SHORT COMMUNICATION

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Zebrafish "personality" influences sensitivity to magnetic fields

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Abstract

How animals integrate different sensory information for orientation is a complex process involving interactions between a variety of internal and external factors. Due to this complexity, each component of a suite of factors is typically studied in isolation. Here, we examine how an internal factor (personality of fish) influences the response of zebrafish (*Danio rerio*) to the magnetic field, while swimming in a flow chamber. Our previous work demonstrated that the orientation to the water current (rheotaxis) of zebrafish individuals is influenced by variations of the magnetic field only when fish are part of a shoal. In this study, we evaluated the rheotactic behavior of 20 fish, grouped in shoals of "proactive" or "reactive" individuals, under magnetic fields of different directions. We found that the magnetic field influenced at which water speed rheotaxis was elicited in zebrafish with "reactive" personality, but not in those with "proactive" personality. These results suggest that fish personality influences response to or weighing of sensory inputs and provides some insight on the variation in behavioral responses to environmental stimuli in both laboratory and natural settings.

Keywords Fish personality · Zebrafish · Orientation · Magnetic field

Introduction

Animals' movement decisions result from their ability to weight and respond to a wide array of sensory information. The animal movement process is shaped by four main interacting factors: the animal's internal state (e.g., hunger, maturity), its navigation capacity (e.g., the ability to select and maintain a direction), its motion capacity (e.g., locomotion biomechanics), and external factors (e.g., time of day, proximity of conspecifics) (Nathan et al. 2008). Each movement "step" is a function of these factors, which may be differentially weighted as animals respond in different contexts. Due to this complexity, the components of movement are typically studied in isolation (Secor 2015; Westley et al. 2018). In particular, how an animal's internal state, such as a behavioral trait, and the external factors experienced interact to influence navigation capacity are seldom explored (Holyoak et al. 2008).

Individual behavioral traits that are consistent over time and across contexts are usually referred to as "personalities" (Wilson et al. 1994; Sih et al. 2004). Personalities can often predict how animals move or explore environments (Fraser et al. 2001; Sasaki et al. 2018). In birds, such as the great tit (*Parus major*), individuals which are bold are usually not sensitive to external stimuli and are rapid explorers, whereas shy birds are more sensitive to external stimuli and are slower in exploration (Marchetti and Drent 2000; Van Oers et al. 2004). Bahamian spiny lobsters (*Panulirus argus*) form groups and show queuing behavior during their autumnal mass migration. The most active individuals usually initiate migration and become queue leaders (Kanciruk and Herrnkind 1978). In fish schools, leadership appears related to the proactive (high locomotor activity, bold, and first

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exploring new environments) or reactive (prudent, sensitive to external stimuli and adjustable to changes in the environment) personalities of individuals (Sih et al. 2004; Schjolden et al. 2006). As such, fish personalities can influence group coordination (Couzin and Krause 2003; King et al. 2009), and thus activities like foraging, predator avoidance, teaching and interacting with competitors (Huntingford 1976; Ward et al. 2004; King et al. 2009; Bode et al. 2010).

Here, we explore whether personality influences the response to environmental cues of shoaling zebrafish (*Danio rerio*). Aquatic animals belonging to diverse taxa display an unconditioned orienting response with respect to water currents, called rheotaxis (Chapman et al. 2011). Rheotaxis is used for a wide array of activities, ranging from the minimization of energetic expenditure with upstream-oriented station holding behavior (Baker and Montgomery 1999), to the interception of food flowing with the water (Montgomery et al. 1995). Water flows also transport chemical cues, which can function as signals or triggers for animal movement behavior. The involvement of rheotaxis in the detection of odors during upstream migration is well known in several species, such as salmon (Thorpe et al. 1981) and juvenile eels (Sola 1995).

Zebrafish is a shoaling species which migrates seasonally between rivers and floodplains (Spence et al. 2008) and displays a robust rheotactic response (Bak-Coleman et al. 2013). Furthermore, this species is able to detect and respond to weak static magnetic fields in the Earth-strength range (Shcherbakov et al. 2005; Takebe et al. 2012; Osipova et al. 2016; Cresci et al. 2017a). The Earth's magnetic field is known to function as a spatial reference system for animal movement coordination and orientation. Animals may spontaneously align their body along magnetic lines when resting or carrying on activities such as building nests (e.g., rodents) or landing (e.g., flying insects) (Begall et al. 2013). Moreover, the magnetic field can be used for compass orientation and as a source of positional information from microscopic to global spatial scales. For example, marine magnetotactic bacteria have motility directed by the magnetic field (Blakemore 1975), while on the scale of few centimeters, juvenile Chinook salmon use the magnetic field when emerging upwards from their gravel nests (Putman et al. 2018). At larger spatial scales, migratory species use the magnetic field both to maintain a compass course (Wiltschko and Wiltschko 2005; Bottesch et al. 2016; Cresci et al. 2017b) and derive "map" positional information (Lohmann et al. 2007; Putman 2015; Naisbett-Jones et al. 2017). In the case of zebrafish, the magnetic field could provide a homogeneous stable reference in turbulent and low visibility waters, possibly helping individual compass orientation and group alignment.

