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## Behavioral titration of a magnetic map coordinate

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**Abstract** Spatial variation in the inclination of the geomagnetic field has been implicated in the map component of homing by eastern red-spotted newts *Notophthalmus viridescens*. Here we show that when newts are exposed to small changes in magnetic inclination, the most dramatic effects on homing orientation occur at values close to the ‘home value’, as predicted by the magnetic map hypothesis (Phillips 1996). Newts reverse the direction of homing orientation over a range of inclination of  $0.5^\circ$  spanning the home value, providing further evidence that magnetic inclination or one of its components (i.e., vertical or horizontal intensity) is used to derive map information.

**Keywords** Magnetic navigation · Migration · Magnetoreception · Homing

### Introduction

There is growing evidence for the involvement of the geomagnetic field in the ‘map’ or geographic-position sense of vertebrates (e.g., alligators, Rodda 1984; newts, Phillips 1986a; Phillips and Borland 1994; Fischer et al.

2001; sea turtles, Lohmann et al. 2001; songbirds, Munro et al. 1997a, 1997b; Beason and Semm 1996; Fischer et al. 2002; and homing pigeons, Beason et al. 1997). In an earlier study, we showed that newts deprived of directional magnetic, olfactory, visual and inertial cues during displacements of 20–40 km from their home pond were able to accurately orient in the home direction using ‘map’ information obtained at the testing site (Phillips et al. 1995). Furthermore, newts exhibited homing orientation towards ponds on both the north-south and east-west axes, suggesting that they may have a bicoordinate map (Phillips 1987; Phillips and Borland 1994; Phillips et al. 1995).

Fischer et al. (2001) obtained evidence that newts use natural spatial variation in magnetic inclination to derive at least one map coordinate. In Fischer et al.’s experiment, newts were displaced from their home ponds 42 km north-northeast to a testing site (home direction =  $207^\circ$ ) where the inclination is slightly steeper than that measured in the vicinity of their home ponds. When exposed to an artificial  $+2^\circ$  change in magnetic inclination that should occur at a location in the same general direction as the testing site, but at a much greater distance, the newts exhibited homing orientation (Fig. 1A) that was indistinguishable from controls tested in the ambient magnetic field (Fig. 1B). In contrast, when newts were exposed to a  $-2^\circ$  change in magnetic inclination that should occur at a location on the other side of the home pond, they oriented roughly opposite the home direction (Fig. 1E). Identical changes in inclination had no effect on shoreward magnetic compass orientation, which does not require map information, suggesting that the change in the direction of homing orientation in Fig. 1E was an effect on the map, rather than compass, component of homing (Fischer et al. 2001).

Although the findings reported by Fischer et al. (2001) provide support for the magnetic map hypothesis, it should be emphasized that use of magnetic map information for short distance homing (i.e., 1–2 km) would place extraordinary demands on the nervous

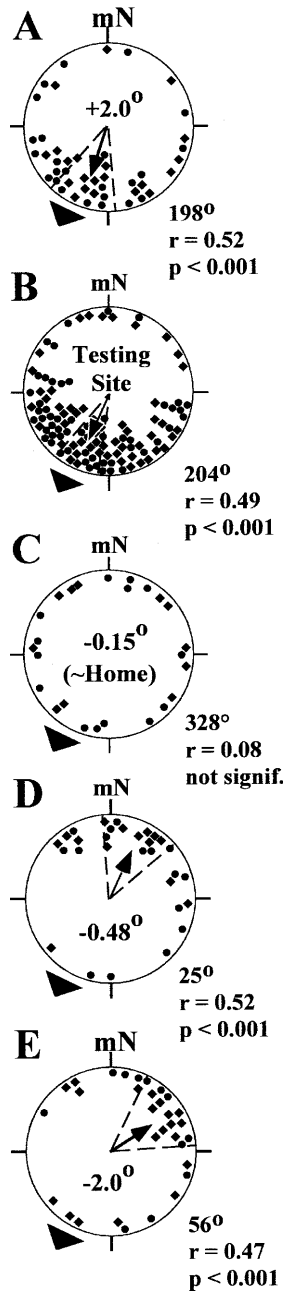
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system. Spatial variation in the magnetic field is extremely weak, i.e., total intensity varies on average only  $3\text{--}5\text{ nT km}^{-1}$  (0.01%) and inclination on average only about  $0.01^\circ\text{ km}^{-1}$ , and could only be detected by comparing successive measurements obtained at different locations (Phillips 1996; Phillips and Deutschlander 1997). In addition, regular temporal variation occurring during the daylight hours, magnetic storms, long-term “secular” changes, and spatial irregularities in the magnetic field make detection of magnetic gradients even more difficult (Lednor 1982; Phillips 1996; Phillips and Deutschlander 1997; Courtillot et al. 1997). In areas where magnetic gradient(s) are too weak and/or irregular to provide reliable map information, magnetic navigation would not be possible and newts would have to

