Magnetic Navigation

JOHN B. PHILLIPS†

Department of Biology, Indiana University, Bloomington, IN 47405, U.S.A.

(Received on 14 September 1993, Accepted in revised form on 26 January 1996)

Recent evidence suggests that some amphibians, reptiles and birds may be capable of homing using information about geographic position (‘map’ information) derived from subtle geographic gradients in the earth’s magnetic field. The “magnetic map” hypothesis faces numerous theoretical difficulties, however, due to the extremely high level of sensitivity that would be necessary to detect natural magnetic gradients, and to the presence of spatial irregularities and temporal variation in the geomagnetic field that might make map coordinates derived from magnetic gradients unreliable. To date, the majority of studies carried out to test the magnetic map hypothesis have involved field observations of the effects on homing orientation of naturally occurring spatial or temporal variation in the geomagnetic field. While providing an important first step, these studies are subject to the criticism that the observed changes in homing orientation could result from effects on a magnetic compass, or some other unidentified component of the navigational system, rather than from effects on a magnetic map. The recent development of experimental systems in which navigational ability can be studied under controlled or semi-controlled laboratory conditions has opened up the possibility of using new experimental approaches to more rigorously test the magnetic map hypothesis. After briefly reviewing the available evidence for the geomagnetic field’s involvement in the map component of homing, a simple graphical model is presented which describes how the home direction derived from a bicoordinate map varies as a function of the value of one of the map coordinates when the value of the second map coordinate is held constant. In studies of homing orientation in which the value of a specific magnetic field parameter (e.g., total intensity, inclination, etc.) can be varied independently of other putative map parameters, the graphical model can be used to generate qualitative predictions about the changes in the direction of homing orientation that should be observed if the magnetic field parameter being manipulated serves as one coordinate of a bicoordinate map. The relationship between the direction of homing orientation and the value of a putative magnetic map parameter can also be used to generate quantitative predictions about characteristics of the local gradient of that magnetic field parameter in the vicinity of the home site (i.e., the alignment and “home value” of the local gradient), which can then be compared with actual measured values. Together, the qualitative and quantitative predictions of the graphical model permit rigorous tests of whether one or both coordinates of a bicoordinate navigational map are derived from the geomagnetic field.

Introduction

Map-based homing or “true navigation” (Griffin, 1952) is the ability of an organism displaced to an unfamiliar location to orient in a direction that would return it to the origin of the displacement (“home”) without reference to familiar landmarks, goal-emanating cues, or directional information obtained during the displacement (e.g., Walcott & Schmidt-Koenig, 1973; Rodda, 1984a,b, 1985; Phillips et al., 1995). Navigational ability requires both a directional (“compass”) sense and a geographic-position (“map”) sense derived from spatial information available at the release site (Kramer, 1953). Vertebrates are known to possess a variety of compass mechanisms (e.g., Ferguson, 1971; Taylor & Auburn, 1978; Wiltschko, 1983; Phillips, 1986b). In contrast, the navigational map (or maps) remains poorly understood (Ganzhorn, 1990; Papi, 1990; Walcott, 1992; Schmidt-Koenig & Ganzhorn, 1991).

†E-mail: phillips@indiana.edu

© 1996 Academic Press Limited
Hypotheses concerning the navigational map have implicated a wide variety of potential sources of positional information including: the solar arc (Matthews, 1968), natural odor sources (Papi, 1976, 1990; Wallraff, 1980), the geomagnetic field (Yeagley, 1947, 1950; Gould, 1980; Moore, 1980; Walcott, 1980; Rodda, 1984a; Phillips, 1986a), and the earth’s gravitational field (Lednor & Walcott, 1984; Dornfeldt, 1991). Of these, all but the “mosaic” olfactory map hypothesis proposed by Papi (1976, 1990) involve detection of gradients of one or more environmental factors (e.g., sun altitude, magnetic field intensity, concentration of airborne odorants, etc.).

A “gradient” map requires an animal to learn the alignment and, possibly, the steepness of one or more environmental gradients in the vicinity of its home range or territory, and to extrapolate the gradients beyond its area of familiarity. A comparison of the value of such a map factor at an unfamiliar site to the “home” value would provide information about the animal’s position along the gradient in relationship to home (Wallraff, 1991). Gradients of two different factors aligned more or less orthogonally would allow bicoordinate position-fixing (i.e., a true navigational).