Shoaling fish display group behavior that appears to be mediated by social and environmental cues in a complex way (Berdahl et al. 2013). Based on the growing literature indicating that "personality" influences how species respond to environmental cues, we hypothesized that fish with "proactive" and "reactive" personality types (Benus et al. 1991; Dahlbom et al. 2012) display a different response to water flows and magnetic fields. To test this hypothesis, we first sorted zebrafish using an established methodology to assign and group individuals that were proactive or reactive (Benus et al. 1991; Koolhaas 2008; Dahlbom et al. 2011; Rey et al. 2013). The proactive/reactive phenotypes are robust and consistent over time and context (Castanheira et al. 2013) and are characterized by a different baseline gene expression (MacKenzie et al. 2009). Individual zebrafish separated using this assay maintains the designated personality trait (proactive or reactive) over a period of at least 10 months (Rey et al. 2013). We then tested fish with the same behavioral trait in a lab-based assay designed to study the influence of Earth-strength magnetic fields on rheotaxis (orientation to water flows) in zebrafish shoals (Cresci et al. 2017a).

Methods

Animals

Adult zebrafish of the short-fin wild-type were provided by a local supply store (CARMAR SAS, S. Giorgio (NA), Italy), and maintained following Cresci et al. (2017a). Both maintenance and experimental temperature was set at 27 °C. Fish were separated into groups of proactive or reactive individuals following the screening protocol described by Rey and co-workers (Rey et al. 2013), which is based on the rate at which individuals explored an unfamiliar, potentially dangerous environment. All the animals used in this behavioral test came from the same maintenance tank and were kept under the same feeding regimes (Tetramin, Tetra, Germany; 47% crude protein content, 6% humidity, 20.1 kJ/g dry mass). No mortality, diseases, or sign of detrimental nutritional state among individuals was observed during maintenance. Moreover, fish were fed ad libitum prior to the transfer to the selecting tank, to limit the possibility that different motivation to search for food would affect animal behavior (Toms et al. 2010). We used a 50-l tank divided into a dark area and an illuminated area, which were separated by a black wall with a circular hole (5-cm diameter) (Supplementary Fig. S1). Fish were randomly selected and placed in the dark box in groups of nine. Individuals which were exploring the bright side of the tank within 10 min were considered proactive and were gently removed. Fish that moved to the bright side of the tank between 10 and 15 min were discarded. The fish that remained in the dark box after 15 min were considered reactive. Similar to Rey et al. (2013), in each behavioral trial, no more than three out of nine fish displayed proactive behavior. Overall, about 20% of animals were proactive, about 70% were reactive, and 10% were discarded. A total number of 72 animals

were tested. Proactive and reactive fish were maintained in separate aquaria and tested within 1 week.

Experimental protocol

Upon designating fish personality, we evaluated the effect of a magnetic field on the rheotactic response of the animals. Previous experiments indicate that zebrafish most strongly respond to magnetic fields during rheotaxis when shoaling (Cresci et al. 2017a). For this reason, the behavioral tests were performed on shoaling fish only, and not on individuals. Animals belonging to the two personality groups were tested inside a swimming tunnel in a shoal of 5 individuals. We tested a total of 20 individuals, selecting at random 2 shoals of 5 proactive fish and 2 shoals of 5 reactive fish for the orientation assay (Cresci et al. 2017a). Each shoal was tested once, under a single magnetic field condition (see below) (Cresci et al. 2017a). Thus, proactive fish were surrounded only by other proactive fish, and reactive fish were surrounded only by other reactive fish. This allowed us to observe the direct effect of the proactive/reactive (leader/subordinate) personality of zebrafish on their sensitivity to environmental information.

