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Magnetic compass orientation in the Eastern red-spotted newt (*Notophthalmus viridescens*)

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Summary. Laboratory tests were carried out to examine the orientation behavior of adult Eastern red-spotted newts (*Notophthalmus viridescens*) to earth-strength magnetic fields. Groups of 30 to 40 newts were housed in water-filled, all-glass aquaria with an artificial shoreline at one end. The aquaria were located in a greenhouse or outdoors adjacent to the laboratory building, and aligned on either the magnetic north-south or east-west axis. Tests were carried out in an enclosed indoor arena. Newts were tested in four horizontal alignments of the magnetic field: the ambient magnetic field (magnetic north at North) and three altered fields (magnetic north rotated to East, South or West). Data were analyzed after pooling the magnetic bearings from all four conditions in such a way as to retain the component of the newts' orientation that was a consistent response to the magnetic field. Elevation of training tank water temperature was used to increase the newts' motivation to orient in the direction of shore. Newts exposed to a training tank water temperature of 33–34 °C just prior to testing exhibited consistent unimodal magnetic compass orientation. The direction of orientation was altered predictably by changing training tank alignment and location relative to the laboratory building. The results provide the first evidence of a strong, replicable magnetic compass response in a terrestrial vertebrate under controlled laboratory conditions. Further, the present study demonstrates that the Eastern newt is able to learn a directional response relative to the earth's magnetic field.

Introduction

Although sensitivity to the earth's magnetic field is a phylogenetically widespread sensory capability involved in many aspects of terrestrial vertebrate orientation, it has proven to be extremely difficult to elicit strong, replicable responses to magnetic stimuli under controlled laboratory conditions (for reviews see Able 1980; Ossenkopp and Barbeito 1978). Much of the evidence for magnetic compass orientation in terrestrial vertebrates has come from laboratory studies of the nocturnal migratory orientation of small passerines. At least seven species of nocturnal migrants have been shown to use the earth's magnetic field to determine a seasonally appropriate migratory direction (Beason and Nichols 1984; Bingman 1983; Emlen et al. 1976; see summary of earlier work by Wiltschko 1983). However, the magnetic orientation observed in these studies is relatively weak, and is only evident in second order analyses.

Outside of the laboratory, magnetic cues have also been shown to influence the orientation of homing pigeons released under overcast skies carrying small coils that alter the magnetic field around the bird's head (Visalberghi and Alleva 1979; Walcott and Green 1974). These studies demonstrate that magnetic cues affect the orientation of birds under natural conditions. Unfortunately, field experiments have the disadvantage that the alignment of the magnetic field can not be precisely controlled. As a consequence, critical tests can not be carried out to determine whether the altered magnetic field is influencing a compass sense, or some other component of the pigeon's navigational system. Moreover, under natural conditions, alternative sources of directional information are available to the birds, so that a nonspecific effect of the altered magnetic field on another sensory system can not be excluded.

In birds, the earth's magnetic field not only provides a source of simple-compass information, but appears to be involved in the calibration of other compass systems, e.g., the star compass (Wiltschko 1983; Wiltschko and Wiltschko 1976)

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and, possibly, the sun compass (Wiltschko et al. 1983; but see Phillips and Waldvogel 1982). Far less evidence exists for magnetic field sensitivity in other terrestrial vertebrate groups. Preliminary evidence indicates an ability to compass orient using the earth's magnetic field in a salamander (Phillips 1977) and a small mammal (Mather and Baker 1981). A correlation between variation in the homing orientation of juvenile alligators and the magnitude of small fluctuations in the geomagnetic field indicates that magnetic field sensitivity may also be present in reptiles (Rodda 1984). However, the claim of an unconscious magnetic sense in humans (Baker 1981) has not been substantiated in attempted replications by other researchers (e.g., Gould and Able 1981).