There has been considerable discussion of the possibility that one or both coordinates of a bicoordinate map are derived from the geomagnetic field, i.e., from geographic gradients in magnetic field parameters such as inclination and total intensity (Gould, 1980; Moore, 1980; Walcott, 1980). Interest in the magnetic map hypothesis was stimulated by studies showing that the initial homeward orientation of homing pigeons *Columba livia* was influenced by natural temporal variation (Keeton *et al*., 1974; Larkin & Keeton, 1976; Kowalski *et al*., 1988) and, possibly also, by spatial anomalies (Walcott, 1978; Kiepenheuer, 1982, 1986; Wagner, 1983; Lednor & Walcott, 1988; but see Dornfeldt 1991, Walcott 1991) in the geomagnetic field. Such variation could produce large errors in estimates of the home direction based on the subtle gradients in the geomagnetic field (see below), but would be too weak to affect the magnetic compass (Wilstschko, 1972).

**Constraints on the Use of Map Information Derived from the Geomagnetic Field**

The use of a bicoordinate map derived from spatial gradients in the magnetic field presents a number of theoretical difficulties (Lednor, 1982; Walcott, 1991). An extremely high level of sensitivity would be required to detect geographic variation in magnetic field parameters such as total intensity or inclination. For example, in the north temperate zone the average geographic variation in total intensity is only about 0.01% km, and in inclination only about 0.005° km.

The difficulty inherent in detecting these extremely weak geographic gradients in the magnetic field is compounded by several factors. For example, large errors in estimates of geographic position could potentially occur as a consequence of spatial irregularities in the magnetic field. As a consequence of such irregularities, local gradients of magnetic parameters such as total intensity and inclination can vary in “steepness” and alignment in different areas. However, even when the local gradients of magnetic field parameters such as total intensity and inclination are extremely regular, it may be difficult for an animal to make fine scale determinations of geographic position. There are several potential sources of error: (a) natural temporal variation in the geomagnetic field (Lednor, 1982; and see below), (b) temperature sensitivity of the underlying magnetoreception system (Yorke, 1979), and/or (c) micro-scale irregularities at or near the earth’s surface (which would not be detected by aeromagnetic surveys). Such sources of error are likely to be especially problematic for amphibians and reptiles that move relatively slowly at ground level and, in many cases, may need to resolve differences in geographic position of as little as a kilometer, or less. Nonetheless, studies of amphibians and reptiles (like those of birds) have provided evidence that is consistent with an ability to derive map information from the geomagnetic field (see below).

**Evidence for the Magnetic Field’s Involvement in the Map Component of Homing**

Rodda (1984a,b, 1985) obtained evidence that yearling American alligators *Alligator mississippiensis* use a route-based mechanism (i.e., path integration), rather than a bicoordinate map, to derive the geographic position information necessary for homing. In contrast, alligators that were in their second year, or older, appeared to rely on site-based information, suggesting that they were using a true bicoordinate (multicoordinate) map. Rodda (1984a) found that the older alligators showed a correlation between “errors” in the direction of homeward orientation and natural temporal variation in the inclination and/or horizontal intensity of the geomagnetic field. In contrast, yearlings showed no effect of temporal variation in the magnetic field. Since both age groups had access to the same sources of compass information, Rodda’s findings point to a possible use of magnetic inclination and/or horizontal intensity by...
older alligators to derive one coordinate of a navigational map.

Rodda’s (1984a) work also suggests that the older alligators may have been comparing the value of one or more magnetic field parameters measured just prior to capture, or averaged over the entire night prior to capture, with the value(s) of these parameter(s) on the following night when they were released at an unfamiliar site. Errors in estimates of geographic position caused by temporal variation in the magnetic field would be reduced by minimizing the time interval between measurements taken at the two locations and/or by taking readings at night when the magnetic field is relatively stable (Rodda, 1984a). Evidence from homing pigeons is also consistent with the possibility that a comparison of magnetic parameters measured immediately before and after displacement plays a role in the map component of homing under some circumstances (Papi et al., 1983).