Experimental setup

A schematic view of the swimming tunnel and the magnetic control apparatus used in the present study is shown in the Fig. S2 of the supplementary material. The tunnel was a non-reflecting Plexiglas cylinder (7-cm diameter, 15-cm length), connected to a SMC Flow switch, and the flow was controlled by a digital feedback system. The whole tunnel was wrapped by an electric coil, as a solenoid (0.83 turns cm^{-1}). The magnetic field was manipulated along the water flow direction (defined as x axis), with the solenoid connected to a power unit to generate static magnetic fields (DC power supply ALR3003D, Elc, France). The intensity and direction of the horizontal component of the magnetic field measured along the major axis of the tunnel in the upstream direction (x axis, $+70°$ of geographic north), was 11 µT; the field along y axis was -25 µT and that of z axis was 55 µT ($F = 62$ µT; $I = 64°$; $D = 44°$). These magnetic conditions were similar to those in the aquarium room for maintenance of animals, measured along the same axes ($x = 22$ µT; $y = -27$ µT; $z = 43$ µT). The manipulated magnetic field was uniform along the swimming tunnel. In our previous work (Cresci et al. 2017a), we observed the maximum variation of behavioral response with fields of -50 µT (the horizontal component of the magnetic field had the same direction of the water flow, i.e., downstream) and $+50$ µT (the horizontal component of the magnetic field had opposite direction with respect to the water flow, i.e., upstream) along the x axis, thus we used these two conditions in the present study (see Supplementary Fig. S3 and Table S1 for details). The magnetic field was measured

with a Gauss/Teslameter (9500 G meter, DC 10 kHz, FWBell, Orlando, USA) equipped with a MO99-2506 probe with a 0.01 µT resolution.

Data analysis and statistics

To determine the rheotactic threshold of each individual in the shoal, water flow rate was increased in a stepwise fashion, from 0 to 2.8 BL (body lengths) s^{-1} (7 steps, 0.4 BL s^{-1} × 10 min each) (Supplementary Fig. S2; (Cresci et al. 2017a). The range of water speed was in the lower range of flow rates that induce continuous oriented swimming in zebrafish (3–15% of Ucrit) (Plaut 2000). From video-recordings (25 frames s^{-1}) of fish orientation in the tunnel, we performed a manual tracking analysis (Tracker 4.84 Video Analysis and Modeling Tool). We tracked the position of the eye of each fish in the shoal, during a period of 10 min per each flow speed used in the study. Through the collected tracks, we determined the individual Rheotactic index (RI), which is the amount of time that the animals spent oriented upstream, as a proportion of the total oriented time (Cresci et al. 2017a), at each flow rate. The RI index varies between 0 and 100%. Values below 50% indicate that the animals spend most of the time swimming downstream (negative rheotactic response); values higher than 50% indicate that the animal spend most of the time swimming upstream (positive rheotactic response). An RI not significantly different from 50% would indicate absence of rheotactic response. Tracking was performed manually at eight-frame intervals (0.32 s). Behavior was blindly recorded and analyzed by trained observers (intra-rater reliability > 0.90). The whole data set is reported in Supplementary material (Table S2). The relationship between RI and flow rate was fit by a logistic-sigmoidal model. As RI values are percent data, an arcsine transformation was applied. Significant differences between curves were tested via a sum-of-squares F test ($p < 0.05$) (Cresci et al. 2017a). Two parameters and their variability were derived from the fit curve. One is the RI$_{plateau}$, which measures the maximal tendency of the animals to orient upstream in the flow range utilized. The other is the rheotactic threshold, i.e., the minimal flow at which a significant rheotactic response can be elicited (Baker and Montgomery 1999), that was interpolated from the sigmoid fitting curves as the flow rate at which the curve displayed the highest rate of slope variation, identified as the positive peak of the second derivative of the curve (Cresci et al. 2017a).

Results

In the present study we changed the direction of the component of the magnetic field aligned with the water flow and examined for effects on the rheotactic response of individual

zebrafish when swimming in shoal. In the proactive animals, there was no significant effect of the direction of the magnetic field on rheotaxis, as one common curve could be fitted to the sigmoidal relationship between RI and flow rate (Fig. 1a, left). In contrast, we observed a pronounced effect of the magnetic field on the rheotactic behavior of reactive individuals (Fig. 1a right). When the magnetic field component along the swimming tunnel was aligned downstream, the threshold was very low (0.72 ± 0.27 cm s^{-1}), and similar to that of proactive fish (Fig. 1b). The threshold was much higher (2.93 ± 0.59 cm s^{-1}) when the magnetic field was aligned upstream (Fig. 1b). Furthermore, the RI$_{plateau}$ value of reactive animals was much lower when the field was oriented upstream (Fig. 1c). This indicates that under these conditions, the full positive

rheotactic response (RI = 100%) of reactive animals could be obtained only at flow rates higher than the highest flow rate used in our study (8.50 cm s^{-1}).

