



Earth-strength magnetic field affects the rheotactic threshold of zebrafish swimming in shoals



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ABSTRACT

Rheotaxis, the unconditioned orienting response to water currents, is a main component of fish behavior. Rheotaxis is achieved using multiple sensory systems, including visual and tactile cues. Rheotactic orientation in open or low-visibility waters might also benefit from the stable frame of reference provided by the geomagnetic field, but this possibility has not been explored before. Zebrafish (*Danio rerio*) form shoals living in freshwater systems with low visibility, show a robust positive rheotaxis, and respond to geomagnetic fields. Here, we investigated whether a static magnetic field in the Earth-strength range influenced the rheotactic threshold of zebrafish in a swimming tunnel. The direction of the horizontal component of the magnetic field relative to water flow influenced the rheotactic threshold of fish as part of a shoal, but not of fish tested alone. Results obtained after disabling the lateral line of shoaling individuals with Co^{2+} suggest that this organ system is involved in the observed magneto-rheotactic response. These findings constitute preliminary evidence that magnetic fields influence rheotaxis and suggest new avenues for further research.

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1. Introduction

Spatial orientation is essential for many of the activities animals undertake, including habitat selection, foraging, and migration (Aidley, 1981; Jander, 1975). Numerous environmental cues are available to animals for orientation and identifying the sensory thresholds by which animals perceive each cue can provide valuable insight to their behavioral ecology (Phillips et al., 2002). Yet, how animals weight different sensory information or how changes in one sensory cue modulates the response to other cues (as likely occurs in nature) remains challenging to determine (Lohmann et al., 2008a; Jorge et al., 2009; Putman et al., 2014a; Beason and Wiltschko, 2015).

For instance, in aquatic environments, rheotaxis (i.e., the unconditioned orienting response to water currents) is especially important for facilitating movement decisions and is observed across diverse taxa (Chapman et al., 2011). In fish, positive rheotactic behavior is widespread (Montgomery et al., 1997; Kanter and Coombs, 2003; Suli et al., 2012) allowing fish to either maintain their upstream-oriented position or move against the current (Baker and Montgomery, 1999). The rheotactic process, necessarily, depends on information coming from

the surrounding environment (Bak-Coleman et al., 2013). In zebrafish, rheotaxis is mediated by several sensory modalities including visual, vestibular, and tactile (Bak-Coleman et al., 2013; Montgomery et al., 2014), each of which requires some frame of reference for fish to gauge the direction of water flow. Given that zebrafish occupy variable freshwater environments with highly turbid waters, such as seasonal floodplains, rice paddies, and slow streams (Engeszer et al., 2007; Spence et al., 2008), multimodal rheotaxis may have an important function for their ecology.

There has been long-standing speculation that the Earth's magnetic field could play a role in rheotaxis (Arnold, 1974). A benefit of using this cue is that the geomagnetic field is ubiquitous, and could provide a stable frame of reference by which current-induced displacement, water direction, or both could be detected. Linking magnetic orientation and rheotactic responses could greatly increase the efficiency of navigation, particularly in dynamic environments (Wyeth, 2010; Endres et al., 2016). Previous studies indicate that diverse animals can detect and use the magnetic field as a stationary cue for positional and compass information (e.g., Walker et al., 1997; Walker et al., 2002; Gould, 2010; Putman et al., 2013; Putman et al., 2014c; Putman et al., 2015). Likewise, zebrafish are known to detect Earth-strength static magnetic fields (Shcherbakov et al., 2005; Takebe et al., 2012; Osipova et al., 2016) and biogenic magnetite, which is associated with magnetoreception

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(Kirschvink et al., 2001), has been found in the region of the lateral line (Dixon, 2011). Neuromast mechanosensors (canal and superficial) are involved in the fish orientation to water flows (Montgomery et al., 1997; McHenry and van Netten, 2007; Suli et al., 2012) and play an important role in the cohesive swimming of fish shoals (Faucher et al., 2010). However, whether magnetoreception and mechanoreception are behaviorally interrelated or whether the magnetic field influences rheotaxis, in general, has yet to be addressed experimentally.

Here we explore the hypothesis that rheotaxis of zebrafish is influenced by the presence and direction of an Earth-strength magnetic field. We performed a series of laboratory-based experiments, using a swimming tunnel that allowed us to quantify the rheotactic threshold of animals while controlling the intensity and the direction of the magnetic field relative to the direction of water flow. Specifically, we evaluated the rheotactic response by a stepwise increase in the velocity of water current and measuring at each step the time spent by the animals oriented upstream. As zebrafish naturally aggregate in shoals and schools (Pitcher and Parrish, 1993), we compared the behavior of individuals swimming alone or as part of a shoal. Furthermore, we examined whether the response of shoaling fish to rheotactic and magnetic stimuli involved the lateral line by also performing experiments with animals pre-treated with cobalt, to inhibit the lateral line functioning (Karlsen and Sand, 1987). We hypothesized that if the geomagnetic field plays a role in rheotaxis, upstream orientation of zebrafish might be influenced by the direction of the magnetic field with respect to water current. Our findings suggest that the rheotactic threshold is affected by the magnetic field in the geomagnetic range when animals swim in a shoal and implicate a possible role of the lateral line in this effect.

2. Materials and methods

2.1. Ethic statement

All animal procedures were approved by the Institutional Animal Care and Use Committee (CESA) of the University of Naples Federico II, Naples, Italy.

