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ORIGINAL ARTICLE

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Magnetic compass mediates nocturnal homing by the alpine newt, *Triturus alpestris*

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Abstract Experiments were carried out to investigate the use of magnetic compass cues in the nocturnal homing orientation of the alpine newt *Triturus alpestris*. Tests were carried out at a site 9 km to the east–northeast of the breeding pond. Newts were tested at night in an outdoor circular arena that provided an unimpeded view of celestial cues, in one of four symmetrical alignments of an earth-strength magnetic field. In tests carried out under partly cloudy skies newts exhibited homeward magnetic compass orientation. Because the moon was visible in some trials, but obscured by clouds in others, we investigated whether the presence of the moon contributed to the scatter in the distribution of magnetic bearings. When the moon was visible, the distribution of magnetic bearings was more scattered than when the moon was obscured by clouds, although in neither case was the distribution significant due, in part, to the small sample sizes. Moreover, when the moon was visible, newts oriented along a bimodal axis perpendicular to the moon azimuth, suggesting that the presence of the moon may have affected the newts behavior. To provide a more rigorous test of the role of magnetic compass cues when celestial cues were unavailable, nocturnal tests were carried out during the following migratory season under total overcast. In the absence of celestial compass cues, the distribution of magnetic bearings exhibited highly significant orientation in the homeward direction. These findings indicate that newts are able to orient in the homeward direction at night using the magnetic compass as the sole source of directional information. Moon light altered the newts' behavior. However, this apparently resulted from the asymmetrical distribution of moon light in the testing arena, rather than the use of an alternative compass.

Keywords Celestial cues · Homing · Magnetoreception · Newt · Orientation · Triturus

Introduction

Homing ability is well established in the alpine newt *Triturus alpestris* (Joly and Miaud 1989, 1993; Diego-Rasilla 2003), and appears to be wide spread in amphibians (Twitty et al. 1966; Phillips 1987; Sinsch 1992). In earlier experiments, alpine newts showed homeward orientation in a visually symmetrical arena after displacements in two different directions from their home pond at distances well beyond their normal range of movement (i.e., 3–9 km, Diego-Rasilla 2003). Such homing ability requires both a source of directional ("compass") information, and a source of positional ("map") information. Previous work suggests that newts may determine compass direction from celestial cues (Landreth and Ferguson 1967; Diego-Rasilla and Luengo 2002; Diego-Rasilla 2003), and from the earth's magnetic field (Phillips 1986a, b, 1987; Phillips and Borland 1994).

Use of directional ("compass") information derived from the earth's magnetic field has been demonstrated in a wide variety of animals (Wiltschko and Wiltschko 1995; Walker et al. 2002; Diego-Rasilla 2004). Nevertheless, magnetic compass orientation by orienting urodeles has been only demonstrated in the Eastern red-spotted newt, *Notophthalmus viridescens* (Phillips 1986a, b,1987; Phillips and Borland 1994; Phillips et al. 1995; Deutschlander et al. 2000), and the cave salamander, *Eurycea lucifuga* (Phillips 1977), and none of these experiments have investigated the role of magnetic compass cues in nocturnal homing orientation.

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Although previous studies showed that the alpine newt could use olfactory cues for short distance (45–110 m) homing to its breeding pond (Joly and Miaud 1993), our previous work provided the first evidence for the use of light and magnetic cues for homing in *T. alpestris*, as well as establishing this species as an excellent model system for studies of long-distance homing ability (Diego-Rasilla 2003). Initial evidence that the earth's magnetic field plays a role in homing was obtained by disrupting the magnetic field with powerful magnets that produced steep gradients that are not present under natural conditions (Diego-Rasilla 2003). Consequently, the change in the newts' orientation behavior observed in these experiments could have been a response to magnetic field intensity or inclination, or to the spatial variation in one or more of these components, and could have resulted from an effect on the map and/or compass component of homing. The experiments reported here were carried out to characterize the use of magnetic compass cues by alpine newts for nocturnal homing orientation. In the present experiments, we used changes in magnetic field alignment, with little or no change in inclination and intensity, to investigate the role of the magnetic field in the compass component of nocturnal homing in both the presence (partly cloudy) and absence (complete overcast) of celestial cues.

