magnetic field simulating gradually decreasing values of intensity and inclination, as experienced by free-flying birds when migrating from Germany to the overwintering sites in Africa. These birds changed from southwesterly directions in the first part of the migration season to southeasterly directions at about the time when the magnetic field values indicated them to be in southern Spain. Migratory birds invariably change their direction from southwest to south when reaching southern Spain to avoid flying over the Atlantic (cf. Gwinner and Wiltschko 1978; Helbig et al. 1989). Another group of pied flycatchers, however, held at the ambient German magnetic field throughout the season, ceased to orient when tested later than mid-October, after first orienting toward the expected southwesterly

direction during the early part of the season. A third group held in the magnetic field found in North Africa was disoriented throughout the season. These experiments suggest that pied flycatchers respond to changing magnetic field values, or values specifying a specific geographic position (or latitude) along their migratory path, with a discrete change in directional heading similar to that found in subsequent work with hatchling sea turtles (see above). In addition, Beck and Wiltschko's (1988) findings suggest that exposure to magnetic field values of the summer breeding grounds may be necessary in conjunction with seasonal cues, such as changing day length, to initiate fall migration.

Observing changes in nonorientation behavior correlated with specific geomagnetic cues might provide indirect tests of the magnetic map hypothesis. Fransson et al. (2001) and Kullberg et al. (2003) took advantage of the tendency for migratory thrush nightingales, *Luscinia luscinia*, to make a stopover in Egypt during their flight from Sweden to central/southern Africa. These birds must cross the barren Sahara desert, thus the stopover in Egypt serves to replenish fat deposits in preparation for the 1500 km desert crossing. To test whether geomagnetic cues might be used to indicate the stopover area, birds were captured in Sweden just before their migration and held either in the ambient magnetic field or in a field that gradually decreased in intensity and inclination until it matched the magnetic field parameters normally found in northern Egypt. Over the following days, the birds tested early in the season and held in the altered "Egypt" field increased in body mass more than controls held at the "Sweden" value. In a second group of birds tested later in the season, body mass increase was similarly high in the experimental and control group. Kullberg et al. (2003) suggest that the birds responded to the changing magnetic field by increasing feeding rate and fat deposition, perhaps in anticipation of the arduous Sahara crossing. The second group, tested late in the season, might have been more time constrained than the early group, thus explaining the lack of difference between the treatment groups. A troubling

aspect of this study is the assumption that variation in feeding rate accurately reflects the birds' perception of geographic position. Could the experimental birds have increased feeding rate as a response to the cessation of change in the magnetic field once it reached the "Egypt" value, not to the value per se? Alternatively, might a change in magnetic intensity, irrespective of its relationship to geographic position, have triggered an increase in feeding rate, perhaps acting as a trigger to increase refueling rate in the same way as decreasing day length triggers the onset of autumn migratory activity? Should further work eliminate these alternative explanations, the question remains whether thrush nightingales respond to specific magnetic field values as boundary or latitudinal markers (as suggested in the studies of pied flycatchers and hatchling sea turtles), or as one component of a uniconordinate (see silvereve discussion) or biconordinate map.

DIRECT EVIDENCE FOR THE MAGNETIC MAP HYPOTHESIS

EASTERN RED-SPOTTED NEWTS

The most direct evidence for magnetic map navigation comes from studies on the Eastern red-spotted newt, *Notophthalmus viridescens*. This species offers several advantages for studies of the geomagnetic field's role in navigation. First, homing behavior is an important feature of newt life history. The eggs and larvae are aquatic and, in most populations, the larval stage is followed by a terrestrial juvenile stage (red eft), which leaves the pond and remains on land as an inhabitant of the forest floor for as long as five to eight years (Gill 1978). Most efts return to their natal pond when they become reproductively mature, with the remainder entering ponds 1–2 km away. In many populations, adults migrate in and out of their pond seasonally. When displaced to another pond, a majority of adult males (and a somewhat smaller proportion of females) return to their home pond at the start of the next breeding season. This "pond fidelity" makes it possible to obtain large numbers of experimental subjects that all attempt to home to the same known destination.

Additionally, newts deprived of directional magnetic, olfactory, visual, and inertial information during displacements of 23–42 km from their home pond (i.e., well beyond their normal range of movement) can orient homeward just as well as controls (Phillips et al. 1995). Newts are thus capable of true navigation, and so must possess some form of map sense used for position fixing at the testing site. Moreover, shoreward "magnetic compass" orientation (which does not involve map information) and homing orientation (which requires map and compass information) can be observed separately under controlled laboratory conditions. Thus it is possible to directly test whether manipulations of geomagnetic components are specific to the map step.

