Evidence for the use of magnetic map information by an amphibian

Biology Department, Indiana University

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The question of whether animals navigate using ‘map’ information derived from one or more spatial gradients in the Earth’s magnetic field has been debated for half a century. Although there is evidence that certain animals possess the sensory abilities necessary to perceive at least two magnetic components that vary spatially, there previously has been no direct test of the use of magnetic map information by experienced adult migrants. Magnetic information could provide information about an animal’s geographic position along a single axis (‘unicoordinate map’) or could be part of a position-fixing system that provides positional information along two nonparallel axes (‘bicoordinate map’) with the second axis being derived from either magnetic or nonmagnetic cues. Here we report that adult eastern red-spotted newts, Notophthalmus viridescens, displaced approximately 45 km NNE of their home ponds oriented in the home direction when exposed either to the ambient magnetic field of the testing site, or to a 2\(^\circ\) increase in magnetic inclination (normally found further from the home ponds in the same general direction as the testing site). When exposed to a 2\(^\circ\) decrease in inclination resulting in a value that would normally be found on the other side of the home ponds from the testing site, however, newts reversed their direction of orientation. The same changes in magnetic inclination had no effect on shoreward magnetic compass orientation, which does not rely on map information. These findings provide support for two critical predictions of the magnetic map hypothesis, and suggest that information about geographic position along at least one axis relative to home may be derived from the magnetic field.

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derived from magnetic field components. A number of vertebrates appear to have the sensory capabilities necessary to detect spatial variation in one or more components of the magnetic field (Larkin & Keeton 1976; Rodda 1984a; Beck & Wiltschko 1988; Walcott 1991; Lohmann & Lohmann 1994, 1996). Until recently, however, critical tests of the magnetic map hypothesis have been lacking due to the inability to study map-based homing under controlled laboratory conditions where individual components of the magnetic field can be manipulated independently (Lohmann & Lohmann 1996; Phillips 1996).

The ability to manipulate one component of the magnetic field, while other potential map parameters (both magnetic and nonmagnetic) remain more or less constant, makes it possible to test several critical predictions of the magnetic map hypothesis. Failure to support any one of these predictions would falsify the hypothesis that the magnetic component being manipulated is used to derive map information (Phillips 1996).

1. Large symmetrical changes in the putative map parameter that result in values that are found on opposite sides of home should produce roughly opposite directions of homing orientation (Fig. 1), provided that the resulting values are within the range that the organism can use for map-based homing. It should be noted, however, that symmetrical changes in one map parameter that result in values falling on either side of the home value can result in perceived home directions that differ by angles that are appreciably less than 180° (Phillips 1996; and see Discussion), especially if the organism is using a bicordinate map. This is because the animal’s perceived position based on a bicordinate map will depend on both the value of the manipulated map parameter and that of the unmanipulated map parameter (Fig. 1).

2. Exposure to the same experimental treatments (as in prediction 1) should have no effect on forms of orientation that do not rely on map information (e.g. shoreward magnetic compass orientation of newts: Phillips 1987; or seasonal migratory orientation of young songbirds without previous migratory experience: Munro et al. 1997a).

3. When tests are carried out with small, incremental changes in the putative map parameter, the most dramatic effects on the direction (or strength) of homing orientation should occur at values close to the ‘home value’ (i.e. the value measured in the vicinity of the animal’s ‘home’; see Phillips 1996).

4. Exposure to altered values of the putative map parameter should produce corresponding changes in the direction of homing orientation that are consistent with the alignment of the local gradient in the vicinity of the animal’s home over the spatial scale that homing normally occurs (Phillips 1996).

Here we report experiments investigating the effects of exposure to changes in magnetic inclination on the shoreward compass and homing orientation of the eastern red-spotted newt, Notophthalmus viridescens, which test predictions 1 and 2 (above).

