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SHORT COMMUNICATION

True navigation by an amphibian

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True navigation, also referred to as map-based homing, is the ability of an organism to return to the origin of a displacement ('home') without access to familiar landmarks or goal-emanating cues, and without knowledge of the displacement route. True navigation requires both a 'map' or geographical position sense and a compass, and has been demonstrated only in vertebrates (e.g. Walcott & Schmidt-Koenig 1973; Rodda 1984a, b, 1985). In the present study, eastern red-spotted newts, *Notophthalmus viridescens*, deprived of directional information during long distance displacement from their home pond were able to orient in the homeward direction, indicating that they are capable of true navigation.

Homing ability appears to be well developed in the family Salamandridae. Western newts, *Taricha rivularis*, return to breeding sites along relatively straight paths after displacements of up to 12 km (Twitty et al. 1966). Eastern red-spotted newts exhibit homeward-directed orientation in an enclosed indoor arena after displacements of 10–50 km (Phillips 1986a, 1987; Phillips & Borland 1994).

In our earlier homing studies (Phillips 1986a, 1987; Phillips & Borland 1994), male eastern newts were displaced from their home ponds to the testing facility in partially covered plastic buckets which provided access to directional cues en route that could potentially have been used to determine the direction of displacement (Phillips 1987). In the experiments reported here, male newts were deprived of visual, magnetic, olfactory and inertial directional cues during displacement from their home ponds in order to determine whether directional information perceived during displacement was necessary for homing orientation.

Male newts were transported in a plastic bucket 26 cm in diameter filled with 8–10 cm of water. The bucket was suspended within a light-tight plywood box by means of a rotatable shaft attached to a handle on the outside of the box. The lid of the box was equipped with foam seals to prevent access to outside air. The handle on the outside of the box was used to rotate the bucket containing the newts 15–20 times/min during the displacement, with the direction of rotation reversed every 2 min. Four vertical plastic vanes attached to the inside bottom of the bucket ensured that the inertia of the water did not prevent the newts from rotating, and reversing direction, as the bucket was turned.

Eight ceramic magnets with a pole strength of approximately 50 mT (Edmund Scientific no. B60,528) were used to prevent the newts from detecting the geomagnetic field during displacement. Five magnets were attached to the bottom of the transport bucket. One magnet underneath the centre of the bucket and two magnets underneath the bottom edge of the bucket 180° apart were aligned with the north-seeking poles up, while the remaining two magnets located underneath the bottom at the edge of the bucket on the perpendicular axis were aligned with the south-seeking poles up. All five magnets attached to the bottom of the bucket rotated when the bucket was turned. Suspended immediately above the surface of the water inside the bucket was a sixth ceramic magnet attached to a single nylon string which rotated freely and erratically owing to the rotation and movement of the bucket as it was carried. Two additional ceramic magnets were fastened to

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the inside of the plywood enclosure approximately 1 cm from the outside of the bucket at the level of the newts with the north-seeking poles pointed inward, and remained stationary as the bucket was rotated. The magnetic intensities to which the newts were exposed during transport ranged from at least 10 times to more than 100 times that of the geomagnetic field, and varied erratically in intensity and direction both spatially and temporally, thus ensuring that the newts were unable to determine the direction of displacement relative to the geomagnetic field.

Since the plywood enclosure was too heavy to carry to the ponds where the newts were collected we left it in the transport vehicle, which was parked less than 0·5 km away, and carried only the bucket directly to the ponds. At the pond, male newts were placed into the bucket directly from the collecting seine. After replacing the lid, we enclosed the bucket in two layers of black plastic, suspended it from a rope which one of us held, and rotated it in the manner described above as we carried it to the vehicle where we placed it inside the plywood enclosure. To control for any directional cues that the newts might have perceived while being seined from the pond and placed in the transport bucket, we varied the direction in which the seine was pulled through the water and the initial departure direction in which the bucket was carried away from the pond at the two collection sites used in these experiments. At one site, to the southeast of the testing facility (home pond direction=103°, distance=23 km), the seine was pulled through the water in the direction towards the testing facility, while the initial departure direction was away from the testing facility. At the second site, to the southwest of the testing facility (home direction 207°, distance=42 km), the seine was pulled through the water in the direction away from the testing facility, while the initial departure direction was towards the testing facility.