Methods

Adult male newts were collected during their seasonal migratory period (Diego-Rasilla 2003) in 2003 and 2004 at the Natural Park of Saja-Besaya (Cantabria, northern Spain; 43°14′8″N, 4°9′59″W). Newts were captured in 2003 from a pond located 9.05 km Southwest (235°) of the testing site, whereas in 2004 newts were collected from a nearby pond located 9.06 km Southwest (232°) of the testing site. The two ponds were separated by 485 m. Newts were captured between 1600 and 1700 (GMT) in 2003 and between 1639 and 1710 (GMT) in 2004. Newts were then placed in completely covered, air tight plastic containers (31×21×17 cm) in which the water depth was 1 cm, kept inside a polyamide backpack, ensuring totally darkness, and transported to the terrestrial test arena by car. At the testing site, animals were held in open tanks (54×35×21 cm) aligned on the north–south geomagnetic axis. In 2003, tests began about 1 h after nightfall. Most of the animals used in the first half of the experiment were tested under a clearly visible moon. Because of an increase in cloud cover, however, most of the newts used in the second half of the test were tested with the moon obscured behind clouds. In 2004, tests were begun about 2 h after nightfall, but under conditions of total overcast. In both years, newts were returned to their pond after testing.

Newts were tested individually in a visually symmetrical terrestrial arena. The test arena consisted of a circular plastic container (57 cm diameter, 28 cm high). The floor and arena walls were thoroughly wiped with a damp cloth between trials to eliminate directional olfactory cues (Fischer et al. 2001), and then they were wiped dry using paper towels.

Just prior to testing, individual newts were placed for 5 min in opaque plastic containers (34×24×16 cm) in which the water depth was 1 cm. They were then put in the center of the arena beneath an opaque, cylindrical plastic container (9.5 cm diameter, 14.5 cm high). They were held in the container for 1 min to overcome effects of handling before the cover was lifted. Once the cylindrical plastic container was lifted, the observers left the testing arena for 5 min during which the newt was permitted to move freely about the arena. The observers then returned to the arena. A newt that remained motionless in the arena center for 5 min was excluded from the subsequent analyses. The directional responses of each newt that left the central area was recorded by the moist trails that it left on the floor of the arena. In all cases, newts that left the central area moved directly from their initial position to the arena wall, tapped against the wall, and then clinging to the wall, proceeded to circle around the arena. Directional responses were recorded to 5° accuracy as the vector of the first point where an animal made contact with the wall.

Each alpine 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) (Phillips 1986a). The three altered fields were produced by means of a doubly-wrapped 1 m cube surface coil (Rubens 1945; for a complete description see Phillips 1986a) surrounding the outside of the arena. An approximately equal number of newts was tested in each of the four magnetic field alignments. In both years, the order of the four horizontal fields (magnetic N=N, S, E or W) was determined using a random number sequence. In 2003 the first individual was tested in magN = N, the next individual in magN = E, followed by one in magN = S and one in magN = W, whereas in 2004 the first individual was tested in magN = W, the next individual in magN = S, followed by one in magN = E and one in magN = N. Testing was carried out double blind. These sequences were repeated until the tests were completed. One experimenter set the horizontal alignment of the field using remote switches, whereas the second experimenter carried in each newt from the tanks and recorded its directional response without knowing the alignment of the magnetic field. The sequence of fields was not revealed to the observer recording the newts' directional responses until after the experiment was completed. If a newt did not reach the orientation criterion within the appropriate time interval, the next individual was tested in the same magnetic field condition.

To determine the relative role of magnetic and non-magnetic cues in the newts' orientation, the absolute or "topographic" bearings were plotted without regard to the alignment of the magnetic field; the use of four symmetrical magnetic field alignments caused any non-magnetic contribution to the newts' orientation to cancel out. To examine the magnetic component of the newts' orientation, the distributions of bearings obtained in the four magnetic field alignments were plotted after first rotating the distributions so that the directions of magnetic north coincided, cancelling out any non-magnetic contribution (Phillips 1986a).

To obtain a measure of the influence of celestial cues on magnetic compass use, in 2003 we compared the topographic and magnetic distributions of bearings obtained from newts tested with and without the moon visible.

Distributions of bearings were analysed using standard circular statistics (Batschelet 1981; Fisher 1995). Mean vector length was estimated and tested for significance using the Rayleigh test for a non-random distribution. Statistics for bimodal distributions were calculated after first doubling each data value and reducing any greater than 360 using modulo arithmetic. Also, a modified Rayleigh test, the *V*-test, was used to test closeness to expected orientation (i.e., the direction towards home), and the Watson U^2-test was used to test for differences between distributions (Batschelet 1981).

Results

In 2003, magnetic bearings obtained in the double blind test were significantly homeward oriented (229°, r=0.36, N=27, P=0.03, Rayleigh test; P=0.004, *V*-test with expected direction = 235°), and the 95% confidence interval (C.I.) for the mean vector included the pond direction of 235° (Fig. 1a—“Combined”, right distribution). The distribution of topographic bearings failed to show significant homeward orientation (209°, r=0.24, N=27, P=0.21, Rayleigh test; P=0.06, *V*-test with expected direction = 235°; Fig. 1a—“Combined”, left distribution).