Our investigation of the use of map information derived from magnetic inclination by eastern red-spotted newts was prompted by several earlier findings. (1) Adult eastern red-spotted newts in many populations are migratory, leaving the water seasonally to avoid temperature extremes and migrating back into ponds at the beginning of the breeding season (Hurlbert 1969; Gill 1978, 1979). (2) Displacement experiments have demonstrated that a majority of adult male newts home back to the pond from which they were captured at the onset of the breeding season (Gill 1979). At these times of year adult male newts held under controlled laboratory conditions switch from shoreward compass orientation to homing orientation relative to the direction of the magnetic field (Phillips 1987; Phillips & Borland 1994). At two different testing locations (Ithaca, New York and Bloomington, Indiana, U.S.A.), newts from two pond directions at each location (distances of approximately 20–40 km) were held in tanks with at least two different shore directions (north, west and east in Bloomington, north and west in Ithaca). During the seasonal migratory period, the newts in each study oriented in the correct homeward directions relative to the magnetic field independently of the shoreward directions (Phillips 1987; Phillips & Borland 1994). Furthermore, the homing responses in these earlier experiments were consistent with the use of a bicordinate map (see Discussion). (3) Route-deprivation experiments indicate that the homeward orientation shown by adult newts during the seasonal migratory periods involves the use of map information obtained at the testing site, rather than path integration, and is exhibited under conditions where nonmagnetic sources of map information (e.g. odours, Papi 1990) are unlikely to be involved (Phillips et al. 1995). (4) Adult eastern red-spotted newts, as well as at least some other vertebrates, appear to have two independent magnetoreception systems: a light-dependent magnetic compass possibly mediated by a photoreceptor-based mechanism (Semm et al. 1984; Semm & Demaine 1986; Phillips & Borland 1992a, b; Wiltschko et al. 1993; Deutschlander et al. 1999a), and a nonlight-dependent mechanism mediated by permanent magnetic material, possibly magnetite, that appears to play a specialized role in the map component of homing (Phillips 1986; Semm & Beason 1990; Phillips & Borland 1994; Beason & Semm 1997; Beason et al. 1997; Munro et al. 1997a, 1997b). (5) Local magnetic field gradients at many locations are stronger and more uniform than the regional gradients and, thus, potentially provide a reliable source of map information for use during short-distance (<5 km) movements (Phillips 1996). Finally, (6) magnetic inclination and horizontal intensity have been implicated as possible sources of map information for short-distance movements in a study of young American alligators, Alligator mississippiensis, which have a range of movement similar to that of adult newts (Rodda 1984a).

METHODS

Experimental Subjects

We collected eastern red-spotted newts from a group of ponds in south-central Indiana (68.3–68.4° inclination)
and transported them ca. 45 km north-northeast (NNE) to our testing facility at Indiana University in Bloomington (68.55° N), well beyond their normal range of movement (i.e. 1–2 km, D. Gill, personal communication). Previous studies have demonstrated that newts from these ponds (as well as newts from a group of ponds in a different ‘home’ direction relative to our testing site) display true navigation under the conditions used in the present experiments (Phillips & Borland 1994; Phillips et al. 1995). Furthermore, because immature newts spend several years away from ponds as terrestrial ‘red efts’ before homing back to ponds as adults to reproduce, the

Figure 1. Four hypothetical grid systems (a–d) derived from gradients of two environmental factors. Solid and dashed lines labelled with Roman numerals (IV–XII) and letters (C–K), respectively, represent isolines of the two map factors that vary spatially. The animal’s home is indicated by +, while the testing site is indicated by a filled circle. Grey shaded lines indicate the isolines corresponding to the values of the two map parameters at the testing site. −Δ and +Δ indicate the changes in the values of the manipulated parameter to which the animals were exposed at the testing site. Hatched areas indicate the isolines corresponding to the altered values of the map parameter. Open circles A and B represent the perceived locations resulting from the two experimental manipulations. The value of the second (i.e. unmanipulated) map parameter is always that of the testing site. Consequently, the perceived locations (A and B) occur at the intersection of the isoline of the unmanipulated map parameter that passes through the testing site and those corresponding to the experimentally produced values of the manipulated map parameter. The location of the isolines is assumed to be determined by extrapolation based on the animal’s prior experience with the gradient of that map parameter in the vicinity of its home pond (see Wallraff 1991; Phillips 1996). Arrows indicate the perceived home direction at each of the sites. In (a)–(c) the gradient of the manipulated map parameter (solid lines) runs directly north-south, and the perceived home direction largely depends upon the alignment of the unmanipulated map parameter (dashed lines). Directions of homing orientation that differ by 180° are only predicted when the value of the unmanipulated parameter (dashed lines) is the same at both the home site and the testing site (as in b). In (c) and (d), the alignment of the unmanipulated map parameter (dashed lines) is the same, while that of the manipulated map parameter (solid lines) differs. A comparison of these two diagrams illustrates that under some conditions the alignment of the manipulated map parameter can vary over a fairly large range with relatively little effect on the perceived home directions.
adults used in the present study were assumed to have had sufficient experience during their natural movements to have learned the spatial pattern(s) of variation in potential map parameters. Newts were returned to their home ponds after testing.

