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Are You Positive? Electric Dipole Polarity Discrimination in the Yellow Stingray, *Urobatis jamaicensis*

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Abstract. It is well established that elasmobranchs can detect dipole electric fields. However, it is unclear whether they can discriminate between the anode and cathode. To investigate this subject, we employed a behavioral assay to determine the discriminatory ability of the yellow stingray, *Urobatis jamaicensis*. We conditioned stingrays with food rewards to bite either the anode ($n = 5$) or the cathode ($n = 6$) of a direct-current dipole located on the floor of an experimental tank. All individuals successfully performed the task after 18 to 22 days. Stingrays were then tested in experimental sessions when they were rewarded only after they identified the correct pole. Stingrays successfully discriminated between the poles at a rate greater than chance, ranging among individuals from a mean of 66% to 93% correct. During experimental sessions, stingrays conditioned to distinguish the anode performed similarly to those conditioned to distinguish the cathode. We hypothesize that the ability to discriminate anode from cathode is physiologically encoded, but its utility in providing spatial information under natural conditions remains to be demonstrated. The ability to discriminate polarity may eliminate ambiguity in induction-based magnetoreception and facilitate navigation with respect to the geomagnetic field.

Introduction

Elasmobranch fishes (sharks, skates, and rays) were first demonstrated to be electrosensitive half a century ago (Dijkgraaf and Kalmijn, 1962; Murray, 1962). In subsequent field and laboratory trials, numerous elasmobranch species have been documented to orient toward and bite at prey-simulating dipole electric fields (Kalmijn, 1971; Tricas, 1982; Kajiura and Holland, 2002; Kajiura, 2003). These trials typically employ a stimulus generator to create a dipole electric field in seawater that replicates the DC component of the bioelectric field of potential prey items. The majority of electroreception research has focused on varying the strength of applied current or the size of the dipole separation (Kalmijn, 1971, 1978; Kajiura and Holland, 2002, Kajiura, 2003; Kajiura and Fitzgerald, 2009). However, it remains unknown whether animals bite preferentially at one pole or the other, or even whether they are able to distinguish between anode and cathode. The ability to distinguish between poles could potentially allow animals to determine the size, orientation, or species-specific bioelectric field characteristics of prey, predators, or potential mates. In addition, the ability to extract polarity information may facilitate orientation to the geomagnetic dipole *via* induction using their electric sense (Kalmijn, 1974; Klimley, 1993; Paulin, 1995; Montgomery and Walker, 2001; Molteno and Kennedy, 2009).

From neurophysiological preparations, elasmobranchs appear to possess the capacity to discriminate between poles of a dipole electric field. Using anesthetized animals, Obara and Bennett (1972) recorded from the primary afferent neurons projecting from the receptor cells lining the ampullae of Lorenzini in two skate species, *Raja oscellata* and *Raja erinacea*. They observed that the resting discharge rate of action potentials was increased by cathodal stimuli and inhibited by anodal stimuli. Tricas and New (1998) found similar results when recording the neural discharge from the hyomandibular nerve in the round stingray, *Urolophus hal-*

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leri. This physiological support for polarity discrimination prompted us to employ a behavioral assay to test whether elasmobranch fishes can be trained to discriminate between the anode and cathode of an electric dipole. A variety of elasmobranchs have been demonstrated to be amenable to classical and operant conditioning (Clark, 1959; Kalmijn, 1982; Schluessel and Bleckmann, 2005, 2012), and for this study we chose a locally abundant species, the yellow stingray, *Urobatis jamaicensis,* which does well in captivity and for which electrosensitivity has been documented (Bedore *et al.,* 2014). The goal of this study was to determine whether the stingrays could be successfully conditioned to preferentially bite at either the anode or the cathode of an electric dipole.

Materials and Methods

Animals

Eleven yellow stingrays, *Urobatis jamaicensis* (Cuvier, 1816), were collected with hand nets off the coast of Boca Raton, Florida. Stingrays were housed at the Florida Atlantic University Marine Science Laboratory (Boca Raton, FL) and maintained in two identical 1.2-m $\times$ 2.4-m tanks, with water depth of about 0.4 m. These indoor tanks were under a controlled lighting regime of 14:10 h light/dark. The tanks were continuously flushed with flow-through seawater at ambient water temperatures of 25–29 °C and salinity of 35 parts per thousand.