To test whether magnetic inclination might provide one component of a magnetic map, Fischer et al. (2001) displaced adult newts 40–45 km north-northeast from their home ponds to the testing facility, where the inclination is slightly steeper than that of the home ponds, and exposed them to the inclination value of the ambient testing facility, or a much steeper altered field of $+2^\circ$ (normally found far to the north and in the same relative direction of the test site), or to a much shallower field of -2° (normally found far to the south of the home pond in the opposite direction from the test site). Magnetic intensity was held constant at the ambient test site value. It was found that newts exposed to the ambient magnetic testing facility field and the altered field of $+2^\circ$ were correctly oriented toward home (i.e., approximately south-southwest); however, those exposed to the -2° inclination value oriented in approximately the reverse direction (Figure 4). This suggests that newts in the -2° group homed in the opposite direction because their perception of geographic position placed them on the opposite side of home. A control experiment demonstrated that newts exhibiting shoreward compass orientation were unaffected by exposure to any of the three inclination conditions, which indicates that the effects of inclination manipulations are specific to the map step of homing. The extreme inclination values used in these experiments would never have been experienced by the newts during the course of their normal movements, demonstrating

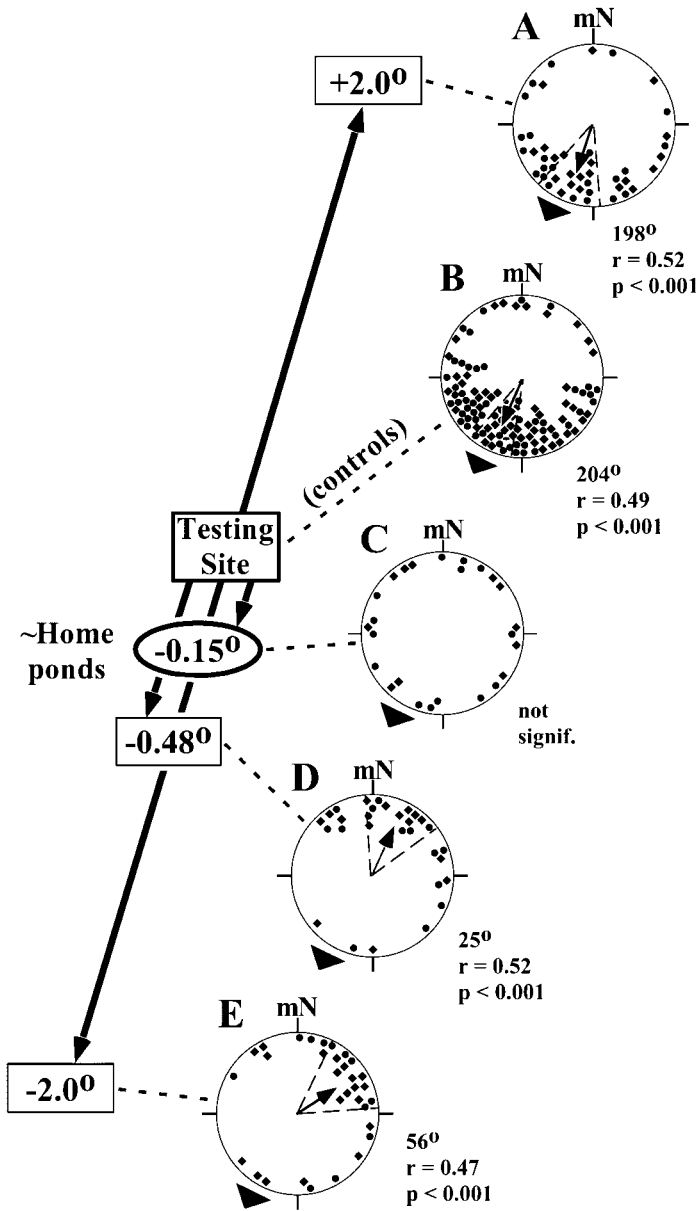


FIGURE 4. ORIENTATION OF EASTERN RED-SPOTTED NEWTS IN MAGNETIC FIELD DIFFERING BY SMALL CHANGES IN MAGNETIC INCLINATION

Magnetic bearings pooled from newts tested in one of four horizontal alignments of the magnetic field (mN at geographic N, E, S, or W). The 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). Data are from Fischer et al. (2001) and Phillips et al. (2002).

that if the interpretation of these results is correct, the newts must have extrapolated their knowledge of the inclination gradient around the home pond to determine their position along the gradient, relative to home.