**Experimental Design**

We exposed groups of newts to one of three different inclination conditions in both outdoor holding tanks and subsequent indoor test arena. We exposed controls to the ambient inclination of 68.5° at our testing site. We exposed experimental newts to an inclination of either 70.5° or 66.5°. The ±2° inclination change simulated a displacement of 200–400 km, depending on the steepness of the local magnetic gradient. An inclination of 70.5° is expected to be found somewhere in the hemicircle north of the pond, beyond the testing site. An inclination of 66.5° should be found somewhere in the hemicircle south of the home pond. For the sake of convenience, we refer to the 70.5° and 66.5° conditions as ‘simulated northward displacement’ and ‘simulated southward displacement’, respectively; however, it should be noted that these two directions are only approximations (see Fig. 1). We predicted that the control (68.5°) and simulated northward displacement (70.5°) groups should display a similar direction of orientation, while the simulated southward displacement (66.5°) group should display an approximately opposite direction of orientation.

**Homing Experiments**

Newts show homeward orientation in the laboratory when collected during the seasonal periods when local populations show migratory behaviour (November–December and May–June). In the present experiments we held newts in two different outdoor tanks (see Deutschlander et al. 2000 for tank description) with shore directions (270° and 360°) that differed from the home direction (207°) so that we could distinguish between homeward and shoreward orientation. The newts were held in outdoor tanks for 4–7 days prior to testing. We manipulated the water temperature of the outdoor tank to increase the strength and unimodality of the homeward orientation (Phillips 1986). This involved maintaining the tank water temperature between 12–18 °C, with less than 2 °C variation within a 24-h period, and less than 3–4 °C variation during the training period (Phillips 1986, 1987; Phillips & Borland 1992a, b). On nights prior to testing, we cooled the water in the outdoor tank to 2–4 °C. At sunrise we elevated the water temperature rapidly to 25 °C, and then more slowly to 30 °C. We then maintained the water temperature at 30 °C for the duration of the test (±0.5 °C). Newts in the Bloomington area have been found living in natural bodies of water at temperatures as high as 34 °C (Phillips & Borland 1994).

**Shoreward Experiments**

Newts collected outside the seasonal migratory periods show shoreward magnetic compass orientation in laboratory experiments (Deutschlander et al. 1999a, b, 2000; Phillips 1987; Phillips & Borland 1992a, b). As in the homing experiments, we held the newts in outdoor tanks with shore directions of 270° and 360° for 4–7 days prior to testing. We maintained the water temperature in the tanks between 18–22 °C, with less than 2 °C variation within a 24-h period, and less than 3–4 °C variation during the training period (Phillips 1986; Phillips & Borland 1992a, b). In the shoreward experiments, the water in the outdoor tank was not cooled down overnight prior to testing (Phillips 1986; Phillips & Borland 1992a, b). At sunrise on the day the newts were tested, we elevated the water temperature rapidly to 25 °C, and then more slowly to 31 °C. We maintained the water temperature at 31 °C for the duration of the test (±0.5 °C) (Phillips & Borland 1992b).

**Training Fields**

Changes in inclination were produced in the outdoor tanks by means of a four-element, cube-surface coil (Merritt et al. 1983), which surrounded each tank, including tanks holding controls. The coils were 182 cm on each side, and the region of the tank occupied by the newts, which was located near the centre of the cube coil, was 66 × 31 × 20 cm, a relatively small volume relative to the overall coil volume. The coil was aligned north–south and angled up towards north (see Fig. 2). The artificial field produced by the coils surrounding the outdoor tanks was approximately 2000 nT, or only about 4% of the ambient field. By adjusting the alignment and intensity of the artificial field, a resultant field was produced with the desired inclination, but little or no change in total intensity (Fig. 2). In the control condition we turned on the coil’s power supply but set the current to zero. Variation in total intensity was ±50 nT, a change of less than <0.1% of the ambient intensity, and did not differ significantly across treatments (Mann–Whitney U test: NS). The inclination of the altered fields varied by ±0.2° within the volume of the tanks occupied by newts, measured with a Develco three-axis magnetometer (model number 105395). This level of precision was possible because: (1) the coil design by Merritt et al. (1983) produces a highly uniform field (Kirschvink 1992), (2) the volume occupied by the newts was very small with respect to the overall coil volume and (3) the tank was centred within the coil, and therefore was located in the most uniform region of the coil’s magnetic field.