The study group consisted of 11 mature animals, 8 females and 3 males, with the following sizes: disc width (mean $\pm$ SD) = 17.8 $\pm$ 0.89 (range 16.2–21.2, $n = 8$) for females and 18.0 $\pm$ 1.82 (range 16.8–18.5, $n = 3$) for males. Training and experiments for anode-conditioned animals ($n = 5$) and cathode-conditioned animals ($n = 6$) took place in separate tanks. All animals were conditioned and tested individually in the tank in which they were housed. Test animals were separated from their tank-mates during conditioning and experimental sessions by a nonconductive barrier fence composed of PVC pipe and plastic mesh. Animal husbandry and behavioral experiments were conducted under Florida Atlantic University IACUC protocol (A12-27).

Experimental apparatus

Stimuli were presented to the rays using a modified version (Fig. 1A) of a previously described apparatus (McGowan and Kajiura, 2009). Two identical dipoles were created on a clear acrylic plate (51 $\times$ 82 cm) (Fig. 1B). Each dipole was created by drilling two holes, 1-mm in diameter, separated by 10 cm, through the acrylic plate. The large separation distance between poles facilitated placement of food at only the selected pole and allowed clear visualization of which pole the rays bit. Affixed to the bottom of the

plate under each hole was a 0.5-m length of seawater-filled polyethylene tubing. At the other end, the tubing was press-fitted to a gold-plated stainless steel connector attached to a shielded underwater cable (Impulse Enterprise, San Diego, CA). The cable terminated into a battery-powered bioelectric stimulus generator outside of the tank. The stimulator was similar to the one described in Kajiura and Holland (2002), but with the addition of a polarity inverter. This apparatus enabled the experimenter to activate one of the two dipoles and switch the direction of current flow on the active dipole.

Conditioning

Five stingrays were conditioned to bite at the anode and six stingrays at the cathode of an electric dipole. At the start of each training session, the acrylic plate was partially buried in the sand on the floor of the tank. To avoid conditioning artifacts from predictable spatial locations, a random number generator was used to determine which of the two dipoles would be activated for each trial bite and with what polarity (Fig. 1A). Only one of the two dipoles was activated at any time; the other remained off as a control treatment. This control protocol follows that previously described in other elasmobranch electroreception work (Kalmijn, 1978; Kajiura and Holland, 2002; Kajiura, 2003).

During a conditioning session, a small piece of thawed shrimp was placed on the selected pole of the dipole and the electric current was applied. The stingray oriented toward and bit at the shrimp/pole, at which time the current was turned off (see supplementary video titled *training bite. mov* at http://www.biolbull.org/content/supplemental/). Each stingray was given 20 feeding opportunities or 30 min, whichever came first. In some conditioning sessions, the individual would not complete the 20 feeding opportunities and would signal satiation by burying in the sand on the floor of the tank; in that case, the session would end for the day. During conditioning, individual progress was recorded as total bites at the correct pole. No negative conditioning occurred. Each stingray was conditioned for 24 sessions.

To determine if (a) the stingrays learned to distinguish between poles and (b) if the rate of learning differed depending on the polarity to which they were conditioned, we used a two-way ANOVA. The factors in the ANOVA model were session and polarity to which rays were conditioned. We also tested for the interaction of the two main factors. Each individual was given the opportunity to participate in each of the 24 sessions. However, the way we recorded conditioning sessions did not allow us to use a repeated-measures ANOVA. To correct for repeated measures, we used the Bonferroni correction to adjust the alpha level from 0.05 to 0.002.