Two further predictions were then tested (Phillips et al. 2002): does the switch to reversed homing happen when newts are presented with inclination values that are just a little less than the home value, and do they stop displaying homing behavior when exposed to the actual home value? As predicted, newts exposed to an inclination value of -0.48° , which is much closer to the home value ($-0.17 \pm 0.04^\circ$) than the -2° condition, continued to exhibit reversed orientation, while newts exposed to the home value oriented randomly (Figure 4). The findings of these series of experiments provide the first direct evidence that a mature, experienced migrant can use magnetic inclination as one coordinate of a navigational map. Future work should include precise geomagnetic surveying at and around the home ponds of the newts to test for a match between the orientation behavior observed in the experiments and the actual gradient pattern.

AUSTRALIAN SILVEREYES

The Australian silvereye, *Zosterops lateralis*, is the only bird species in which the magnetic map hypothesis has been directly tested (Fischer et al. 2003). The Tasmanian race *Z. l. lateralis* undertakes seasonal migrations from the Tasmanian breeding grounds to overwintering sites along the southeast coast of mainland Australia in southern and central New South Wales, as far north as Queensland. Direct evidence that adult birds rely on magnetic map information comes from a study that tested the birds' responses to experimental manipulations of the magnetic field that simulated displacements to different locations along the migratory path (Fischer et al. 2003). Adult silvereyes, captured on their breeding grounds in Tasmania, were transported to Armidale, New South Wales, north-northeast. The birds were tested on five to six nights over a period of two weeks during the Australian autumn in artificially altered magnetic fields simulating displacements to ar-

east north (SimN) or south (SimS) of Armidale. In the SimN and SimS conditions, the vertical component of the magnetic field was decreased or increased by 12% causing corresponding changes in the total intensity and inclination angle of the magnetic field around the cages (Figure 5). To minimize the likelihood of an effect on the magnetic compass, the manipulations that were used resulted in less than 10% change in the total intensity of the magnetic field. Birds were exposed to the altered magnetic field values for a minimum of six days prior to testing, and were held in the altered fields between tests (see Wiltschko 1968). In southeastern Australia, the gradients of all three components (vertical intensity, total intensity, and inclination) decrease to the north-northeast, paralleling the study population's migratory route.

Silvereyes in the SimS condition oriented toward the north-northeast, the seasonally appropriate migratory direction exhibited by the birds in the control condition (i.e., the ambient field of Armidale). In contrast, birds in the SimN condition ceased to show directed orientation in the overall distribution of data obtained over the five to six nights of testing (Fischer et al. 2003). A later reanalysis of these data, however, prompted by Mouritsen's (2003) proposal that migratory birds might use uniconordinate map information to derive north-south position and major topographic features (e.g., mountains, coastlines) to determine their east-west position, suggested that the silvereyes response in the SimN condition may be more complex than initially realized. The results of this reanalysis indicate that birds in the SimN condition exhibited an initial phase of easterly orientation, which would bring them to the coastline in southeastern Australia, followed by a significant shift in orientation, resulting in a southward tendency that approached significance ($0.1 > p > 0.05$). There was no evidence for a comparable change in the orientation of birds in the SimS condition. Fischer et al. (2003) considered several alternative explanations for the effect of the SimN condition and concluded that the most likely explanation was an effect on the map. Consistent with this conclusion, a more recent experiment (Deutschlander, Phillips, Fischer,