**Testing Facilities**

The Animal Orientation Research Facility at Indiana University was designed specifically for studies of magnetoreception and magnetotactic orientation. The building is constructed of largely nonmagnetic materials. The floor of the test room is uncoupled from the rest of the building to minimize vibrations and the walls and ceiling are heavily insulated to prevent the inside temperature from varying when the building utilities are turned off. Utilities were turned off during testing to minimize vibrations and electromagnetic disturbance.
adjacent room to observe the newt’s movements on a video monitor.

The fields in the indoor test arena were generated by means of five cube-surface coils (Rubens 1945). Two coils aligned orthogonally in the horizontal plane were used to produce the four symmetrical horizontal alignments of the magnetic field (Phillips 1987). Two additional, horizontally aligned cube-surface coils and a vertical cube-surface coil were used to increase or decrease the horizontal and vertical components (respectively) of the four fields to alter inclination with negligible change in total intensity (i.e. ± 50 nT, a change of <0.1% of the ambient intensity).

We manipulated the alignments and intensities of the horizontal and vertical components of the magnetic field to produce four symmetrical horizontal alignments of the magnetic field (i.e. magnetic north at north, east, south or west) with the same inclination to which the newts were exposed in the outdoor tanks, 70.5° or 66.5° (variation ± 0.1° measured at the centre of the arena).

**Testing Protocols**

For testing, we removed a newt from the shallow end of the training tank by grasping it gently by the base of the tail. We placed it in a small plastic transport container freshly rinsed with water from the training tank and placed the transport container inside a bag consisting of four layers of black cloth to exclude light, and then carried it to the testing room. Upon entering the testing room, we removed the newt from the transport box in total darkness and gently placed it in the release device from a constant direction that was the same in all tests. Newts that struggled violently or received rough handling at any time during transportation to the test arena were not tested. After placing the newt in the release device, the observer left the room. Curtains covering the exit door prevented light from entering the room while the observer was leaving. The arena was then illuminated by opening a shutter in the outer room. After a 60-s delay, the newt was released. We measured the newt’s directional response at the point at which it first contacted a 20-cm radius circle centred on the release device. The arena surface was thoroughly wiped with a damp sponge after each trial to eliminate directional olfactory cues. We discontinued trials if a newt did not leave the centre of the arena within 10 min, if the newt exited immediately (i.e. <1 s), indicating that it was startled by the lowering of the release device, or if the newt did not reach the 20-cm radius circle in 15 min (Phillips 1986; Phillips & Borland 1992b, 1994).

Pooling the magnetic bearings from an approximately equal number of newts tested in each of the four field alignments made it possible to factor out any consistent nonmagnetic bias (Phillips 1986).

A typical test lasted 4–6 h and yielded two to eight bearings. Normally, a similar number of newts in each test failed to meet the time criterion described previously. Therefore, to achieve the balanced design necessary to factor out any nonmagnetic bias (Phillips 1986) it was
necessary to pool data from a series of tests carried out under the same experimental conditions, each involving a new group of newts.

We analysed the data according to the procedures in Batschelet (1981). We determined significance of individual distributions by the Rayleigh test (95% confidence limits show the region of error for the mean vector bearing) and we made comparisons between distributions using the Watson $U^2$ test (Batschelet 1981).