A

video
camera

water level

stimulus
generator

acrylic plate

B

1

A   B

10 cm

2

A

B

20 cm
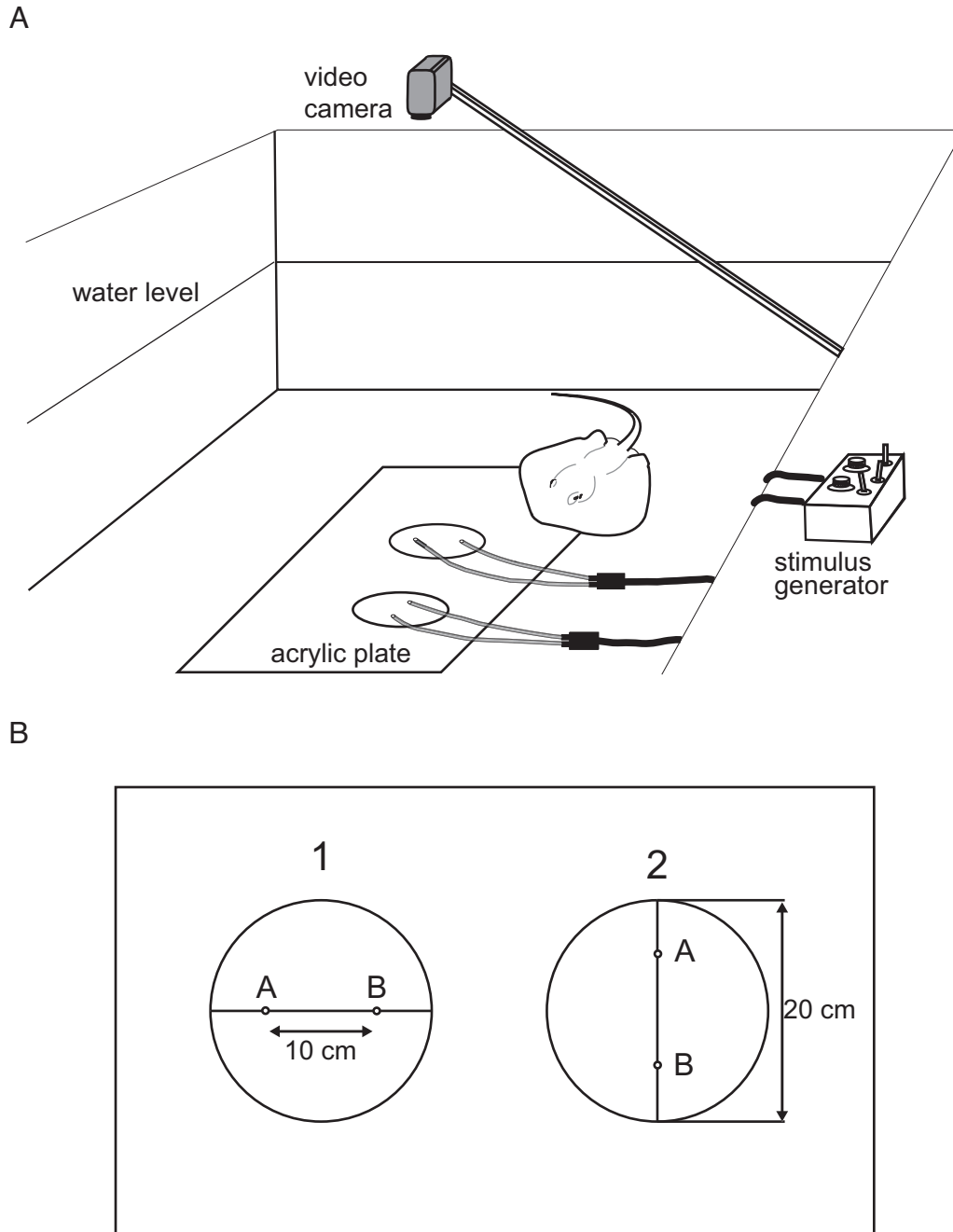
Figure 1. Experimental apparatus used for training and experimental testing. (A) An acrylic plate was placed at the bottom of a tank. Two pairs of dipoles were located on the plate. A stimulus generator produced a DC electric field to simulate the bioelectric field of a stingray's natural prey. All training and experimental trials were recorded with an overhead digital video camera. (B) Acrylic dipole plate used for training and experimental trials. Two dipoles (1 and 2) were controlled by a stimulus generator outside the tank, which allowed the experimenter to select A or B as the anode or cathode. A random number generator was used to assign the polarity during each training and experimental trial. Only one dipole would be activated at any time. The anode and cathode poles were spaced 10 cm apart to facilitate visualization of which pole the stingray was biting.