Additional support for the use of the geomagnetic field to derive geographic position has come from studies of hatchling sea turtles. Lohmann & Lohmann (1994) found that hatchling loggerhead sea turtles exposed to values of magnetic inclination that would normally be encountered at the northernmost (i.e., 60°) and southernmost (i.e., 30°) extremes of their range, shifted the direction of magnetic compass orientation to a new heading that might help to prevent them from being displaced beyond their normal range by ocean currents. At an intermediate value of inclination (i.e., 45°) corresponding to the center of their range where movement is largely due to passive displacement by ocean currents, as well as at more extreme (i.e., 15° and 75°) values of inclination, hatchlings failed to exhibit a consistent direction of orientation. These data do not suggest that hatchling sea turtles have a bicoordinate map, which presumably would require a knowledge of the geographic variation in the magnetic field built up through experience during normal long distance movements. Rather, Lohmann & Lohmann (1994) suggest that the response of hatchling sea turtles to magnetic inclination may represent an innate “recognition” mechanism that helps prevent young turtles from straying beyond the boundaries of their normal range into regions where conditions (e.g., water temperatures) are not favorable for survival. If this interpretation is correct, the geomagnetic field provides hatchling sea turtles with a rudimentary sense of geographic position.

Further experimental evidence for the use of geographic position information derived from the magnetic field has come from recent studies of a migratory bird, the silvereye Zosterops lateralis (Fischer et al., in preparation). Adult silvereyes were captured on their breeding grounds in Tasmania off the southern coast of Australia prior to the onset of the fall migration and then transported to Armidale, New South Wales, approximately half way to the northern boundary of the population’s winter range on the eastern coast of Australia. They were held indoors in the ambient magnetic field until they exhibited migratory activity. When tested indoors in the ambient magnetic field of Armidale, silvereyes exhibited seasonally appropriate, northeasterly orientation as demonstrated previously in this species (Wiltschko et al., 1993, 1994). One group was subsequently exposed to a decrease of approximately 12% in the vertical intensity of the magnetic field resulting in values of magnetic inclination, vertical intensity, and total intensity comparable to those that occur in the vicinity of the northern boundary of the population’s winter range (“simulated northern displacement”). The second group was exposed to an increase in vertical intensity of approximately 12% resulting in values of the three magnetic field parameters comparable to those normally experienced near the beginning of their fall migration from Tasmania (“simulated southern displacement”). Both experimental manipulations produced changes in total magnetic field intensity (approximately 9.5%) that were below values that have been shown to affect the magnetic compass in another migratory bird (Wiltschko, 1972). Although there was no difference in the orientation of the two groups when they were housed and tested in the ambient magnetic field of Armidale (control condition), their orientation after exposure to the simulated northern and southern displacements differed significantly. Silvereyes exposed to the simulated southern displacement continued to show seasonally appropriate migratory orientation to the north-northeast that was stronger than in the control condition, although this difference was not statistically significant. In contrast, the responses of birds exposed to the simulated northern displacement were randomly distributed (i.e., they failed to exhibit a consistent direction of migration, as might be expected in the final stages of migration), and differed significantly from the distribution of responses that they exhibited in the control condition and from the distribution of responses exhibited by the second group of birds tested in the simulated southern displacement condition. These findings are consistent with the possibility that silvereyes used magnetic inclination and/or intensity to derive one coordinate of a bicoordinate map. However, the data do not rule out an alternative explanation, which is that silvereyes fly in a fixed northeasterly compass.
direction during the fall migration until they encounter specific values of magnetic inclination and/or intensity associated with the northern boundary of the population’s winter range. This second alternative is similar to the “range boundary” hypothesis suggested by Lohmann & Lohmann (1994) to explain effects of changes in magnetic inclination on the orientation of young sea turtles.