The testing procedures have been discussed in detail elsewhere (Phillips 1987; Phillips & Borland 1994). All tests were carried out in the Orientation Research Facility's laboratory building at Indiana University, Bloomington, during May and June. For 3–8 days prior to the tests, the newts were held indoors in 110-litre all-glass aquaria on a natural photoperiod, and fed salmon pellets (Rangen) three times per week. Newts from one of the collecting sites were then divided into three groups that were placed into separate water-filled outdoor tanks located 12–16 m from the laboratory building. Groups remained in the outdoor tanks for 5–10 days prior to testing. The three tanks were aligned so that an artificial shore at one end of each tank was pointed towards the laboratory building. One tank was placed to the south of the building with the shore at the north end. The second tank was placed to the west of the building with the shore at the east end. The third tank was placed to the east of the building with the shore at the west end. Water temperature in the outdoor tanks was maintained at between 12 and 16°C until the night prior to testing. As in previous studies of homing by eastern newts (Phillips 1987; Phillips & Borland 1994), a rapid drop in water temperature during the night prior to testing was used to elicit unimodal homeward orientation. The water temperature in the tank to be tested was lowered to 2–4°C overnight and then rapidly warmed to 31·5°C on the following morning. Testing was begun once the water temperature reached 28°C. After the three groups from one collecting site were tested, newts from the second site were divided into three groups and the sequence was repeated.

Testing was carried out in a circular (66 cm diameter), visually uniform indoor arena illuminated by a remote 150-W xenon arc lamp which produced full spectrum visible and near-ultraviolet light (Phillips & Borland 1994). A newt was removed from the training tank and carried into the laboratory building in a light-tight container for testing. The newt was then placed in a release device at the centre of the testing arena in total darkness. The arena light was turned on and, after a 60-s delay, the newt was released. The newt's directional response was measured where it first contacted a circle of radius 20 cm centred on the release device. A roughly equal number of newts was tested in each of four symmetrical alignments of an earth-strength magnetic field, i.e. magnetic north at north, east, south or west (Table I). For analysis, the magnetic bearings obtained in each of the four alignments of the magnetic field were pooled (Phillips 1986b). Within 1–2 weeks after the tests were completed, the newts were returned to the ponds from which they were collected.

Previous experiments in which newts had access to directional information both during displacement and at the testing site have demonstrated an

Table I. Directional responses of newts

Magnetic direction of shore	Test field (mN)	Absolute bearing	Magnetic bearing	Magnetic bearing relative to shore
Home direction=207°				
270°	180°	193°	13°	103°
270°	270°	138°	228°	318°
270°	90°	4°	274°	4°
90°	360°	176°	176°	86°
90°	270°	131°	221°	131°
90°	180°	52°	232°	142°
90°	90°	241°	151°	61°
90°	360°	154°	154°	64°
90°	180°	84°	264°	174°
90°	270°	217°	307°	217°
90°	90°	281°	191°	101°
90°	360°	229°	229°	139°
360°	90°	280°	190°	190°
360°	180°	80°	260°	260°
360°	360°	252°	252°	252°
360°	270°	85°	175°	175°
360°	180°	87°	267°	267°
360°	90°	218°	128°	128°
Home direction=103°				
270°	90°	244°	154°	244°
270°	180°	334°	154°	244°
270°	270°	4°	94°	184°
270°	360°	142°	142°	232°
270°	90°	196°	106°	196°
270°	180°	223°	43°	133°
270°	270°	352°	82°	172°
270°	360°	136°	136°	226°
90°	180°	351°	171°	81°
90°	90°	298°	208°	118°
90°	270°	70°	160°	70°
90°	360°	132°	132°	42°
360°	360°	31°	31°	31°
360°	90°	144°	54°	54°
360°	180°	296°	116°	116°
360°	270°	243°	333°	333°
360°	90°	19°	289°	289°
360°	360°	179°	179°	179°
360°	270°	58°	148°	148°