When we examined the orientation of newts with the moon visible, both the distribution of topographic bearings (197°, r=0.24, N=16, P=0.41, Rayleigh test; P=0.15, *V*-test with expected direction = 235°; Fig. 1a—“Moon visible”, left distribution) and the distribution of magnetic bearings (232°, r=0.29, N=16, P=0.26, Rayleigh test; P=0.05, *V* test with expected direction = 235°; Fig. 1a—“Moon visible”, center distribution) were indistinguishable from random. When the bearings were plotted as deviations from the azimuth of the moon, however, the distribution was significant along a bimodal axis perpendicular to the moon azimuth (87–267°, r=0.55, N=16, P=0.01; Fig. 1a—“Moon visible”, right distribution). The topographic bearings of newts tested when the moon was not visible were also randomly distributed (226°, r=0.26, N=11, P=0.48, Rayleigh test; P=0.11, *V* test with expected direction = 235°; Fig. 1a—“Moon behind clouds”, left distribution), while the magnetic bearings were more strongly clustered than in the “Moon visible” condition, though this result is not significant (227°, r=0.45, N=11, P=0.11, Rayleigh test; Fig. 1a—“Moon behind clouds”, right distribution). However, using the *V*-test, the magnetic bearings of newts tested when the moon was not visible were significantly homeward oriented (P=0.02, *V*-test with expected direction = 235°) and the 95% C.I. (171°, 283°) included the pond direction. The two distributions of magnetic bearings (“Moon visible” and “Moon behind clouds” conditions) were not significantly different (U^2=0.044, P>0.05, Watson U^2-test).

In 2004, the topographic bearings of newts tested under overcast conditions were randomly distributed (341°, r=0.16, N=17, P=0.64, Rayleigh test; P=0.62, *V*-test with expected direction = 232°; Fig. 1b—“Total overcast”, left distribution), while the magnetic bearings were strongly oriented (244°, r=0.57, N=17, P<0.01, Rayleigh test; P<0.001, *V*-test with expected direction = 232°; Fig. 1b—“Total overcast”, right distribution), and the 95% C.I. included the pond direction.

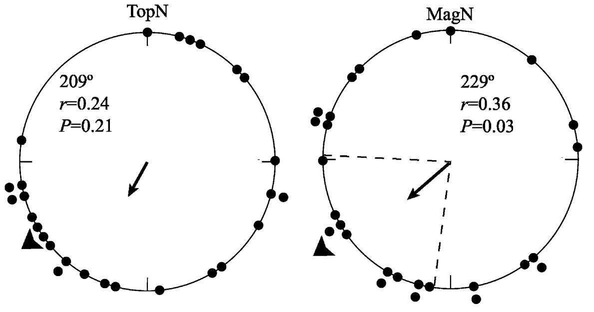
Discussion

A variety of amphibians, including newts, have been shown to use daytime celestial cues for compass orientation (Ferguson and Landreth 1966; Landreth and Ferguson 1966, 1967, 1968; Ferguson et al. 1967; Taylor and Ferguson 1970). More recent work on alpine newts (Diego-Rasilla 2003) suggests that celestial compass cues may also play a role in nocturnal orientation. Thus, newts appear to rely on a multisensory orientation system similar to that found in birds (Able 1991). By testing newts in four symmetrical alignments of the magnetic field, while simultaneously allowing them to view the night time sky, we were able to investigate the relative contribution of magnetic and non-magnetic cues to the newts’ nocturnal homing orientation. Under total overcast and under partly cloudy skies when the moon and large portions of the sky were obscured by clouds, the magnetic compass provided the primary source of directional information used by newts in the present experiments for nocturnal homing orientation. In conjunction with evidence from Eastern red-spotted newts (earlier references), the responses of alpine newts suggest that the magnetic compass is a well-developed component of the orientation/navigation system in this group of salamanders.

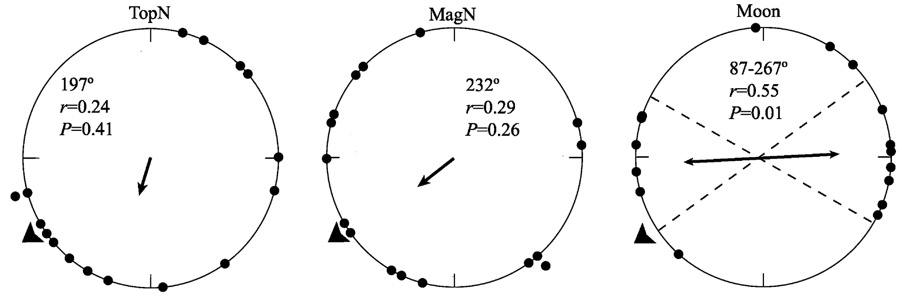
Scatter in the distribution of magnetic bearings was greater when the moon was visible, although this difference was not significant. Nevertheless, the orientation of the newts perpendicular to the moon’s azimuth (Fig. 1a—“Moon visible”, right distribution) suggests that the presence of the moon have affected the newts’ behavior. Such an effect could have resulted from the use of celestial compass information or from a response to some other feature of the surroundings that was visible to the newts in the test arena only when illuminated by moonlight. Neither of these possibilities, however, can readily explain the bimodality in the distribution of bearings relative to the moon’s azimuth. A more likely explanation is that newts were attracted to the boundary between the region of the testing arena opposite the moon illuminated by direct moonlight and the region toward the moon that was shaded by the side of the arena. This type of response may be the result of a behavioral tendency to follow edges (e.g., to avoid open areas with increased exposure to predators), and/or of processing mechanisms in the visual system such as lateral inhibition (Carew 2000) that sharpens the contrast between areas of light and dark, and causes an area in shadow adjacent to an area of bright illumination to appear