Preliminary data from a study of the homing orientation of eastern newts is also consistent with the possibility that a magnetic field parameter, i.e., magnetic inclination, may be involved in the map. Initial results suggest that small (i.e., 2') changes in magnetic inclination have a significant effect on the direction of homing orientation by newts, but have no effect on shoreward magnetic compass orientation which does not require map information (J. A. Fischer, J. B. Phillips & S. C. Borland, research in progress). If replicable, these results would be consistent with the possibility that magnetic inclination is used to derive one coordinate of the navigational map. It must be kept in mind, however, that in order for newts to derive useful information about geographic position within their normal range of movement (i.e., <5 km), they would have to detect differences in magnetic inclination that are a hundred to a thousand times smaller than the manipulations used in these experiments (i.e., 0.02°–0.002°, depending on the steepness of the local gradient in the vicinity of their home pond). Moreover, since magnetic inclination is measured relative to gravity, a gravitational reference system with a comparable level of sensitivity would be required.

Evidence for the Involvement of a Specialized Magnetoreception Mechanism in Homing

Results of behavioral experiments (e.g., Phillips, 1986a; Phillips & Borland, 1994; Munro et al., submitted) and neurophysiological experiments (e.g., Semm et al., 1984; Semm & Demaine, 1986; Beason & Semm, 1987; Semm & Beason, 1990) suggest that some vertebrates may have two distinct magnetoreception mechanisms. One putative mechanism appears to be light-dependent and to provide compass information. The second putative mechanism appears to be non-light-dependent and to play a specialized role in the map component of homing. In eastern newts, the use of the geomagnetic field for shoreward orientation (which requires only a compass) and homing (which requires both a map and compass) have been found to be affected differently by changes in the vertical component of the magnetic field (Phillips, 1986a) and in the wavelength of light (Phillips & Borland, 1994, and unpublished data). The wavelength-dependent effects of light on shoreward magnetic orientation by newts suggest that this compass response is mediated by a light-dependent, possibly photoreceptor-based, magnetoreception mechanism (Phillips & Borland, 1992a,b,c). In contrast, homing orientation by newts exhibits properties that are consistent with the involvement of both the light-dependent magnetic “compass” and a non-light-dependent magnetic inclination or intensity detector that may be used to derive map information from the geomagnetic field (Phillips & Borland, 1994; and unpublished data). The results of recent experiments with migratory silveryeyes are also consistent with the presence of light-dependent magnetic compass, and a non-light-dependent (possibly magnetite-based) magnetoreception mechanism that is used to derive map information (Wiltshko et al., 1993, 1994; Munro et al., submitted).

Neurophysiological studies of birds have provided support for the presence of two distinct magnetoreception mechanisms, although to date replication of these results has proven difficult (P. Semm, personal communication). Recordings from the central nervous systems of birds have yielded evidence for light-dependent responses to directional magnetic stimuli in visual centers (e.g., the optic tectum, and nucleus of the basal optic root; Semm et al., 1984; Semm and Demaine, 1986). In addition, single-unit responses to small (<1%) changes in magnetic intensity have been reported in the trigeminal nerve system of the bobolink Dolichonyx oryzivorus (Beason & Semm 1987, Semm & Beason, 1990). Unlike the responses recorded in the visual system, the trigeminal nerve responses appear to be independent of light and visual input. The trigeminal nerve innervates the anterior region of the head where particles of the mineral magnetite have been localized in a number of vertebrate groups (Kirschvink et al., 1985). This suggests that a magnetite-based receptor may underlie the non-light-dependent responses reported by Semm & Beason (1990). Support for this possibility has come from a recent study by Beason & Semm (1996) in which they obtained evidence that blocking the ophthalmic branch of the trigeminal nerve with an anesthetic eliminated shifts in the direction of orientation by migratory bobolinks caused by exposure to a brief, high-intensity magnetic pulse. This type of “pulse remagnetization” treatment should alter the response of a magnetoreception mechanism mediated by single-domain particles of magnetite that are fixed (i.e., not free to rotate) with respect to the surrounding tissue. (Kalmijn & Blakemore, 1977, 1978). In Beason & Semm’s (1996)
study, blocking the trigeminal nerve did not prevent bobolinks from maintaining a consistent direction of orientation in the absence of usual cues, suggesting that pulse remagnetization did not affect the magnetic compass. These findings are consistent, therefore, with a magnetite-based receptor associated with the ophthalmic branch of the trigeminal nerve that is somehow involved in deriving map information. Moreover, recordings from the trigeminal nerve (Semm & Beason, 1990) have provided evidence for the high level of sensitivity that would be necessary to derive map information from the subtle geographic gradients in the magnetic field.