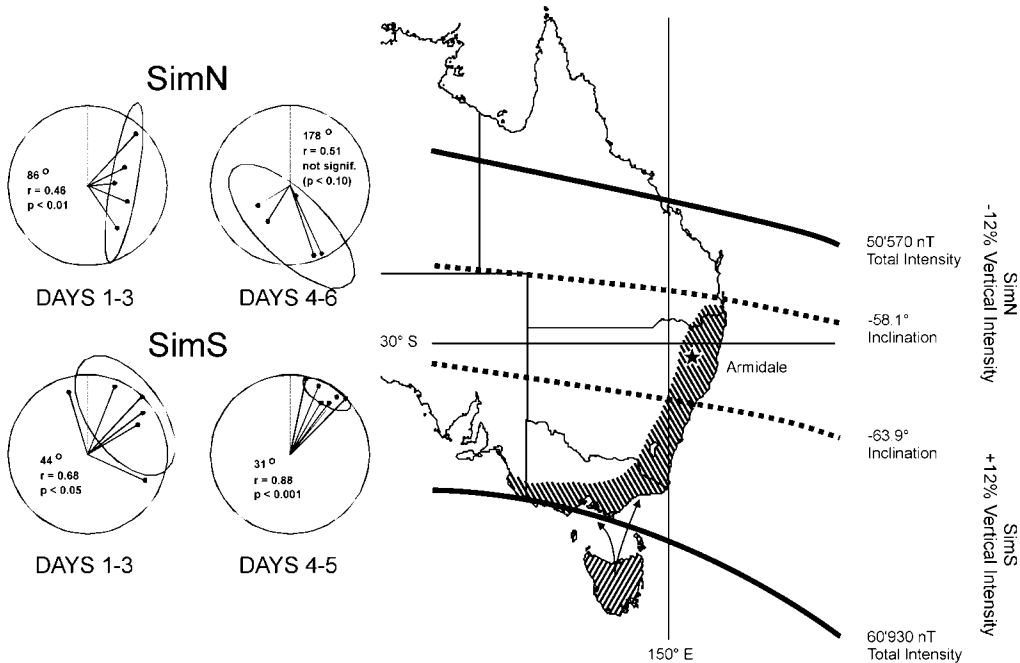


FIGURE 5. ORIENTATION OF AUSTRALIAN SILVEREYES AFTER SIMULATED DISPLACEMENT

Position of the geomagnetic field values after artificially changing the vertical intensity of the geomagnetic field of Armidale by $\pm 12\%$. SimN = simulated northern displacement; SimS = simulated southern displacement. Geomagnetic field values for Armidale (30° 30' S, 151° 42' E) according to DGRF90 for 1 May 1994: 55700 nT total intensity, -61.3° inclination. Data from Fischer et al. 2003.

and Munro, unpublished data), in which birds were exposed to larger simulated displacements, found that the effect of the SimN condition was only observed in experienced adult birds that use map information. Young birds collected prior to their first migration, which do not rely on map information, showed no effect from the SimN or SimS treatments. As discussed previously, pulse remagnetization experiments have also provided evidence that silvereyes use magnetic map information. In these experiments, the migratory orientation of adult silvereyes (Wiltschko et al. 1994, 1998), but not that of inexperienced young birds (Munro et al. 1997a,b), was affected by pulse remagnetization, which suggests that a magnetoreception mechanism involving single-domain or interacting superparamagnetic particles of magnetite is involved in obtaining map information.

SPINY LOBSTERS

Only vertebrates have been considered as potential candidates for true navigation using

geomagnetic maps, and so perhaps the most remarkable development is recent work strongly mirroring our studies with newts, but in an arthropod migrant, the spiny lobster, *Panulirus argus*. The long-distance migrations (up to hundreds of kilometers) of spiny lobsters from the shallows to deep water breeding grounds are well known (Herrnkind 1980), and individuals regularly make nighttime foraging trips of several hundred meters before returning to their home den. Moreover, previous work demonstrated that spiny lobsters have a magnetic compass sense used to set a course, even in darkness (Lohmann et al. 1995). Thus the ability of lobsters to sense the magnetic field, taken in conjunction with evidence for homing from unfamiliar areas (Creaser and Travis 1950), strongly suggests spiny lobsters as a potential candidate for magnetic map navigation. Boles and Lohmann (2003) began by testing whether spiny lobsters can perform true navigation (as defined above). Lobsters were displaced

in one of three different directions by boat or truck in sealed water-filled containers and tested in a circular arena at "unfamiliar" locations 12–37 km from their capture site. The lobsters oriented in the correct homeward direction despite the lack of visual, inertial, and olfactory cues during displacement. Route-based magnetic cues were then also excluded using strong magnets to disrupt the geomagnetic field during the outward journey, again with no effect on the lobsters' ability to orient homewards. This was followed by a simulated displacement experiment in which lobsters were exposed to values of magnetic inclination and intensity that would normally be found about 400 km north or south of the capture site. Lobsters, which were exposed to the simulated north-displacement, oriented approximately south, while individuals exposed to the simulated south-displacement oriented approximately north. Each group oriented in the direction that would return them to the capture site.

Because both magnetic inclination and intensity were varied, it is not possible to determine which component of the magnetic field was used by the lobsters to determine their location, or even if a location was determined. If, as is likely, the magnetic parameter(s) used by the lobsters runs approximately north/south, then the lobsters could have oriented in the correct direction even though they may have only known their position along the y-axis, with no knowledge of their position along the x-axis. Therefore further work is required to test whether lobsters possess a bicoordinate map. Their ability to perform true navigation after displacement in multiple directions, however, would suggest that a unicoordinate map sense is inadequate to explain the navigational feats in this species.