Experimental sessions

After each ray was subjected to 24 conditioning sessions, experimental sessions were initiated. The experimental ses- sions consisted of 4 acclimation bites, in which food was provided at the dipole to which the rays were conditioned, and 10 unrewarded (experimental) bites (see Gerstein,
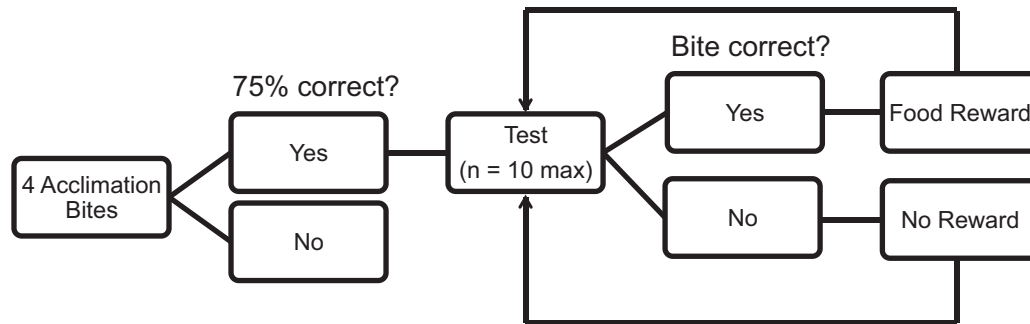
Figure 2. Flowchart of experimental protocol. Experimental sessions began with four acclimation bites, at least three needed to be correct, to alert the stingray to the presence of food. The acclimation bites were identical to a training bite (with food reward). Following three correct acclimation bites (75% correct), stingrays were allowed a maximum of 10 experimental bites (food reward following a correct choice) to test their ability to discriminate between the anode and cathode poles. If the stingray bit at the correct pole to which it was trained, a food reward was given on that pole. Incorrect bites were followed by another experimental bite without a food reward. If the stingray failed to achieve 75% successful bites at the correct pole during the acclimation period, no further testing was attempted with that individual on that experimental day.

1994; Gerstein *et al.*, 1999) (Fig. 2). An acclimation bite was identical to a conditioning bite in which a small piece of shrimp was placed on the randomly selected pole to which the ray had been conditioned. The acclimation bites were used to alert the rays to the presence of food and motivate them to feed. A ray needed to correctly complete at least three of the four acclimation bites to continue on to the experimental session. If the ray failed to bite at the correct pole of the dipole more than once during the acclimation period, it was returned to the holding area until the next session.

Once a stingray successfully completed the four acclimation bites, the experimental session began. During each experimental bite, a randomly assigned pole was activated without a food incentive. After a motivated stingray bit at either pole of the dipole, the stimulator was immediately turned off (see supplementary video titled *experimental_trial.mov* at http://www.biolbull.org/content/supplemental/). A bite was scored as correct if the stingray bit at the pole to which it was conditioned (Fig. 2). After each correct experimental bite, stingrays were rewarded (reinforcing the learned behavior) with a piece of shrimp on the correct and activated dipole. A bite was scored as incorrect if the ray bit at the opposite pole to which it was conditioned; incorrect experimental bites were not rewarded. During each experimental session, rays were given 10 opportunities to bite at the activated dipole. Experimental sessions took place on 6 days, such that each stingray had 60 opportunities overall to bite at the correct pole.

All statistical tests were conducted in JMP, ver. 8.02, SAS Institute, Inc. Each data set was tested for a normal distribution using a Shapiro-Wilk *W* test ($a = 0.05$). If the data were normally distributed, a Student's *t*-test was applied ($a = 0.05$), against a mean of 0.5 (50% chance). If the data were not normally distributed, a nonparametric Wil-

coxon signed rank test was used ($a = 0.05$) against a mean of 0.5 (50% chance).

