



Evidence of light-dependent magnetic compass orientation in urodele amphibian larvae



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ABSTRACT

Experiments were conducted to investigate whether larval palmate newts undertake orientation toward or away from the home shoreline (y-axis orientation) using the geomagnetic field to steer the most direct route, and if they accomplish this task through a light-dependent magnetoreception mechanism similar to that found in anuran tadpoles and adult newts. Larval palmate newts trained and then tested under full-spectrum light showed bimodal magnetic compass orientation that coincided with the magnetic direction of the trained y-axis. In contrast, larvae trained under long-wavelength (≥ 500 nm) light and then tested under full-spectrum light displayed bimodal orientation perpendicular to the trained y-axis direction. These results offer evidence for the use of magnetic compass cues in orienting urodele amphibian larvae, and provide additional support for the light-dependent magnetoreception mechanism since they are in complete agreement with earlier studies showing that the observed 90° shift in the direction of magnetic compass orientation under long-wavelength light (≥ 500 nm) is due to a direct effect of light on the underlying magnetoreception mechanism. This study is the first to provide evidence of a light-dependent magnetic compass in larval urodeles.

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1. Introduction

Larval amphibians have been shown to have a well-developed compass sense that enables them to orient efficiently between shallow and deeper waters (Pough et al., 2004; Wells, 2007). Landreth and Ferguson (1966) referred to this movement along an axis perpendicular to a shoreline as y-axis orientation; they referred to the shoreline as the x-axis. Larval amphibians orient towards or away from shallow water in response to abiotic and biotic factors affecting their growth and survivorship (Bancroft et al., 2008; Harkey and Semlitsch, 1988). For example, water temperature varies with depth, time of day, and cloud cover, and temperature is a major factor influencing larval differentiation and growth rate (Atlas, 1935; Bancroft et al., 2008; Castañeda et al., 2006; Lillywhite et al., 1973; Wells, 2007). Larval amphibians find optimal temperatures by moving along the y-axis (Ultsch et al., 1999). Furthermore, although shallow shores of ponds are warmer and have more abundant food

resources than deep waters (Zug et al., 2001), shallow margins are also the preferred microhabitat of aquatic insect predators, such as dragonfly larvae and dytiscid beetles (Bancroft et al., 2008; Fairchild et al., 2003; Holomuzki, 1986). Consequently, larval amphibians may reduce predation by being able to escape directly to deep water when a predator is encountered (Stebbins and Cohen, 1997).

Celestial cues seem to be of primary importance for y-axis orientation in many adult amphibians, both anurans (Ferguson, 1967, 1971; Ferguson et al., 1965, 1967, 1968; Ferguson and Landreth, 1966; Landreth and Ferguson, 1966, 1967) and urodeles (Adler and Taylor, 1973; Taylor and Adler, 1973, 1978). In addition, larval bullfrogs, *Lithobates catesbeianus* (Auburn and Taylor, 1979; Justis and Taylor, 1976), as well as larval salamanders, *Ambystoma* sp. (Taylor, 1972; Tomson and Ferguson, 1972) have been also shown to use celestial cues for y-axis orientation.

Use of the Earth's magnetic field information for compass orientation by amphibians (Diego-Rasilla, 2004; Diego-Rasilla and Rodríguez-García, 2007; Sinsch, 2006) can be advantageous because it can be used in contexts where visual cues are not available (Goodenough et al., 2010; Rozhok, 2008). However, evidence for y-axis magnetic compass orientation among adult amphibians has only been reported in Eastern red-spotted newts,

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Notophthalmus viridescens (Phillips, 1986a,b), while among larval amphibians it has been reported for three species of frogs (*Lithobates catesbeianus*, *Pelophylax perezi* and *Rana temporaria* (Diego-Rasilla et al., 2013; Diego-Rasilla and Phillips, 2007; Freake et al., 2002), and one species of urodele, *Lissotriton boscai* (Rodríguez-García and Diego-Rasilla, 2006).

Y-axis magnetic compass orientation in amphibians has been shown to be mediated by a light-dependent magnetoreception mechanism (Deutschlander et al., 1999a,b; Diego-Rasilla et al., 2010; Phillips and Borland 1992a, 1999b; Phillips and Borland, 1999b; Phillips et al., 2001). Furthermore, the light-dependent magnetic compass exhibits similar features in larval frogs and adult newts (Deutschlander et al., 1999a,b; Diego-Rasilla et al., 2010; Phillips et al., 2001, 2010). In both groups, the light-dependent magnetic compass relies on a magnetoreception system receiving two antagonistic inputs, i.e., a high-sensitivity short-wavelength mechanism and a low-sensitivity long-wavelength mechanism (Phillips et al., 2010). Y-axis magnetic compass orientation of larval frogs and adult newts tested under natural light is indistinguishable from the orientation of those tested under short-wavelength light, showing that full-spectrum light preferentially excites the more sensitive short-wavelength input, whilst the long-wavelength input is excited by wavelengths >500 nm (Deutschlander et al., 1999a; Diego-Rasilla et al., 2010). The antagonistic inputs produce a wavelength-dependent 90° shift in the direction of y-axis magnetic compass orientation that has been shown to result from a direct effect of light on the underlying magnetoreception mechanism (Diego-Rasilla et al., 2010, 2013; Phillips and Borland, 1992a).