In contrast to studies providing support for the existence of magnetic sensitivity, many experiments have failed to obtain evidence for this sensory capability in a variety of vertebrates (e.g., Lemkau 1976; Kreithen and Keeton 1974; Griffin 1982). Undoubtedly, many other failures have not been published. A majority of these unsuccessful attempts to demonstrate magnetic sensitivity have two features in common: (1) subjects were not required to exhibit a natural behavior (e.g., a directional goal-oriented movement) and (2) little, if any, attention was paid to eliciting an appropriate motivational state in the experimental subjects. The elevated motivational state associated with long distance migration is undoubtedly one reason that studies of the migratory orientation of birds (earlier references) and teleost fish (Quinn et al. 1981; Quinn 1980; Tesch 1974) have been successful in demonstrating the use of magnetic cues.

The present study is an attempt to demonstrate a magnetic compass in the Eastern red-spotted newt (*Notophthalmus viridescens*) and, in doing so, to develop an experimental approach to elicit strong, replicable magnetic compass orientation in a terrestrially moving vertebrate under controlled laboratory conditions. The Eastern newt is a small salamander that is widely distributed in the eastern United States (Conant 1975). The larvae are aquatic. Adults are primarily aquatic, although in some populations adults leave the water seasonally to avoid extreme water temperatures (D. Gill, pers. comm.). In contrast, the intermediate juvenile ('eft') stage is fully terrestrial, leaving the water at the end of the larval stage and remaining on land as an inhabitant of the forest floor for up to 8 years before reentering a pond as an adult (Gill 1978, 1979, and pers. comm.; Healey 1973, 1974).

Amphibians have been used in a variety of studies examining the sensory basis of vertebrate orientation behavior because of the ease with which they learn to orient in a fixed compass direction with respect to a natural or artificial shoreline (Y-axis orientation; reviewed by Adler 1976; Ferguson 1971). Eastern newts that are housed in a training tank and exposed to moderate water temperatures exhibit weak *bimodal* magnetic orientation (Phillips submitted). In the present study, training tank water temperature was elevated just prior to testing, causing newts to exhibit consistent *unimodal* compass orientation in the direction of the artificial shoreline. Under natural conditions, high water temperature causes newts to leave the water and seek shelter in cooler refuges on shore (D. Gill, pers. comm.). Thus, manipulation of water temperature provided a convenient means of increasing the newts' motivation to orient in a shoreward direction.

Methods

Adult male newts were collected from ponds located 20.5 km East (100°) and 12 km South (190°) of the laboratory. The newts were transported to the laboratory in two liter, translucent plastic containers filled with 10 cm of pond water. The plastic containers were placed inside a styrofoam cooler that admitted diffuse light, but obscured landmarks and celestial cues. The newts were maintained in 110 l, all glass aquaria with shelter at one end (30 to 40 per tank). The aquaria were located in a greenhouse attached to the laboratory building or, during the warmer months, outdoors adjacent to the building, and exposed to the natural light-dark cycle. Prior to testing each group was placed in a training tank for a period of 5 to 7 days.

Two different training configurations were used: (1) tanks aligned along the magnetic north-south axis and located to the south of the laboratory building and (2) tanks aligned along the magnetic east-west axis and located to the west of the laboratory building. Preliminary tests indicated that the directionality of the newts' trained compass response was influenced by *both* the alignment of the training tank and its location relative to the laboratory building. Thus, in the present experiments, both of these factors were varied simultaneously to maximize the difference in orientation exhibited by newts exposed to the two training conditions.

The training tank design used in these tests is illustrated in Fig. 1. A bank of three to five heat lamps (depending on air temperature) was used to elevate the water temperature on the day of testing. During the 5 to 7 days before testing, the water temperature in the training tank was maintained between 18 and 27 °C. Early in the morning of the test day (6:00 to 7:00 EST), the heat lamps were turned on and testing was initiated once the water temperature reached 32 °C (usually between 9:30 and 11:30 EST). Voltage to the lamps was controlled by a rheostat and lowered once the water temperature reached 33.5° to maintain the temperature within a ±0.5° range. In the present series of experiments, each group of newts was exposed to elevated water temperature and tested only once after being housed in each training tank alignment (i.e., along the north-south or east-west axis).