(a) 2003

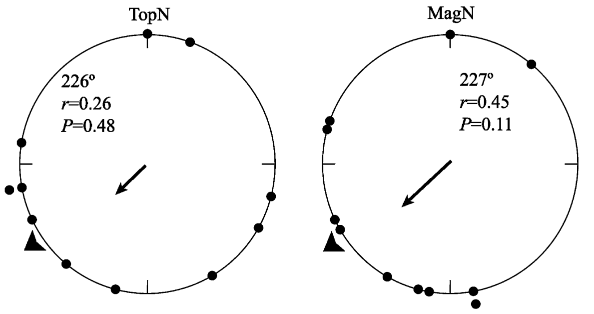
Combined



Moon visible



Moon behind clouds



(b) 2004

Total overcast

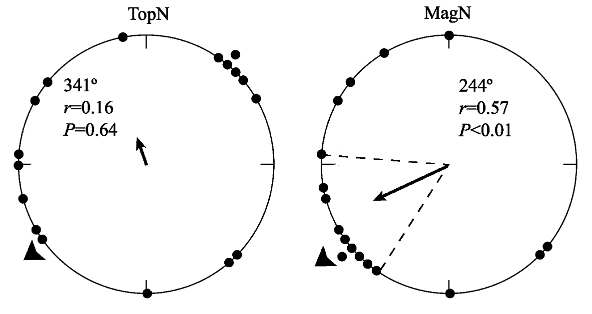


Fig. 1 Orientation responses of the alpine newts, *Triturus alpestris*. Each data point represents the direction of movement of an individual newt tested only once in one of four horizontal alignments of the magnetic field (i.e., magN = N, magN = E, magN = S, magN =W). Single-headed and double-headed arrows at the center of each plot indicate the mean vector and mean bimodal axis, respectively, for each distribution. The length of each arrow is proportional to the mean vector length (r), with the radius of the circle corresponding to r=1 (single-headed arrows) or with the diameter of the circle corresponding to r=1 (doubled-headed arrow). Dashed lines indicate the 95% confidence intervals for the mean vectors. The arrowhead outside each circle indicates the magnetic bearing from the testing site to the home pond of the newts. Circular distributions on the left show the topographic bearings of newts (i.e., the distribution of bearings with respect to topographic directions ignoring the alignment of the four test magnetic fields), and in the center the magnetic bearings obtained in the four magnetic field alignments. Circular distribution on the right shows the bearings plotted as deviations from the azimuth of the moon. **a** Newts tested in 2003 when the moon was visible, was not visible, and combined. **b** Newts tested in 2004 under overcast conditions

darker than a comparable area in the center of a large area of shadow.

By comparison, the absence of direct moon light not only reduced a potential source of compass information, but also reduced the overall light, at least at wavelengths visible to humans (pers. observ.). Since the mechanism of magnetoreception underlying the magnetic compass in newts appears to involve a light-dependent process (Phillips and Borland 1992a, 1994; Deutschlander et al. 1999; Ritz et al. 2002), this finding suggests that nocturnal light levels, even in the absence of direct moon light, are sufficient for the magnetic compass to operate. Earlier experiments have shown that both the homing orientation of alpine newts (Diego-Rasilla 2003) and the shoreward magnetic compass orientation of Eastern red-spotted newts (Phillips and Borland 1992b) are eliminated in total darkness. Therefore, the newts' magnetic compass appears to operate under dim nocturnal light levels, but not in total darkness, as also appears to be in case of migratory birds (Wiltschko and Wiltschko 2002).

In summary, magnetic compass cues appear to play a predominant role in the nocturnal homing orientation of alpine newts, at least under partially cloudy skies when the moon is obscured by clouds and under total overcast. Further experiments carried out under more natural conditions (e.g., eliminating the opaque walls of the arena that produce shadows when the moon is visible) and/or under totally clear skies are needed to determine whether one or more celestial compass cues, in addition to the magnetic compass, play a role in the nocturnal homing orientation of alpine newts.

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