### RESULTS

The newts exposed to the 68.55° (controls) and 70.5° (simulated north displacement) inclination conditions showed significant orientation in the homeward direction. The two distributions were not significantly different (Watson $U^2$ test: $U^2=0.068$, NS; Fig. 3, Table 1). In contrast, newts exposed to the 66.5° (simulated southward displacement) inclination condition showed

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**Table 1. Homing orientation data**

<table>
<thead>
<tr>
<th>Shore direction</th>
<th>Home direction</th>
<th>N</th>
<th>Deviation from home</th>
<th>Deviation from shore</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>70.5°</td>
<td>270°</td>
<td>24</td>
<td>210°+3°</td>
<td>−60°</td>
<td>0.520</td>
<td>0.001</td>
</tr>
<tr>
<td>360°</td>
<td>207°</td>
<td>21</td>
<td>186°−21°</td>
<td>−174°</td>
<td>0.569</td>
<td>0.001</td>
</tr>
<tr>
<td>Combined*</td>
<td>207°</td>
<td>45</td>
<td>198°−9°</td>
<td>−5°</td>
<td>0.520</td>
<td>0.001</td>
</tr>
<tr>
<td>68.55°</td>
<td>270°</td>
<td>30</td>
<td>206°−1°</td>
<td>−64°</td>
<td>0.499</td>
<td>0.001</td>
</tr>
<tr>
<td>360°</td>
<td>207°</td>
<td>32</td>
<td>187°−20°</td>
<td>−173°</td>
<td>0.348</td>
<td>0.025</td>
</tr>
<tr>
<td>Combined*</td>
<td>207°</td>
<td>62</td>
<td>198°−9°</td>
<td>−5°</td>
<td>0.420</td>
<td>0.001</td>
</tr>
<tr>
<td>66.5°</td>
<td>270°</td>
<td>12</td>
<td>52°+155°</td>
<td>+142°</td>
<td>0.533</td>
<td>0.031</td>
</tr>
<tr>
<td>360°</td>
<td>207°</td>
<td>20</td>
<td>60°−147°</td>
<td>+60°</td>
<td>0.429</td>
<td>0.023</td>
</tr>
<tr>
<td>Combined*</td>
<td>207°</td>
<td>32</td>
<td>56°−151°</td>
<td>−3°</td>
<td>0.470</td>
<td>0.001</td>
</tr>
</tbody>
</table>

$N$: number of newts in treatment; $\phi$: mean vector bearing of pooled distribution of magnetic bearings; $r$: mean vector length; $P$: probability, Rayleigh test (Batschelet 1981).
significant orientation in approximately the opposite direction; 95% confidence limits include the direction opposite home as well as the directions opposite the mean vector bearings of newts tested in inclinations of 68.5° and 70.5°. Furthermore, the distribution of magnetic bearings from newts tested in the 66.5° condition was significantly different from that of newts tested in either the 68.5° condition or the 70.5° condition (Watson U² test: 68.5° versus 66.5°: U²=0.06, NS; 70.5° versus 66.5°: U²=0.044, NS; Baschelet 1981). These findings indicate that the newts’ magnetic compass was unaffected by the changes in magnetic inclination (Table 2).

**DISCUSSION**

Our findings support two critical predictions of the magnetic map hypothesis. Exposure to values of magnetic inclination on either side of the value at the newts’ home pond produced roughly opposite directions of homing orientation (prediction 1, see Fig. 1), but had no effect on shoreward magnetic compass orientation (prediction 2). Furthermore, since the inclination at the testing site was higher than that of the home ponds, a further increase in inclination (i.e. in the 70.5° condition) would be expected to occur at locations on the same side of the home ponds as the testing site but at a greater distance. In contrast,

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**Table 2. Shoreward compass orientation data**