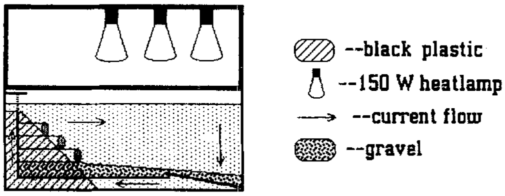

Fig. 1. Training tank design (side view). Training tanks consist of 110 l, all-glass aquaria with one end partially enclosed in black plastic. Four rows of progressively shorter 5 cm diameter plastic tubes provide an artificial shoreline at the enclosed end. The bottom of the tank is covered with coarse gravel that slopes up towards the shore. Heat lamps (150 W) located above the tank are used to elevate water temperature. An air-driven circulation system prevents a thermal gradient from forming and produces a current flowing from the shallow to the deep end of the tank

The newts were tested in an enclosed cylindrical arena (70 cm high × 80 cm diameter) located inside the laboratory building. The walls and roof of the arena were constructed of aluminum and wood, and were painted flat black. The floor was made of frosted plexiglass. The arena was illuminated by a light source consisting of a 12 V/100 W quartz/halogen bulb and two frosted Pyrex diffusers, positioned above a 4.5 cm diameter opening centrally located in the roof of the arena. The arena was enclosed in aluminum screening to provide electromagnetic shielding, and fluorescent lights in immediately adjacent rooms were turned off to reduce electromagnetic noise. The legs of the arena rested on a flagstone base that was isolated from vibrations.

For testing, a newt was removed individually from the training tank and placed in a clear plastic container that had been freshly rinsed with tank water. The newt was carried 2 to 3 m away from the tank along the tank axis with the plastic box held so that the newt faced in the direction of movement. The plastic container was then placed inside a light-tight bag made out of four layers of heavy black cloth and carried into the laboratory.

In the room used for testing, the newt was removed from the carrying container in total darkness and placed from a constant direction into a release device consisting of a small (8 cm high × 5 cm diameter) plexiglass cylinder in the center of the arena floor. After closing the top of the arena, the arena light was turned on. The release device was raised using a hydraulic mechanism, following a delay of 30 s. The newt's movements were observed by means of its silhouette which was visible through the frosted plexiglass floor of the arena and reflected in a mirror located beneath the arena. Prior to the beginning of each test, the arena was carefully leveled. Before the training tank water temperature reached 32 °C, two to four newts were tested in different alignments of the magnetic field (see below). This pretesting revealed any pronounced nonmagnetic bias in the test arena, which was then corrected by further adjustment of the slope of the arena floor or realignment of the light source.

Directional responses were recorded to 5° accuracy where the newt first contacted a circle of 10 cm radius. In preliminary tests, unimodal orientation was evident at both 10 and 30 cm. However, because the newts often remained in the center area for several minutes and then moved very slowly, the 10 cm criterion distance was used in order to increase the number of bearings that could be obtained from each group. The directional heading at 10 cm did not show a significant relationship to the direction that the animal was facing at the time of release, in fact, newts frequently circled one or more times before leaving the area under the release device.

A small number of newts that reached the outside of the arena (30 cm) in less than one minute were excluded from further analysis. In several earlier test series, the directional headings of newts scoring in less than one minute were randomly distributed. Most of these individuals were disturbed by the release device being raised and would freeze for 20 to 30 s and then move rapidly in a relatively straight line to the outside of the arena. In contrast, a majority of newts scoring in greater than one minute moved in short bursts (covering 3 to 5 cm) separated by pauses of a few seconds to several minutes, and often circled initially.