The Need for Critical Tests of the Magnetic Map Hypothesis

The available evidence for the involvement of the geomagnetic field in the map component of homing is intriguing. Nevertheless, legitimate concerns remain: (1) the extremely high levels of sensitivity that would be required to detect the subtle geographic variation in magnetic field parameters such as inclination and total intensity, especially in organisms that move over relatively short distances (i.e., < 5 km); (2) the effects of temporal and spatial unpredictability in the magnetic field on the ability to derive meaningful information about geographic position from the gradients in these magnetic field parameters; and (3) in the case of magnetic inclination, the requirement of a gravitational reference system with a comparably high level of sensitivity. The possibility that there are alternative explanations for findings that appear to support the involvement of the geomagnetic field in the map component of homing must, therefore, be given serious consideration, even if these alternative explanations are not immediately apparent. As a consequence, data suggesting that the effects of small changes in magnetic inclination and/or total intensity are specific to homing and that a specialized magnetoreception system may be involved in homing (see earlier discussion) are not sufficient to demonstrate the magnetic field's involvement in the map.

The present paper presents a simple graphical model of bicoordinate navigation that can be used to test whether a specific parameter of the geomagnetic field (e.g., inclination or total intensity) serves as the basis for one coordinate of a bicoordinate map. This model generates specific, falsifiable predictions about the qualitative changes in the direction of homing orientation that should occur when the value of a map parameter derived from the magnetic field is manipulated independently of other putative map parameters. In addition, the relationship derived from the model between the direction of homing orientation and the value of a putative magnetic map parameter can be used to make quantitative predictions about the alignment of the local gradient and the "home" value of that parameter in the vicinity of the home site for comparison with actual measured values. A determination of the "match" between the predicted and actual measured values provides an additional critical test of a specific magnetic field parameter's role in providing one of the map coordinates. While the graphical model was specifically developed for tests of the magnetic map hypothesis, in principle it can be used to investigate the involvement of any environmental factor in a gradient map, provided that the value of this factor can be manipulated independently of other putative map factors during tests of homing orientation.

A Graphical Model of Bicoordinate Navigation

Figure 1(a) shows a hypothetical coordinate system derived from gradients of parameters C-K and IV-XIX. Solid lines are the isometric contours of the two parameters showing that the steepness and orientation of the gradients may vary in different regions. Dashed lines indicate the isometric contours extrapolated from the local gradients within the animal's area of familiarity (hatched area) which are used by the animal to estimate its position relative to home at an unfamiliar site. When an animal is released at an unfamiliar site, the animal's actual position relative to home (closed circle labeled "testing site") may differ from the position derived from the extrapolated map coordinates (open circle) resulting in a predictable error in the estimate of home direction.

Figure 1(b) shows the predicted orientation of an animal that uses the extrapolated coordinate system in Fig. 1(a) to determine its position relative to home. Curved lines labeled C'-H' in Fig. 1(b) indicate the estimate of homeward direction (vertical axis) for several values of parameter C-K as the value of the second parameter IV-XIX (horizontal axis) is varied. In other words, curves (C'-H') indicate the estimates of home direction that would be derived by an animal at different locations along one of the contours of parameter C-K [see home directions indicated by small arrows along extrapolated contour lines E' and F' in Fig. 1(a)].