Discussion

The results suggest that the personality of zebrafish significantly affects the way these animals respond to magnetic field direction in relation to water flow. Specifically, the findings suggest that reactive individuals are more sensitive to the magnetic field than proactive. This work may have implications for understanding variation in individual responses in orientation in both laboratory and natural settings.
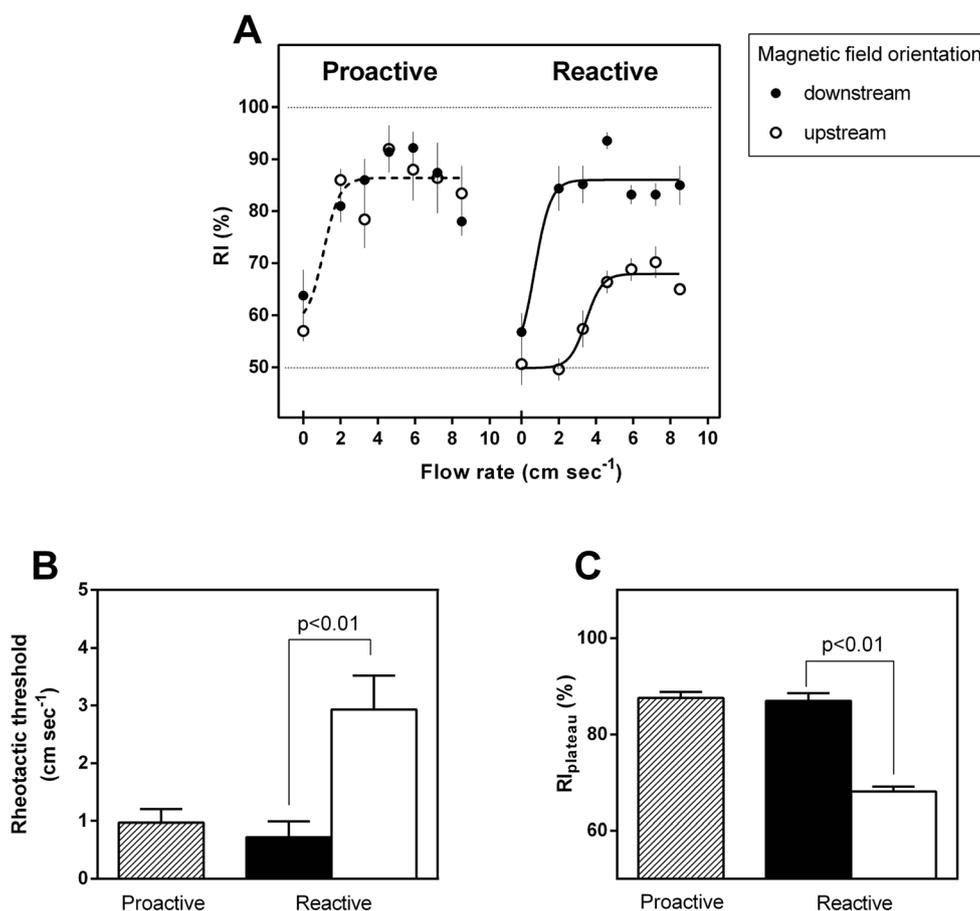
Fig. 1 Rheotactic response in zebrafish. **a** Rheotactic index (RI) vs water flow rate in shoaling proactive and reactive zebrafish at the two induced magnetic field conditions (50 μT, headed downstream or upstream of the water current). RI is the percentage of time that each fish spent oriented upstream. Each value is the average (± SE) of the RI at each flow rate of the five individuals composing the shoal. The square-root, arcsine-transformed data were fit to a logistic-sigmoidal model to test for significance. The dashed curve on the proactive plot indicates that data were fit to one common curve (no effect of the magnetic field, sum-of-squares *F* test, *P* = 0.476), whereas the two curves in the reactive plot show a significant effect of magnetic field (sum-of-squares *F* test, *P* < 0.001). **b** Rheotactic threshold values derived from the curves in panel A.