rely on other cues/strategies to derive their geographic position relative to home (e.g., path integration). Given these difficulties, a convincing case for the use of a map coordinate derived from magnetic inclination, requires support from multiple experiments testing all of the critical predictions of the magnetic map hypothesis (Phillips 1996; Fischer et al. 2001). In the present experiments, newts from the ponds used by Fischer et al. (2001) were exposed to small decreases in inclination resulting in a value either close to or slightly less than the home value. The magnetic map hypothesis predicts that changes in a putative map coordinate should have the most dramatic effect on homing at values closest to the home value (Phillips 1996). Moreover, at the home value, homing orientation should be distinct from that exhibited at extreme values of the map coordinate (e.g., Fig. 1A, E) and, for animals relying on a bicoordinate map, should depend on the value of the second (as yet unidentified) map coordinate. Newts should be disoriented if the value of a second map coordinate also equals the home value<sup>1</sup>, while they should exhibit an intermediate direction of homing orientation if the second map coordinate indicates a location other than home (Phillips 1996).

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<sup>1</sup>In practice, disorientation is likely when the values of both map coordinates approximate the home values because variation in the altered fields in the holding tanks should result in uncertainty and/or differences between individuals (depending on where in the tank they measure the magnetic field) in their perceived location relative to home.

## Materials and methods

Adult male newts were collected during the seasonal migratory periods from ponds 42 km south-southwest of our testing site (home direction = 207°). The value of inclination in the vicinity of the ponds was  $0.17 \pm 0.04^\circ$  lower than the value in the holdings tanks at our testing site. A detailed description of holding and testing procedures can be found in Fischer et al. (2001). Briefly, newts were held for 4–7 days in water-filled, outdoor tanks at a temperature of 14–16°C. Controls were exposed to the ambient inclination and total intensity of the testing site. In the experimental conditions, the same cube-surface coils used by Fischer et al. (2001) were used to expose the newts to changes in magnetic inclination of either  $-0.15 \pm 0.03^\circ$  or  $-0.48 \pm 0.04^\circ$ . The total intensities of the resulting fields differed by less than 30 nT from that of the ambient field at the testing site, were consistently higher than the values measured in the vicinity of the newts' home ponds, and did not differ significantly between treatment groups ( $P > 0.20$ , Mann-Whitney  $U$ -test).

During the night prior to testing, newts in the outdoor tank were exposed to a rapid drop in water temperature to 1–2°C. The following morning, the tank water was rapidly elevated to a temperature of  $30 \pm 0.5^\circ\text{C}$ . These manipulations of water temperature have been shown to increase the strength of homing orientation (see Phillips 1987 for discussion of the role of temperature fluctuations in triggering the newt's homing response). Newts were then removed from the tank and tested individually in a terrestrial, visually-symmetrical, indoor arena in one of four horizontal alignments of the magnetic field (magnetic north at north, east, south or west), which matched the values of inclination and intensity experienced by the newts in the outdoor holding tanks. The arena surface was thoroughly wiped with a damp cloth between trials to eliminate any directional olfactory cues. Data were analyzed after pooling the magnetic bearings from an approximately equal number of newts tested in one of the four magnetic field alignments (each newt was tested only once) to factor out any consistent non-magnetic bias from the pooled distribution of magnetic bearings (Phillips 1986b).

## Results

Controls exposed to the ambient magnetic field of our testing site oriented in the homeward direction ( $213^\circ$ ,  $r = 0.57$ ,  $n = 42$ ,  $P < 0.001$ ; data included in Fig. 1B). Newts exposed to a change in inclination of  $-0.15 \pm 0.03^\circ$ , resulting in values that overlapped the home value, failed to exhibit a consistent direction of orientation (Fig. 1C). In contrast, newts exposed to a change in inclination of  $-0.48 \pm 0.04^\circ$ , resulting in values slightly lower than the home value, reversed their direction of orientation relative to controls. Thus, the reversal in orientation occurred over a range of approximately  $0.5^\circ$  spanning the home value (Fig. 1B versus D,  $P < 0.001$ , Watson  $U^2$ -test), while there was no difference ( $P > 0.10$ ) in the orientation of newts exposed to values differing by  $1.5^\circ$  (Fig. 1D versus E) and  $2.0^\circ$  (Fig. 1A versus B) that did not span the home value.