ability to orient in the home direction after displacements of 10–50 km (Phillips 1986a, 1987; Phillips & Borland 1994), which is considerably beyond their normal range of movement (i.e. 2–3 km; D. Gill, personal communication). In the present experiment, in which newts were deprived of directional information during displacement, the distributions of magnetic bearings obtained from newts collected from the two sites were homeward oriented (Fig. 1, Table I). When the magnetic bearings were pooled with respect to the direction of the shores in the outdoor tanks (shore direction=0°), there was no evidence of shoreward compass orientation (see Phillips 1986b; Phillips & Borland 1992) in the data obtained from newts collected from either the southeast (156°; Rayleigh test: $r=0{\cdot}27$, $N=19$, $P>0{\cdot}10$) or southwest (145°; $r=0{\cdot}33$, $N=18$, $P>0{\cdot}10$) sites.

Figure 1 shows that eastern newts were able to orient in the homeward direction at an unfamiliar

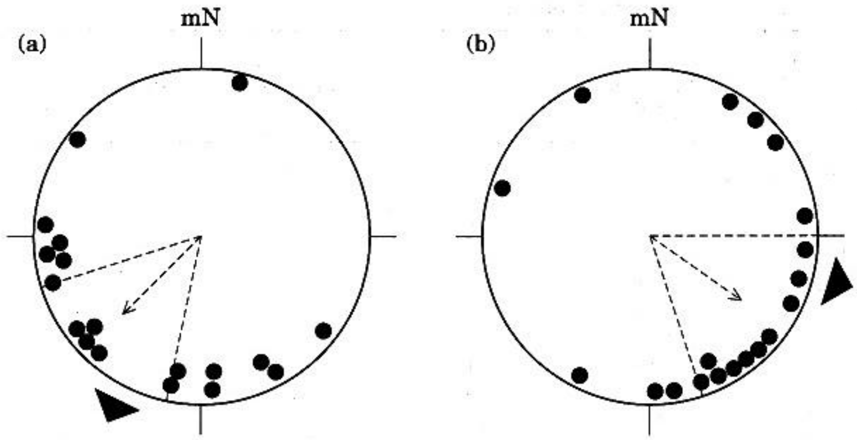

Figure 1. Homing orientation of eastern newts after elimination of directional information during displacement from their home pond. (a) Newts collected from a pond to the southwest of the laboratory (home direction=207°, distance=42 km; mean bearing ± 95% confidence intervals=221 ± 31°; $r=0.59$, $N=18$, $P=0.001$). (b) Newts collected from a pond to the southeast (103°, 23 km; mean bearing ± 95% confidence intervals=126 ± 37°; $r=0.52$, $N=19$, $P=0.005$). The two distributions are significantly different ($U^2=0.344$, $P<0.005$). Each data point indicates the magnetic bearing of a single newt tested only once in one of the four symmetrical magnetic field alignments (i.e. magnetic north (mN)=north, south, east or west). The arrowhead at the edge of each circle diagram indicates the magnetic direction of the home pond. The arrow at the centre of each diagram indicates the mean vector bearing. Dashed lines indicate the 95% confidence intervals for the mean vector bearings. The length of each of the central arrows is proportional to the mean vector length (r); the radius of each diagram corresponds to $r=1$. Statistics after Batschelet (1981).

site without reference to directional information perceived during displacement. Displacement distances 10–20 times the newt's normal range of movement make it unlikely that the newts were using familiar landmarks or goal-emanating cues to determine the home direction. The present findings suggest, therefore, that the newts were able to use 'map' information available at the testing site, presumably obtained while they were housed in the outdoor tanks prior to testing (see Phillips 1986a, 1987). Experiments are currently underway to investigate the sensory basis of the newt's navigational map. With this first evidence for newts, true navigation has now been demonstrated in amphibians, reptiles and birds and may, indeed, be widespread among vertebrates.

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