The rheotactic threshold is the flow rate at which the curve displayed the highest rate of slope variation (Cresci et al. 2017a). A pairwise comparison of thresholds in reactive animals shows a significant difference between the magnetic treatments (*t* test, *P* < 0.01), while one common value is reported for proactive. **c** Maximal RI (RI$_{plateau}$) in shoaling proactive and reactive zebrafish at the two induced magnetic field conditions (50 μT, headed downstream or upstream of the water current). The asterisk indicates a significant difference from 100% (sum-of-squares *F* test, *P* < 0.01). Shaded bars: indicate threshold and RI when there is no effect of the magnetic field (one common value for both magnetic conditions); black bars: fish exposed to a downstream-oriented magnetic field; white bars: fish exposed to an upstream-oriented magnetic field

A lower rheotactic threshold might be considered advantageous in environments with slow moving water, given that rheotactic response benefits the interception of downstream-drifting prey (Gardiner and Atema 2007), and provides directional information for migratory behavior (Thorpe et al. 1981). The relatively high rheotactic threshold observed in reactive fish when the horizontal component of the magnetic field was aligned upstream might be correlated with their more careful behavior. It is interesting to note that under these conditions reactive animals not only started to orient upstream at faster flow speeds, but their level of rheotactic response remained relatively low throughout the whole range of water flows used (low $RI_{plateau}$, Fig. 1c). This suggests that the flow rate necessary to induce a full rheotactic response in reactive animals is well higher than the highest flow utilized in the present study. This result implies that the modulation of magnetic field may affect the response of reactive animals in a wide range of water flow conditions and is a sign of higher flexibility, which can be beneficial in complex and less predictable environments (Koolhaas 2008; MacKenzie et al. 2009). In the natural habitat of zebrafish, the speed of the flow varies greatly across environments, from more turbulent rivers (Spence et al. 2008) to paddies, ponds, and floodplains where the water is still or slow moving (Engeszer et al. 2007). The rheotactic threshold of proactive fish was independent of the magnetic treatment, possibly indicating a more consistent and less flexible orientation to water flows than their reactive counterparts. When sources and direction of food supply are more predictable, proactive fish might gain advantage by the higher consistency of their behavior. For example, dominant individuals of Atlantic salmon (*Salmo salar*) grow faster and are able to obtain the best feeding in structurally simple environments with predictable food supplies (Reid et al. 2012). Interestingly, aggressive/dominant individuals of brown trout fry (*Salmo trutta*) have lower fitness in complex habitats compared to subordinate conspecifics (Höjesjö et al. 2004).

In earlier experiments on shoals with fish that were not grouped according to personality, the lowest rheotactic threshold was displayed when the horizontal component of the magnetic field had the same direction as the water flow, while the $RI_{plateau}$ was not affected by the magnetic field, being $92.9 \pm 1.1\%$ and $98.9 \pm 3.1\%$ for the downstream- and upstream-oriented magnetic field, respectively (see supplementary Fig. S4) (Cresci et al. 2017a). Compared to this earlier work, our present results show that by considering fish personality, it is possible to observe different responses to water flow and magnetic field direction that may be important for movement, orientation and group cohesion. Thus, taking fish personality into account we gain more information and possibly a different perspective on fish movement behavior, that otherwise would be missed. The rheotactic threshold of shoals composed of both proactive and reactive individuals is affected by magnetic fields (as in the reactive fish), while the $RI_{plateau}$

is independent of the magnetic field (as in proactive fish) (Cresci et al. 2017a). This may suggest that a subdivision of roles between proactive and reactive fish exists during orientation to water flows, and the responses of reactive fish may shape the shoal response at low water flow rates, while the response of proactive fish may shape the shoal response at higher flow rates, possibly assuming a leading role (Couzin et al. 2005). However, we caution that our study represents a limited experiment on this topic under laboratory conditions. Further studies are needed to examine the ecological relevance of the behavior displayed by zebrafish under different magnetic fields and water flows.

Although these results represent preliminary observations under laboratory conditions, they imply that fish with different behavioral traits may respond differently to cues which are relevant for orientation such as the magnetic field and water currents. This different sensitivity to the environment could be important for movement decisions of shoaling fish when performing activities such as feeding, exploration, or risk taking (Huntingford 1976; Van Oers et al. 2004). Our study shows that considering fish personality reveals patterns not captured in previous studies, which underscores the importance of taking this variation into account when studying movement behavior.

Author's contribution A.C. proposed the original hypothesis of the study and designed it together with C.A.; he participated to data analysis and drafted the manuscript. R.DR. participated to the study design and was responsible of the theoretical and experimental aspects of the magnetic field manipulation. M.S. and S.F. performed the experiments, collecting, and analyzing the experimental data. C.A. conceived the study together with A.C., designed and coordinated the study, and helped draft the manuscript. N.P. participated in results evaluation and helped draft the manuscript. All authors gave final approval for publication.

Compliance with ethical standards

Competing interests The authors declare that they have no competing interests.

Ethics All animal procedures and experiments were aimed to minimize the number of animals used to test the focal hypothesis and were approved by the Institutional Animal Care and Use Committee (CESA) of the University of Naples Federico II, Naples, Italy.

Data accessibility The data supporting this article are available as part of the Supplementary Material.

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