Each newt was tested only once in one of four magnetic field conditions: the ambient magnetic field (magnetic north at North) and three altered fields (magnetic north rotated to East, South or West). The three altered fields were produced by means of a doubly-wrapped cube-surface coil (Rubens 1945; see Fig. 2), and closely resembled the natural field in dip angle and total intensity (±5%; a Bell model #240 magnetometer was used to measure magnetic field strength and direction). The first individual was tested in magN = N, the next individual in magN = E, followed by one in magN = W and one in magN = S. The sequence of four magnetic field conditions was repeated using fresh, previously untested newts until the test was terminated (approximately one hour prior to sunset). If a newt did not reach the 10 cm criterion within the appropriate time interval, the next individual was tested in the same magnetic field condition. The sample size obtained from each group was determined by the number of newts that could be tested in one day. When the next test of a new group of newts was carried out, the sequence of magnetic field conditions was started where the previous test had left off. Consequently, data pooled from an entire test series included approximately equal numbers of bearings from newts tested in each of the four alignments of the magnetic field.

The advantage of this type of symmetrical design is that the data can be pooled by rotating the four distributions so that the magnetic norths coincide to factor out consistent nonmagnetic bias (Fig. 3). The pooled distribution retains the component of orientation that is a consistent response to the magnetic fields. Thus, it is unlikely that orientation evident in the pooled data is an artifact of a nonmagnetic directional cue.

Two tests (one in which the training tank was aligned north-south and located to the south of the laboratory building, and one in which the training tank was aligned east-west and located to the west of the laboratory building) were carried out double blind. One experimenter set the horizontal alignment of the field using remote switches located in an adjacent room; the order of the four horizontal fields (magnetic N = N, E, S or W) was determined using a random number sequence. The second experimenter carried in each newt from the training tank and recorded its directional response without knowing the alignment of the magnetic field.

Statistical procedures. The distribution of the pooled *magnetic* bearings from the four magnetic field conditions were analyzed according to the statistical procedures described in Batschelet (1981). Rayleigh's test was used to determine whether a distribution exhibited significant orientation. The V test was used to test for orientation with respect to a predicted direction. To determine whether the difference between two distributions was significant, the Watson U^2 test was used.

Results

Groups held in tanks aligned along the north-south axis and located to the south of the laborato-