A criticism common to both the newt and lobster studies is that the simulated displacement distances exceed the distances over which they are known to perform true navigation and, therefore, are not representative of the real world. Current experimental design constraints make it necessary to simulate substantial distances to ensure that the signal is greater than the noise. Comparable studies using other animal models with normal movement patterns over the scale used in

the newt and lobster experiments would strengthen support for the magnetic map hypothesis.

SOME THOUGHTS ON DESIGNING EXPERIMENTS

Critical tests of the magnetic map hypothesis are most likely to come from animal models that exhibit map-based homing under carefully controlled laboratory conditions. In particular, the ability to produce precise alterations in the magnetic field to simulate artificial displacements and exclude alternative cues is essential. It is also important to test whether manipulations of the geomagnetic field act on the map step of homing, rather than exerting a nonspecific effect on the compass step. This is especially relevant considering the wide range of animals now known to possess a magnetic compass sense (Wiltschko and Wiltschko 1995a).

To date, many studies have used a much more indirect approach by testing magnetically impaired animals in the field. When the impaired animals are still able to complete the navigational task, this is often taken as sufficient evidence that magnetic cues are not used for navigation. Given the evidence from several species for the use of multiple sources of navigational information, however, it is premature to conclude that magnetic map cues do not play a role. The process of migration is likely to consist of several navigational components, normally used at various ontogenetic stages over different distance scales or at different localities (Phillips 1996). In other words, alternative cues may suffice to mediate homeward orientation when reliable magnetic information is unavailable, but this does not demonstrate that a magnetic map sense is nonexistent. There is a specific concern over the interpretation of experiments that have attempted to test the magnetic map hypothesis in adult long-distance migrants, such as sea turtles (Papi et al. 2000; Luschi et al. 2001; Hays et al. 2003), albatrosses (Mouritsen et al. 2003; Bonadonna et al. 2005), and petrels (Benhamou et al. 2003). In all of these cases, the movements of control and experimental individuals were tracked using satellite telemetry, and the authors have gener-

ally concluded that magnetic map cues are not used for short- and medium-scale navigation because animals fitted with strong magnets were able to reach feeding or nesting grounds just as well as controls (Papi et al. 2000; Benhamou et al. 2003; Mouritsen et al. 2003; Bonadonna et al. 2005). It is essential to consider whether the presence of a satellite transmitter attached to the animal distorts the geomagnetic field sufficiently to render a magnetic map sense inoperable. The static and dynamic fields produced by these units are very rarely reported in the studies; indeed, it is likely that in most cases they have never been measured. However, the transmitters do produce a significant artificial field. Papi (2001) reports that the Telonics ST10 transmitter produces a continual static field component of 40000 nT at 3 cm, 20000 nT at 6 cm, and less than 10000 nT at 8 cm. When the sea turtle surfaces, the transmitter signal produces a static field of about 720000 nT at 3 cm from the transmitter for 360 ms every 50 s, together with a dynamic field at 401.650 MHz. In several studies, the transmitter was attached to the head of some sea turtles (Papi et al. 2000; Luschi et al. 2001). If the magnetoreceptor is located in the head (e.g., near the ethmoidal region in which innervated magnetite particles have been located in several species; Beason and Nichols 1984; Kirschvink et al. 1985; Fleissner et al. 2003), the static artificial field would add components of several thousand nT to the ambient field, producing changes in inclination/intensity corresponding to distances of thousands of kilometers. Attempts have been

made in some studies to minimize the effect of the transmitter by attaching the transmitter to the carapace rather than the head (Papi et al. 2000; Hays et al. 2003). It is not clear, however, whether this is sufficient to eliminate an effect on the animal's navigation system(s). Hays et al. (2003) state that "such an effect is excluded in the present experiments, since the transmitters were attached to the carapace" (p S6). Yet, altered fields of a comparable Telonics transmitter extend 40 cm from the transmitter (Ken Lohmann, personal communication). This could still affect a magnetoreceptor located in the head of an adult turtle (and certainly in a bird), by adding small field components of ten nT or more (representing distances of a few km). Moreover, any head movements would introduce an additional and unpredictable dynamic component to the static component; this temporally varying component of the magnetic field may be interpreted as a magnetic storm, causing magnetic map cues to be treated as unreliable. Under these circumstances, it is possible that both control and experimental sea turtles would forgo magnetic cues. Caution is warranted, therefore, in assessing the value of these studies as tests of the magnetic map hypothesis. This concern applies to any field-based study using tracking equipment with electromagnetic components.

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