Alternatively, curves C'-H' indicate estimates of home direction that would be derived if the animal remained at the "testing site" in Fig. 1(a) and the values of parameters C-K and IV-XIX were
Fig. 1. (a) A hypothetical grid system derived from gradients in two environmental factors. Solid lines indicate actual spatial variation in the environmental factors. Dashed lines indicate grid system extrapolated by an animal from the gradients within its area of familiarity (shaded area). (b) Variation in the animal's estimates of the home direction derived from the extrapolated grid system shown in (a) as values of the two map parameters vary, due either to changes in the animal's position or due to experimental manipulation of the map parameters (see text).
manipulated experimentally. If, for example, the value of parameter IV-XIX is manipulated while the values of other possible map parameters (including parameter C-K) remain unchanged, the expected changes in homing orientation at the “Testing site” in Fig. 1(a) are shown by the curve labeled “F” in Fig. 1(b). If the value of parameter IV-XIX is decreased [indicated by arrow labeled “−” directed away from the “Testing site” in Fig. 1(b)], the animal’s estimate of the home direction would undergo a clockwise rotation eventually reaching an asymptote at a direction roughly opposite to the actual home direction. In contrast, if the value of parameter IV-XIX was increased [indicated by arrow labeled “+” by a comparable amount, there would be little or no effect on the estimated home direction. For a second home site located between isometric contours E and F, but in the opposite direction from the “Testing site” [i.e., a home site located above the testing site near the top of Fig. 1(a)], the predicted changes in the direction of homing orientation resulting from changes in the value of parameter IV-XIX would be roughly the reverse of those shown in Fig. 1(b), i.e., an increase in the value of parameter IV-XIX would produce a counterclockwise rotation of the animal’s estimate of the home direction, while a decrease in the value of parameter IV-XIX would have little or no effect. These qualitative predictions of the model would hold true even if the map parameter that is not manipulated has not been identified and/or is derived from an entirely different sensory modality [see curve F’ in Fig. 1(b)].

Curve E’ in Fig. 1(b) indicates the changes in the estimates of home direction that will occur if the value of parameter C-K at the testing site is held constant at a new value while parameter IV-XIX is varied. Comparison of curves E’ and F’ in Fig. 1(b) illustrates another qualitative prediction of the model. Because isometric contours E and F are on opposite sides of the “home” site [see Fig. 1(a)], a given change in the value parameter IV-XIX near the home value of this parameter will result in opposite directions of rotation (i.e., clockwise vs. counterclockwise) of the animal’s estimate of home direction. It should be noted that all of the qualitative predictions of the model outlined here, and in the previous paragraph, can be tested even if no information is available about the local

†In this equation, $a$ is the angular deviation of the direction of homing orientation from the isometric contour of the map parameter that is held constant [see Fig 1(a)], $y$ is the difference between the value of the parameter being manipulated and the home value of that parameter, and $C_x$ is the difference between the value of the parameter that is held constant and the home value of that parameter.

magnetic gradient(s) in the vicinity of the “home” site (see below), provided that the range of values of the relevant magnetic field parameter(s) used in testing is large enough to span the “home” value(s).

When experimental manipulation of a putative map parameter leads to the qualitative changes in homing orientation predicted by the map model, the map model can also be used to estimate characteristics of the local gradients of putative map parameters in the vicinity of the animal’s home pond or territory for comparison with actual measured values. For example, when experimental subjects are tested at several values of a putative map parameter (e.g., magnetic field intensity) while other possible map parameters remain constant, a curve of the general form $a = \arctan \frac{C_x}{y}$ can be fitted to the data†. If this is repeated at several different values of a second putative map coordinate, a family of curves like that shown in Fig. 1(b) can be generated. As shown in Fig. 1(b), these curves can be used to estimate the alignment of the local gradients of both map parameters in the vicinity of the animals’ home, and the “home” values of each of the parameters relative to the value at the testing site [compare values indicated in Fig. 1(b) to hypothetical gradients in Fig 1(a)].

If only one putative map parameter can be manipulated (e.g., if a second putative map parameter has not been identified), characteristics of the local gradient of the manipulated parameter in the vicinity of the home site can still be estimated provided that homing tests are carried out at a fixed site where the values of other potential map parameters remain more or less constant. A single curve of the general form given above can be fit to the experimental data obtained under these conditions [similar to curve F’ in Fig 1(b)]. The coordinates of the point where this curve would intersect the family of curves generated if both map parameters were manipulated indicate the home isometric contour alignment and the home value of the manipulated parameter [see Fig. 1(b)]. These coordinates can be estimated by solving for the value of the manipulated parameter where the instantaneous rate of change in home direction (i.e., the first derivative or “slope” of the curve) is maximum or, alternatively, where the second derivative of the equation (i.e., change in slope) is equal to zero.

The quantitative predictions of the map model outlined above are quite robust. Therefore, even if manipulation of a specific parameter of the magnetic field at the testing site is found to affect the direction of homing orientation, failure to find agreement between the predicted and actual measured
characteristics of the local gradient in the vicinity of the “home” site would falsify the hypothesis that the manipulated parameter was the basis for one of the coordinates of a bicoordinate map.