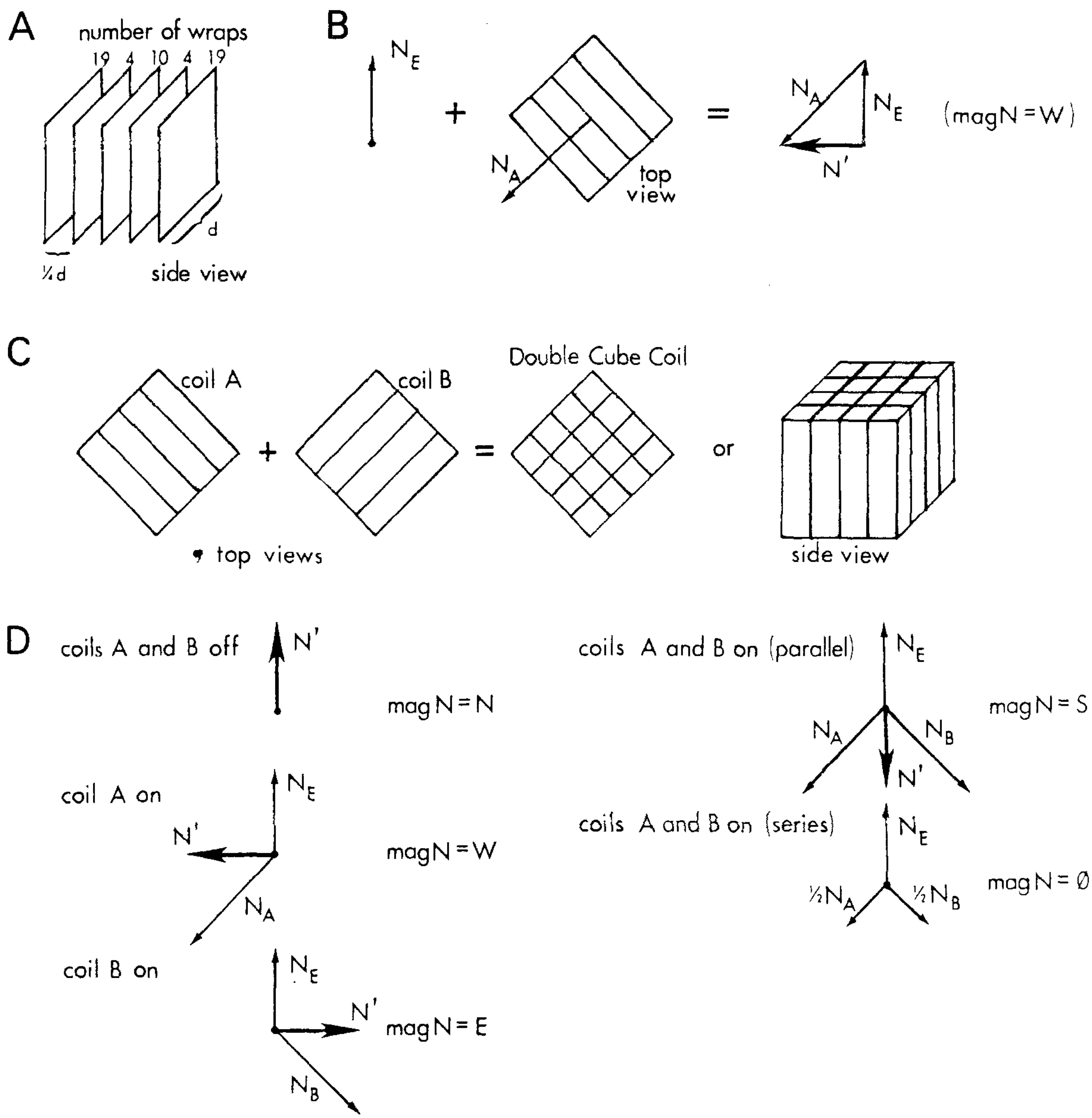

Fig. 2. Production of altered magnetic fields. **A** Schematic design of cube-surface-coil of Rubens (1945). Number of wraps in each coil element and their relative spacing is shown. **B** Coil alignment necessary to shift the horizontal magnetic component 90° counterclockwise. The coil is aligned to produce an artificial field N(A) 135° from geomagnetic north N(E). Increasing the artificial field strength until the resultant field (N′) is rotated 90° reproduces the horizontal intensity of the earth's magnetic field. Because the vertical component is unchanged, the vertical and horizontal magnetic vectors sum to produce the same inclination (or dip-angle) and total intensity as the natural field. **C** Double cube-coil, consisting of two perpendicularly aligned cube-coils wrapped on the same structural frame. **D** Equal resistances of the two coils (A and B) permit a constant setting of the voltage-regulated power supply to produce four altered horizontal magnetic components (including cancelling the horizontal component) in addition to the natural field

ry building exhibited northward magnetic orientation (tested February through August) (Fig. 4A). The compass direction of the pond in which the newts were collected did not influence this response; northward magnetic orientation was evident both in newts collected to the east (solid symbols) and to the south (open symbols) of the laboratory. Groups held in the east-west aligned tanks that were located to the west of the laboratory building exhibited unimodal eastward orientation (tested June through August; only newts collected from a pond located to the east of the laboratory were used in these tests) (Fig. 4B). The distributions of magnetic bearings of newts exposed to the two different training conditions were significantly different ($P < 0.05$, Watson U^2 test). In both