## Discussion

The findings shown in Fig. 1 are consistent with the predictions of the magnetic map hypothesis. Since the value of magnetic inclination at our testing site is steeper

than that at the newts' home pond, a further increase in inclination should result in a perceived geographic position in the same general direction from the home ponds, but at a greater distance and, thus, should cause newts in this condition to exhibit homing orientation that differs least from controls (Fig. 1A). In contrast, a decrease in inclination that results in a value that is less (i.e., shallower) than the home value should result in a perceived location on the other side of the home ponds from the testing site (although not necessarily in precisely the opposite direction; Fischer et al. 2001), resulting in homing orientation that differs most from controls (Fig. 1D, E). In addition, the change in homing orientation per unit change in the value of magnetic inclination should be greatest near the home value (Fig. 1B–D). At a value that approximates the home value, newts should either exhibit a direction of orientation that is intermediate between the directions exhibited by newts exposed to extreme values of the map coordinate (Fig. 1A, E), or be disoriented as they are in Fig. 1C (Phillips 1996). The home value, therefore, should fall within the range of values to which the newts in Fig. 1C were exposed (i.e.,  $-0.15 \pm 0.03^\circ$ ), which is in good agreement with the value actually measured in the vicinity of their home ponds (i.e.,  $-0.17 \pm 0.04^\circ$ ). These findings provide further evidence that magnetic inclination or one of its components (i.e., horizontal or vertical intensity) is used to derive information about geographic position. However, because of the unprecedented precision of measurement required for newts to use magnetic navigation for homing from distances of 1–2 km, a convincing case for magnetic navigation will require additional critical tests of the magnetic map hypothesis (Phillips 1996).

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## References

- Beason RC, Semm P (1996) Does the avian ophthalmic nerve carry magnetic navigational information? *J Exp Biol* 199:1241–1244
- Beason RC, Wiltschko R, Wiltschko W (1997) Pigeon homing: effects of magnetic pulses on initial orientation. *Auk* 114: 405–415
- Courtyllot V, Hulot G, Alexandrescu M, Mouël JL le, Kirschvink JL (1997) Sensitivity and evolution of sea-turtle magnetoreception: observations, modeling and constraints from geomagnetic secular variation. *Terra Nova* 9:203–207
- Fischer JH, Freake MJ, Borland SC, Phillips JB (2001) Evidence for the use of magnetic map information by an amphibian. *Anim Behav* 62:1–10
- Fischer JH, Munro U, Phillips JB (2002) Magnetic navigation by an avian migrant? In: Berthold P, Sonnenschein E, Gwinner E (eds) *Avian migration*. Springer, Berlin Heidelberg New York (in press)

- Lednor AJ (1982) Magnetic navigation in pigeons: possibilities and problems. In: Papi F, Wallraff HG (eds) Avian navigation. Springer, Berlin Heidelberg New York, pp 109–119
- Lohmann KJ, Cain SD, Dodge SA, Lohmann CMF (2001) Regional magnetic fields as navigational markers for sea turtles. *Science* 294:364–366
- Munro U, Munro JA, Phillips JB, Wiltschko R, Wiltschko W (1997a) Evidence for a magnetite-based navigational ‘map’ in birds. *Naturwissenschaften* 84:1–3
- Munro U, Munro JA, Phillips JB, Wiltschko W (1997b) Effect of wavelength of light and pulse magnetization on different magnetoreception systems in a migratory bird. *Austr J Zool* 45:189–198
- Phillips JB (1986a) Two magnetoreception pathways in a migratory salamander. *Science* 233:765–767
- Phillips JB (1986b) Magnetic compass orientation in the eastern red-spotted newt (*Notophthalmus viridescens*). *J Comp Physiol* 158:103–109
- Phillips JB (1987) Homing orientation in the eastern red-spotted newt (*Notophthalmus viridescens*). *J Exp Biol* 131:215–229
- Phillips JB (1996) Magnetic navigation. *J Theor Biol* 180:309–319
- Phillips JB, Borland SC (1994) Use of a specialized magnetoreception system of homing by the eastern red-spotted newt *Notophthalmus viridescens*. *J Exp Biol* 188:275–291
- Phillips JB, Deutschlander ME (1997) Magnetoreception in terrestrial vertebrates: implications for possible mechanisms of EMF interactions with biological systems. In: Stevens RG, Andrews LE, Wilson BW (eds) The melatonin hypothesis: electric power and the risk of breast cancer. Battelle Press, Columbus, Ohio, pp 111–172
- Phillips JB, Adler K, Borland SC (1995) True navigation by an amphibian. *Anim Behav* 50:855–858
- Rodda GH (1984) The orientation and navigation of juvenile alligators: evidence of magnetic sensitivity. *J Comp Physiol* 154:649–658