<table>
<thead>
<tr>
<th>Shore direction</th>
<th>Home direction</th>
<th>N</th>
<th>φ</th>
<th>Deviation from home</th>
<th>Deviation from shore</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>70.5°</td>
<td>270°</td>
<td>8</td>
<td>254°</td>
<td>+47°</td>
<td>−16°</td>
<td>0.74</td>
<td>0.008</td>
</tr>
<tr>
<td>360°</td>
<td>207°</td>
<td>8</td>
<td>356°</td>
<td>+149°</td>
<td>−4°</td>
<td>0.575</td>
<td>0.064</td>
</tr>
<tr>
<td>Combined*</td>
<td>207°</td>
<td>16</td>
<td>349°</td>
<td>−11°</td>
<td>0.650</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>68.5°</td>
<td>270°</td>
<td>7</td>
<td>290°</td>
<td>+83°</td>
<td>+20°</td>
<td>0.630</td>
<td>0.057</td>
</tr>
<tr>
<td>360°</td>
<td>207°</td>
<td>10</td>
<td>357°</td>
<td>+150°</td>
<td>−3°</td>
<td>0.504</td>
<td>0.079</td>
</tr>
<tr>
<td>Combined*</td>
<td>207°</td>
<td>17</td>
<td>8°</td>
<td>+8°</td>
<td>0.544</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td>66.5°</td>
<td>270°</td>
<td>8</td>
<td>255°</td>
<td>+48°</td>
<td>−15°</td>
<td>0.665</td>
<td>0.025</td>
</tr>
<tr>
<td>360°</td>
<td>207°</td>
<td>9</td>
<td>10°</td>
<td>+163°</td>
<td>+10°</td>
<td>0.504</td>
<td>0.104</td>
</tr>
<tr>
<td>Combined*</td>
<td>207°</td>
<td>17</td>
<td>357°</td>
<td>−3°</td>
<td>0.566</td>
<td>0.003</td>
<td></td>
</tr>
</tbody>
</table>

N: number of newts in treatment; φ: mean vector bearing of pooled distribution of magnetic bearings; r: mean vector length; P: probability, Rayleigh test (Batschelet 1981).

*Combined, pooled distribution of magnetic bearings rotated so that shore directions coincided at 360°.

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**Figure 4.** Effects of changes in magnetic inclination on the shoreward magnetic compass orientation of newts. Magnetic compass orientation of newts exposed to (a) a 2° increase in magnetic inclination; (b) ambient magnetic inclination; and (c) a 2° decrease in magnetic inclination. There were no significant differences between any of the distributions (Watson U² test: a versus b: U²=0.07, NS; b versus c: U²=0.06, NS; a versus c: U²=0.044, NS; Baschelet 1981). Magnetic bearings were pooled from each of the four magnetic field alignments used in testing, and rotated so that the shore direction is at the top of each distribution (360°). ◆: Bearings for newts held in an outdoor tank with a shoreward direction to the west (270°); •: bearings for newts held in an outdoor tank with a shoreward direction to the north (360°).
an inclination of 66.5° would be expected to occur at locations on the other side of the home ponds from the testing site. Therefore, the finding that newts exposed to the 66.5° inclination, rather than those exposed to the 70.5° inclination, showed a significant difference in orientation relative to controls, is also consistent with the magnetic map hypothesis. Although the mean vector bearing of the 66.5° group was not exactly opposite that of the 68.55° and 70.5° groups, the 95% confidence limits include the opposite directions; indeed a deviation of 180° would only be expected if the newts were relying on a unicoordinate map (see below), or alternatively, if the value of an additional (unmanipulated) factor used to derive a second map coordinate was the same at both the testing site and at the home ponds (see Fig. 1b).

The absence of an effect of either inclination condition on the newts’ shoreward magnetic compass response supports the conclusion that the difference in the homing orientation of newts in the 70.5° and 66.5° groups occurred because their perception of geographic position placed them on different sides of home. These findings provide evidence that magnetic inclination, or one of its components (i.e. vertical or horizontal intensity), may be used to derive map information, and may provide one coordinate of a navigational map. This is consistent with earlier evidence that newts are capable of map-based homing (Phillips et al. 1995; and see below). If the newts had relied on route-based cues to establish their geographic position relative to home (e.g. ‘path integration’), the 2° decrease in inclination (Fig. 3c) should not have affected their choice of home direction.

It should be noted, however, that we have not demonstrated responses to the extremely small changes in magnetic inclination that newts would have to detect in order to use a magnetic map within their normal range of movement (1–2 km), that is, changes approximately 100 times smaller than were used in the present experiments. Producing such small changes in inclination reliably with existing coil systems is not yet feasible. However, experiments are underway using progressively smaller changes in magnetic inclination to determine whether the reversal in the direction of homing orientation occurs near the ‘home value’ of magnetic inclination, as the map model predicts (prediction 3). In addition, we have recently initiated an attempt to map magnetic inclination in the vicinity of the newts’ ponds to determine whether there is the necessary correspondence between the newts’ behaviour in the laboratory setting and the gradient around the home ponds (prediction 4). The difficulty of making such measurements, which are likely to require several years of work with sophisticated instrumentation, underscores the extraordinary level of precision with which newts would have to measure the spatial variation in magnetic inclination in order to derive map information.