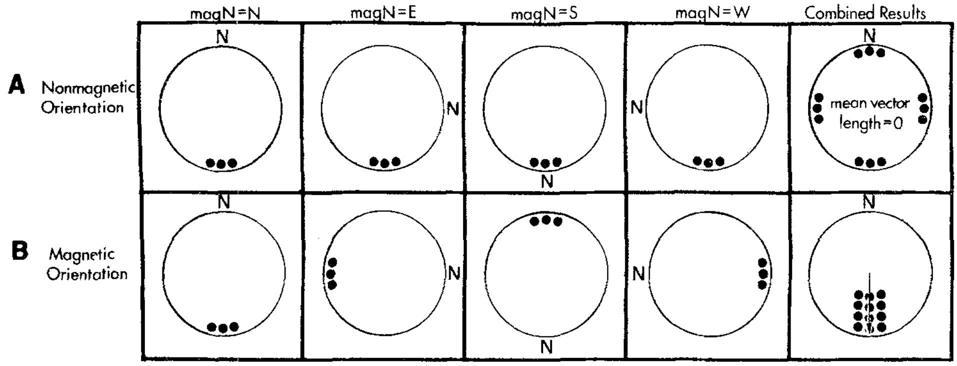

Fig. 3. Magnetic testing format. Equal numbers of newts are tested in each of the four horizontal alignments of the magnetic field (e.g., first newt in magN = N, second newt in magN = E, third in magN = S, fourth in magN = W, and then this sequence is repeated with four new animals). In subsequent analysis, data from the four conditions are combined by rotating the bearings so that the magnetic norths coincide (i.e., 90° is subtracted from the actual headings of newts tested in magN = E, 180° from the headings of newts tested in magN = S and 270° from the headings of newts tested in magN = W). If the newts are orienting with respect to a geographically-fixed (nonmagnetic) cue, the pooled data will be uniformly distributed **A**. However, if the newts are exhibiting a consistent directional response relative to the magnetic fields, the pooled data will be nonrandomly distributed **B**

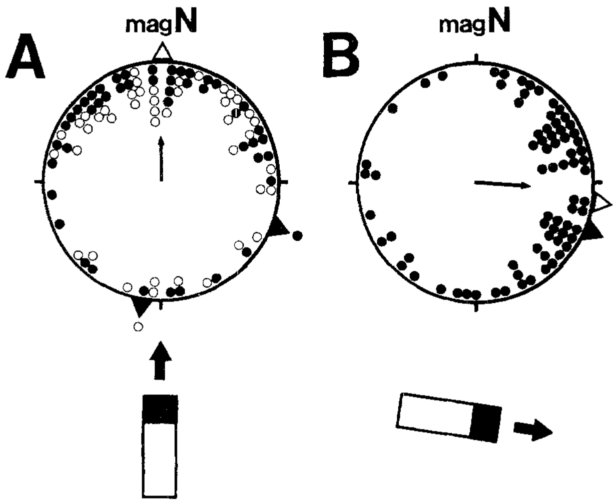

Fig. 4. Unimodal magnetic orientation. Each data point is the magnetic bearing of a single newt tested in one of the four horizontal alignments of the magnetic field (see Fig. 3). Arrow in the center of each distribution is the mean vector bearing calculated for the pooled data. An open arrowhead at the edge of each circle indicates the expected direction of orientation, a closed arrowhead indicates the compass direction from the laboratory to the pond in which the newts were collected. Inset below each distribution shows alignment of the training tank and direction from the training tank to the laboratory building (*solid arrow*). **A** Newts held in north-south tanks located to the south of the laboratory building, exhibited significant northward orientation (359°, $r = 0.39$, $P < 0.0001$, Rayleigh's test; $P < 0.0001$, V test with expected direction = 360°). This northward orientation was evident both in tests of newts collected from ponds located to the east (closed symbols – 354°, $r = 0.42$, $P = 0.0002$, $P(360°) < 0.0001$) and to the south of the laboratory (open symbols – 7°, $r = 0.37$, $P = 0.002$, $P(360°) = 0.0004$). **B** Newts held in east-west tanks located to the west of the building exhibited eastward orientation (92°, $r = 0.46$, $P < 0.0001$, $P(100°) < 0.0001$; only newts collected to the east of the laboratory were used in these tests)

cases, the newts exhibited a compass response that would have carried them away from water had they been on the shoreline of the training tank (insets Fig. 4).