Finally, if subjects are collected from two home sites that are located in roughly the same direction from the testing site, but differ in the alignments of the local gradients of at least one of the map parameters, this difference should lead to predictable differences: (a) in the direction of homing orientation by subjects exposed to the ambient magnetic field at the testing site, (b) in the response to manipulation of the relevant map parameters at the testing site, and (c) in the corresponding estimates of the characteristics of the local gradients at the two sites derived from the map model (Fig. 1).

Testing the Predictions of the Bicoordinate Map Model

Tests of the magnetic map hypothesis using the graphical model of bicoordinate navigation require observations of the direction of homing orientation under a series of different values of a specific parameter of the magnetic field with other potential map parameters held constant. When artificial changes in the magnetic field are used (an alternative approach involving the use of natural geographic variation in the magnetic field is discussed below), the study organism must be able to obtain map information while confined to a restricted “laboratory” area where the magnetic field can be manipulated using stationary coils. Stationary coils allow production of precise changes in a specific parameter of the magnetic field, while leaving other parameters unchanged. In contrast to stationary coils, coils attached to the study organism vary in alignment as the organism moves, resulting in continuously and unpredictably varying changes in all parameters of the magnetic field (e.g., Walcott & Green, 1974).

The choice of an appropriate experimental system may also make it possible to greatly reduce, or eliminate, the possibility that experimental subjects have access to alternative (i.e., non-magnetic) source(s) of map information. For example, the likelihood that olfactory cues (Papi, 1976, 1990) could be used to derive map information instead of, or in addition to, magnetic cues can be greatly reduced if subjects can be displaced to a testing site under conditions that prevent access to natural odors (e.g., Wallraff & Sinsch, 1988, Phillips et al., 1995), and if subjects can be held and tested indoors or in enclosures that minimize access to outside air (Munro et al., submitted, in preparation; Phillips & Borland, 1994; Phillips et al., 1995). In some systems, when manipulation of a putative map parameter is found to affect homing orientation, experiments can be carried out to determine whether manipulation of this parameter also affects orientation behaviors that do not require map information (e.g., shoreward magnetic compass orientation of eastern newts; Phillips, 1987). Such experiments would provide a control for an effect on a component of the navigational system other than the map.

When selecting a study animal, the normal range of its movements should be an important consideration. Aeromagnetic surveys suggest that the geomagnetic field could serve as a source of map information for relatively long distance (i.e., greater than 50–75 km) and, at least at some locations, for relatively short distance (i.e., less than 5–10 km) movements. In general, however, the geomagnetic field is unlikely to be a reliable source of map information at intermediate distances (i.e., 10–50 km), e.g., the distances typically used in studies of pigeon homing. At these intermediate distances, the local and regional gradients of total intensity (the only magnetic field parameter for which aeromagnetic surveys are generally available) tend to be comparable in magnitude, but to vary in relative direction. Over this range of distances, therefore, an organism displaced in any direction relative to its home will tend to encounter values of total intensity that are both higher and lower than the home value (Lednor, 1982), i.e., the variation in total intensity would provide little, if any, useful information about geographic position relative to home. Therefore, a magnetic map that made use of total intensity (or any other magnetic parameter that exhibits a similar pattern of spatial variation) would generally be of little value at these intermediate displacement distances.

Spatial irregularities in the magnetic field may be less problematic at distances greater than 50–75 km (e.g., distances covered by many migratory birds) and also, at least at some locations, at distances less than 5 km (e.g., distances covered by many amphibians and reptiles). For example, aeromagnetic surveys suggest that local gradients of magnetic total intensity are relatively uniform within a 3–5 km radius of many of the ponds around Bloomington (IN, U.S.A.) where we have found a large population of eastern newts, that home using true navigation (Phillips & Borland,
migratory birds caught en route usually not the case, for example, when studying long distance displacement (see earlier discussion). Over longer distances (i.e., distances of more than 50–75 km), aeromagnetic maps suggest that the regional gradient of magnetic total intensity tends to predominate and could, in theory, provide information about geographic position for large scale movements, e.g., for a migratory bird attempting to locate its summer or winter range.