Previous experiments of palmate newts, *Lissotriton helveticus*, have also demonstrated that migrating adults use the calls of anurans as a guidance mechanism to locate breeding ponds, particularly for short-distance orientation under an overcast sky (Diego-Rasilla and Luengo, 2007), an ability also demonstrated in adult marbled newts, *Triturus marmoratus* (Diego-Rasilla and Luengo, 2004), and smooth newts, *Lissotriton vulgaris* (Pupin et al., 2007). Furthermore, palmate newts are capable of long-distance homing at night using the magnetic compass as the only source of compass information (Diego-Rasilla et al., 2008). However, no attention has been paid so far to the orientation behaviour of larval stages of this species.

Here, we investigate whether larval palmate newts are able of using the Earth's magnetic field to orient along a learned y-axis and, if so, whether this task is mediated by a light-dependent magnetoreception mechanism similar to that found in the earlier experiments with other species and developmental stages of amphibians (Diego-Rasilla et al., 2010, 2013; Freake and Phillips, 2005; Phillips and Borland, 1992a).

2. Material and methods

2.1. Subjects and study site

Palmate newt (*Lissotriton helveticus*) larvae were collected from a permanent pond located in Barros (Cantabria, northern Spain; 43°17'7"N, 4°4'41"W; 61 m a.s.l.). Twenty-five palmate newt larvae were collected in 2010 (19 August) and 56 in 2011 (27 July), and allowed to learn the direction of an artificial shore in an outdoor tank for four and five days, respectively. In 2010 one group of 13 larval newts was trained under long-wavelength light ($\lambda \geq 500$ nm) and a second group of 12 larvae was trained under natural (i.e., full-spectrum) skylight. Similarly, in 2011 one group of 28 larval newts was trained under long-wavelength light ($\lambda \geq 500$ nm), whereas a second group of 28 animals was trained under natural skylight. In both experiments, all animals were subsequently tested under full-spectrum lighting conditions.

2.2. Procedure

2.2.1. Training protocols

Testing protocols, as well as training and testing apparatus have been described elsewhere (Diego-Rasilla et al., 2010; Diego-Rasilla and Phillips, 2007). Training and testing took place in an open area completely shaded by a group of hazels, *Corylus avellana* (43°17'07"N, 4°4'44"W; elevation 59 m). Larvae were trained under natural light–dark cycle in water-filled outdoor tanks and exposed to natural variation in light intensity. Animals tested in the experiments were returned to their home pond after testing.

The y-axis training tanks consisted of two 96 l all glass aquaria (length, 0.81 m; width, 0.31 m; height, 0.41 m), each one with a sloping bottom (~25° slope) providing a gradient of water depth from the deep end to the shallow end. Water depth at the shore end was 1 cm. The sides of each aquarium were covered with 1.5 cm thick wooden boards to prevent light penetration from the sides of the tanks, whereas the tops of the aquaria were covered with transparent window glass (transmission ≥ 370 nm). Training tanks were filled with tap water treated with aquarium water conditioner (TetraAcqua AquaSafe®, Tetra GmbH, Germany). Each day the aquarium water was partly replaced with fresh treated water; this was done at the time of maximum temperature (i.e., 14, 00–16, 00 GMT), thus maintaining the water temperature of the training tanks between 19 and 23 °C. Larval newts were fed frozen bloodworms, which were placed in the shallow end of the tank daily.

Two different training configurations, with perpendicular shore directions, were used in experiments carried out in 2010. One training tank was aligned along the magnetic north–south axis, with shore facing North, and the other training tank was aligned along the east–west axis, with shore to the East. The top of the N–S training tank was covered with a ≥ 500 nm long pass filter, comprised of one layer of a spectral filter (Lee no. 101; Lee Filters®, Andover, Hants, UK) placed between two transparent methacrylate sheets (82 cm × 42 cm, 0.4 cm thick), while the E–W tank was covered with glass only.

In 2011 two training tanks were aligned along the magnetic north–south axis, with shore facing North. The top of one of them was covered with a ≥ 500 nm long pass filter, comprised of one layer of a spectral filter (Lee no. 101; Lee Filters®, Andover, Hants, UK) placed between two transparent methacrylate sheets (82 cm × 42 cm, 0.4 cm thick), while the other tank was covered with glass only.

In 2010, the two groups of 13 and 12 larvae were introduced into the shallow end of each training tank (N–S and E–W training tanks, respectively) on 19 August, and allowed four days (i.e., from 19 to 23 August) to learn the y-axis direction before testing. In 2011, two groups of 28 animals were introduced into the shallow end of each training tank on 27 July and allowed five days (i.e., from 27 to 1 August) to learn the y-axis direction.

After training, larvae were tested individually in a water-filled outdoor arena for magnetic orientation under natural (i.e., full-spectrum) skylight conditions. In both 2010 and 2011, all larvae were tested on a single day during daylight hours.

2.2.2. Testing apparatus and protocols

Each animal was tested only once in one of the 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) produced by means of a double-wrapped cube surface coil (Rubens, 1945). The testing apparatus was a circular, featureless arena open only to the sky (circular plastic container, 43 cm diameter and 24 cm high) enclosed within the double-wrapped coil powered by a dual DC power supply (Protek 30158) used to alter the alignment of the Earth's magnetic field. The sides of the apparatus were covered with a black cotton

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