Short-term temporal variation in the geomagnetic field (occurring over time scales of hours to days) could further complicate the use of magnetic inclination for navigation (Phillips & Deutschlander 1997). However, newts could increase the accuracy of map measurements by taking readings at dawn or dusk, or during the night (when the field is most stable), or average multiple readings over extended periods of time, as suggested by Rodda’s (1984a) findings from young American alligators.

Variation over months to years potentially creates an even greater problem for newts navigating using the geomagnetic field (Courtillot et al. 1997). However, such change could be distinguished from spatial variation in the magnetic field during periods when newts remain at the same location, as may be the case for extended periods of time in the terrestrial ‘eti’ stage of the newt, and/or might be factored out of estimates of geographic position if the change is regular over the time scale that newts may remain away from ponds.

Is There a Second Map Coordinate?

The question remains whether our findings point towards the use of a bicoordinate map, or whether use of a unicoordinate map, or even nonmap information is sufficient to explain our results. Several factors point to the probable use of a second map coordinate: (1) In both New York and Indiana, newts with home directions that differed by about 90° showed significantly different directions of homeward orientation that coincided with the respective home directions. Such accurate position fixing is unlikely using just a unicoordinate map. A bicoordinate map could only explain these findings in the unlikely situation that the local gradients at the four pond sites (two in New York, and two in Indiana) were all aligned in the same relationship to the testing sites (i.e. the gradient at each of the pond sites was aligned parallel to the direction of the testing site, with the value of the map parameter, that is, the inclination or one of its components, increasing towards the testing site). Since the pond/testing site directions differed by 90° both in Indiana and New York, this is indeed unlikely. (2) An alternative strategy of combining a unicoordinate map with nonmap information such as path integration is also unsatisfactory since the earlier route-deprivation experiment carried out in Indiana demonstrated that preventing newts from having access to directional information during displacement from the home pond (which would be necessary for path integration), did not impair the homing orientation of newts from either of two home sites that differed in direction by 90° (Phillips et al. 1995). (3) The changes in inclination used in this experiment are too large to have ever been experienced by the newts, whose normal range of movement is 1–2 km (D. Gill, personal communication). The 2° inclination change is approximately two orders of magnitude greater than the change in inclination expected over such a distance (based on the regional gradient). So newts could not have homed using pilotage, based on a familiar inclination value (i.e. a magnetic ‘landmark’) encountered during their normal movements. Thus, although the findings from this study are consistent with the use of either unicoordinate or bicoordinate map information, the more likely explanation is that magnetic inclination (or one of its components) provides one coordinate of a bicoordinate map.
Future Directions

In addition to testing the effects of changes in other magnetic field components to determine their role (if any) in providing a second map coordinate, it will also be of considerable interest to study the homing of newts collected from other sites, because local gradients may differ from the regional gradient in both steepness and direction (Phillips 1996). At some localities, the local gradients may not be regular enough to provide reliable information about geographic position, raising the possibility that newts may not be able to home at these sites, or that they home using alternative sources of sensory information and/or homing mechanisms (e.g. path integration; Wallraff 1980, 1990; Rodda 1984a; Papi 1990). Therefore, comparison of the homing behaviour of newts collected from different localities would be expected to show that newts make flexible and opportunistic use of more than one type of homing mechanism depending on local conditions, as also appears to be the case in birds (Wiltschko et al. 1989; Walcott 1992). In addition, mapping of the spatial variation in the magnetic field around pond sites is needed, because differences in the direction of local and regional gradients should result in predictable errors in the direction of homing orientation when newts are displaced beyond the range of the local gradient; local field mapping will also provide information that can be used to help identify other potential map parameters (Phillips 1996).

In summary, the findings reported here provide the first direct experimental support for the magnetic map hypothesis in experienced adult migrants (see also Beck & Wiltschko 1988; Lohmann & Lohmann 1996). Given the extraordinary precision of measurement that would be required for newts to derive map information from the magnetic field and the problems caused by spatial and temporal variation, however, additional tests of the magnetic map hypothesis are clearly needed (Phillips 1996). Further investigation of the geomagnetic field’s role in animal navigation will help to resolve one of the most enduring mysteries in animal behaviour, the nature of the geographic position or ‘map’ sense.

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References


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