Many species of amphibians and reptiles that home over relatively short distances (i.e., distances of less than 5–10 km) are well-suited for tests of the magnetic map hypothesis. This is because large numbers of individuals can be collected from a single home site [e.g., a small pond in the case of some populations of the eastern newt (Gill, 1978, 1979; Phillips, 1987, Phillips & Borland, 1994); or a restricted area within a larger body of water in the case of young American alligators (Rodda, 1984a,b, 1985)]. The map model requires observations of the effects of varying the value of a putative map parameter or parameters on experimental subjects that are attempting to home to the same site (Fig. 1).

In addition, when the home site is known (which is usually not the case, for example, when studying migratory birds caught en route to their summer or winter range), the local values of the relevant magnetic field parameters in the vicinity of the home site can be measured for comparison with predicted values derived from the map model.

When studying an organism that moves over relatively short distances (e.g., many species of amphibians and reptiles), local magnetic topography should be an important consideration in the selection of a study population. The likelihood that individuals from a given population would be able to rely on magnetic map information will depend on characteristics of the local magnetic field gradient(s). Aeromagnetic maps suggest that in some areas local gradients of magnetic total intensity (and presumably other magnetic field parameters) are extremely weak and/or irregular and, therefore, would not provide a reliable source of map information. If the geomagnetic field provides the sole source of one or both coordinates of a bicoordinate navigational map, individuals collected from such areas should fail to exhibit map-based homing. Alternatively, if the geomagnetic field provides one source of map information and, in addition, there is a second, non-magnetic (e.g., olfactory) source of map information or an alternative mechanism for deriving geographic position (e.g., path integration; Wiltschko & Wiltschko, 1982; Rodda, 1984a, 1985), individuals collected from areas where the local magnetic gradient(s) are weak or irregular should fail to exhibit the changes in the direction of homing orientation predicted by the map model when exposed to different value(s) of the relevant magnetic field parameter(s).

To determine whether the geomagnetic field provides an independent source of map information when alternative sources of map or geographic position information are present, tests of individuals collected from sites where local gradients of the relevant magnetic field parameter(s) are suitable for deriving one or both map parameters would have to be carried out under conditions that exclude these alternatives (see earlier discussion).

In principle, it should be possible to apply the map model to homing orientation data obtained from a large number of different sites where the values of specific magnetic field parameters vary naturally (e.g., data from studies of regional patterns of “release site biases” exhibited by homing pigeons Columba livia; Windsor, 1975; Gruter et al., 1982; Ganzhorn, 1990). This would require precise measurements of the relevant magnetic field parameters from each of the sites. Moreover, in order to apply the map model, orientation data would have to be available from several sites where the values of one of the putative map parameters fell within a narrow range (i.e., where the value of this parameter would have a more or less constant value), while the value of a second putative map parameter varied over a range that spanned the home value of that parameter [see Fig. 1(b)]. This approach would only be successful, therefore, if the parameters underlying both of the actual map coordinates were included in the analysis. In contrast, when experimental manipulation of a specific magnetic field parameter is carried out at a fixed testing site where other potential map parameters (both magnetic and non-magnetic) are effectively constant, the map model can be used to determine whether the manipulated parameter provides one coordinate of a bicoordinate map even when a second putative map parameter has not been identified.

**Conclusion**

The graphical model presented here makes both qualitative and quantitative predictions about the
changes in homeward orientation that should occur when the value of one or both of the factors used to derive the coordinates of a bicoordinate “gradient” map are manipulated. Experiments investigating whether manipulation of magnetic field parameters such as inclination and total intensity produce changes in the direction of homing orientation that conform to the predictions of the graphical model will provide critical tests of whether these magnetic field parameter(s) serve as the basis for one or both coordinates of a navigational map.

I would like to thank Charles Baube, S. Chris Borland, Mark Deutschlander, Janette Fischer, Ursula Munro, and an anonymous reviewer for critical feedback on earlier drafts of this manuscript. Support was provided by NSF IBN 92-12102 and IBN 95-07826.

REFERENCES


GOULD, J. L. (1980). The case for magnetic sensitivity in birds and bees (such as it is). Amer. Sci. 68, 256–267.


J. B. PHILLIPS