2.2. Animals

Adult zebrafish of the short-fin wild-type were provided by a local supply store (CARMAR SAS, S. Giorgio (NA), Italy). Animals were maintained in 200 l tanks, at a density of 1 animal per 2 l. Main water parameters in the maintaining tanks were monitored daily: temperature 27°–28 °C; conductivity < 500 μ S; pH 6.5–7.5; $\text{NO}_3^- < 0.25$ mg/l. Animals were fed once a day with commercial pelleted fish food (Tetramin, Tetra, Germany; 47% crude protein content, 6% humidity, 20.1 kJ/g dry mass) and displayed a normal shoaling behavior. Experimental individuals were selected randomly from the maintenance tank. All experiments were performed at the same time of the day (9.30–13.00), during March and October 2014. The average weight of selected animals was 0.76 ± 0.1 g (Mean \pm s.d., $N = 45$).

2.3. Swimming tunnel and magnetic field control

The swimming apparatus for zebrafish was from M2M Engineering Custom Scientific Equipment (Naples, Italy). As schematically shown in Fig. 1A, water flow was continuously measured by a SMC Flow switch flowmeter and controlled by a digital feedback system. Water in the swimming apparatus was identical to the maintenance water, was continuously aerated (oxygen content ~ 7.9 mg/l) and its temperature was maintained at 27 °C via a TECO 278 thermo-cryostat. The tunnel was a non-reflecting Plexiglas cylinder (7 cm diameter, 15 cm length) (Fig. 1B). Micro-turbulence in the tunnel was avoided by two perforated Plexiglas plates.

The intensity and direction of the horizontal component of magnetic field in the lab, measured along the major axis of the tunnel in the upstream direction (x axis, +70° of geographic north, Fig. 1C and E), was 11 μ T; the field along y axis was -25 μ T and that of z axis was 55 μ T ($F = 62$ μ T; $I = 64^\circ$; $D = 44^\circ$). These magnetic conditions were similar to those in the aquarium room for maintenance of animals, measured along the same axes ($x = 22$ μ T; $y = -27$ μ T; $z = 43$ μ T). No variation in the lab magnetic field was observed during the period of experimentation, being likely below the measurement equipment resolution (92 nT). For geographic context, the International Geomagnetic Reference Field (IGRF-12) predicted the geomagnetic field at site of the lab (40°N, 14°E) to be $F = 45.8$ μ T; $I = 56.1^\circ$; $H = 25.6$ μ T; $D = 2.91^\circ$ at the time of testing (www.geomag.nrcan.gc.ca).

We manipulated the magnetic field along one dimension, the same axis as the water flow (Fig. 1C, i.e., the x-axis) (one-dimensional magnetic field manipulation, according to Tesch, 1974). The magnetic field intensity and direction along the tunnel major axis were modified by wrapping the swimming tunnel with a solenoid (0.83 turns cm^{-1}) connected with a power unit to generate static magnetic fields (DC power supply ALR3003D, Elc, France). Fields of -50 μ T, 0 μ T and $+50$ μ T were utilized in order to observe the effect of field direction with respect to the water flow (y and z components were unchanged, see Fig. 1E). Positive induced magnetic field along the x axis was oriented opposite to the water current direction (upstream). The manipulated magnetic field did not vary along the swimming tunnel. The magnetic field was measured with a Gauss/Teslameter (9500 Gauss meter, DC 10 kHz, 0.092 μ T resolution, FW Bell, Orlando, USA).

2.4. Experimental protocol

We used a mixed design with one within-subject factor (flow speed) and three between-subject factors (solitary vs in-shoal swimming, magnetic field and cobalt pre-treatment). A repeated-measure design was used to manipulate flow within each animal group – magnetic field combination.

Animals were tested inside the magnetic swimming tunnel solitary or in a shoal of 5 individuals. Animals were acclimated for 1 h (Fig. 1D). During acclimation, the water flow was 1.73 cm s^{-1} . This flow rate was sufficient, according to preliminary experiments, to maintain the oxygen supply for the animals. After acclimation, we started the test with the induced magnetic field. At first, animals stayed for 10 min with no water current. Successively, we exposed the fish to a stepwise increase in the velocity of water current, from 1.95 cm s^{-1} to 8.45 cm s^{-1} (about 0.7–2.9 BL s^{-1}). The flow rate increased by 1.3 cm s^{-1} (about 0.4 BL s^{-1}) every 10 min for six times (60 min in total). The range of water speed was in the lower range of flow rates that induce continuous oriented swimming in zebrafish (3–15% of U_{crit}) (Plaut, 2000).

2.5. Experimental groups

Only naïve fish were used, and each fish experienced only one magnetic field condition. A first group was made of 15 animals that swam alone in the tunnel (mean body weight: 0.78 ± 0.05 g, standard length, 3.10 ± 0.05 cm); this group was divided in 3 sub-groups of 5 animals. Each sub-group was tested with a different magnetic field induced along the axis of water flow: -50 μ T, $+50$ μ T and a null magnetic field, 0 μ T (see above). A second group was made of 15 animals which were let to swim in groups of 5 animals (mean body weight: 0.80 ± 0.05 g; standard length, 3.00 ± 0.05 cm); each of the three groups was tested with a different induced magnetic field: -50 μ T, $+50$ μ T and a null magnetic field, 0 μ T (see above). These animals were tested in order to observe how the magnetic field affects the rheotactic orientation of individual zebrafish in the shoal, which is the natural state of aggregation for this species. Finally, as the integrity of lateral line may be important for the interaction of individuals in a shoal (Faucher et

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