Trained magnetic compass orientation was evident in the tests in which directional responses were recorded by an observer who was not aware of the alignment of the magnetic field. The magnetic bearings obtained in the double blind test of newts housed in a training tank aligned on the north-south axis (included in Fig. 4A) were significantly oriented in a northward direction (337°, $r = 0.50$, $n = 13$, $P = 0.03$, $P(360°) = 0.01$). The double blind test of newts housed in a tank aligned on the east-west axis (data included in Fig. 4B) yielded easterly orientation (75°, $r = 0.45$, $n = 15$, $P = 0.04$, $P(100°) = 0.01$). The two distributions were significantly different ($P < 0.05$, Watson U^2).

Discussion

Several factors contribute to the suitability of the Eastern newt as an experimental subject for laboratory studies of orientation behavior. A large number of studies have demonstrated that amphibians will exhibit compass orientation with respect to their home shoreline (Y-axis orientation) even after they have been transported long distances and are tested in an entirely different context (reviewed by Adler 1976; Ferguson 1971). In the present study, this delay in the response to the animal's immediate surroundings may have been an important factor in minimizing the disruptive effect of the test arena on the newts' behavior. Further-more, in contrast to other more highly mobile vertebrates, movements over very short distances, such as those made within the test arena, are behaviorally relevant to these small, slow-moving salamanders. Finally, the natural history of the Eastern newt suggested that water temperature could be used to increase the motivation of this species to orient in a shoreward compass direction.

Nevertheless, in order to obtain consistent responses to the magnetic field it was necessary to minimize nonmagnetic asymmetries in the test apparatus. A slope in the arena floor of as little as 1–2° produced a clear nonmagnetic bias in the newts' orientation. Nonmagnetic biases were also observed in response to a slight misalignment of the arena light source and to disturbances elsewhere in the laboratory building. This type of bias greatly increased the scatter in the pooled distribution of magnetic bearings. However, the use of the four horizontal magnetic field conditions (see Methods) made it possible to factor out any consistent nonmagnetic bias from the subsequent analysis.

In an earlier study, newts tested without exposure to elevated water temperature exhibited weak *bimodal* magnetic orientation. This bimodal response varied seasonally. During the winter months, the newts exhibited a trained compass response. However, at the onset of the Spring migration (April–early May in the Ithaca area), they switched to orienting along an axis coinciding with the direction of the pond in which each group was collected (Phillips, submitted). Bimodal magnetic orientation has also been reported in the savannah sparrow, *Passerculus sandwichensis* (Bingman 1981), and chum salmon, *Oncorhynchus keta* (Quinn and Groot 1984). Quinn and Groot, however, found that salmon switch from bimodal to unimodal orientation in response to an increased rate of nondirectional water flow in a radial flow tank, presumably because of an increased motivation to orient.

The unimodal orientation exhibited by newts in response to an elevation of water temperature is presumably an attempt to escape unsuitable water conditions. As in Quinn and Groot's (1984) study of migrating salmon, increasing the newts' motivation to orient caused them to switch from bimodal to unimodal orientation. Natural populations of newts respond to high water temperature (that may reach 40 °C during late summer in some parts of this species' range) by seeking shelter on shore beneath debris, tufts of vegetation, etc. Shade provided by this cover, coupled with evaporative cooling, maintains the ambient temperature as much as 10 to 12 °C below water temperature (D. Gill, pers. comm.). In the present series of experiments, the strength of the newts' response after exposure to high water temperature, as well as the absence of a seasonal change in behavior, reflects the overriding importance of responding to conditions that pose a direct threat to survival.

Conclusions

Eastern newts exhibit replicable individual responses to earth-strength magnetic fields under controlled laboratory conditions. The strength of these responses is comparable to that exhibited with respect to other better known sources of directional information (e.g., the sun, Ferguson 1971; polarized light, Taylor and Auburn 1978). Moreover, due to the disruptive effects of even slight nonmagnetic biases in the test arena on the newt's behavior, data from the present experiments may underestimate the accuracy of the newt's magnetic compass. Consequently, the earth's magnetic field is likely to be an important source of directional information for newts under natural conditions.

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