By chance alone, stingrays had a 50% probability of biting at the pole to which they were trained. We performed two types of statistical test to determine if rays significantly exceeded the 50% threshold. Data were pooled by *conditioning group* (anode and cathode) to include all sessions for all individuals within a group. The proportion of correct bites in the anode-conditioned group was tested against a mean of 0.5 using a *t*-test, as data were normally distributed. This analysis was repeated with the pooled data from the six individuals in the cathode-conditioned group.

To determine the performance of *individual rays* within the anode- and cathode-conditioned groups, we performed a second statistical test. The mean proportion of correct bites for each of the 11 individuals was tested against a mean of 0.5 using either a *t*-test for normally distributed data or a Wilcoxon signed rank test for those violating normality. The mean for each individual comprised correct bites from all six experimental sessions (only five sessions in two individuals). Because the individual observations for each ray are not independent, the results should be interpreted cautiously.

Results

Eleven yellow stingrays were successfully conditioned to discriminate between the anode ($n = 5$) and cathode ($n = 6$) of an electric dipole after 24 training sessions ($F_{3,278} = 54.217$, $P < 0.0001$ uncorrected, and well below the Bonferroni adjusted alpha of 0.002; Fig. 3). Conditioning session was the only significant factor ($F = 160.08$, $P < 0.0001$). The polarity to which the rays were trained to bite and the interaction between polarity and training session were not significant. By the end of 18 sessions, the five
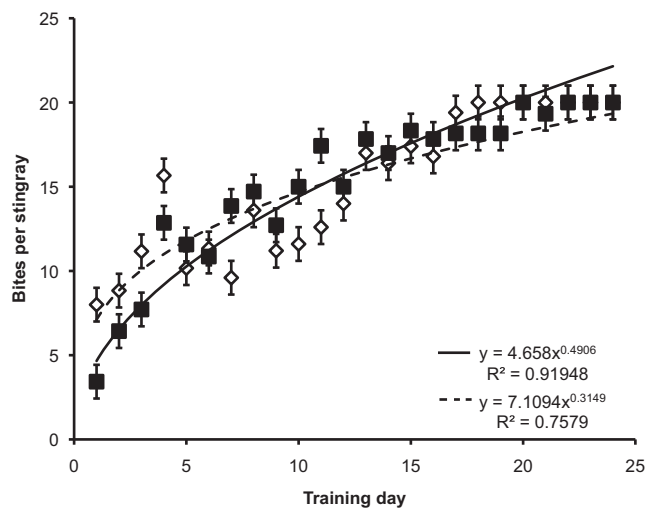
Figure 3. Stingrays are successfully conditioned to bite at the pole to which they were trained (anode or cathode). All stingrays conditioned to the anode were participating in all 20 training bites after 18 days (white diamonds), and all stingrays conditioned to the cathode were participating in all 20 training bites after 22 days (black squares). Data are mean ± 1 S.D., and regression line is a power fit.

Table 1

All 11 stingrays discriminate the anode or cathode of an electrical dipole at a level better than chance

Specimen	Normally distributed?	*t*-test *P*-value	Wilcoxon signed rank *P*-value
	Anode-trained individual		
1	Yes	**0.0003**	**0.0156**
2	Yes	**0.0037**	**0.0313**
3	Yes	**0.0004**	**0.0156**
4	No	–	**0.0313**
5	Yes	**0.0171**	0.0625
	Cathode-trained individual		
6	No	–	**0.0156**
7	Yes	**0.0050**	**0.0156**
8	No	–	**0.0156**
9	Yes	**0.0389**	0.0625
10	Yes	**0.0343**	0.0625
11	No	–	**0.0156**

Distributions significantly different from a mean of 0.5 (50% chance) with *P*-values in **bold**.

Distribution not normally distributed disqualifies the *t*-test, hence no *P*-value given.

anode-conditioned stingrays were consuming 20 pieces of shrimp, the maximum number offered per session. They often accomplished this task within the first 10 of the 30 allotted min in the session. Likewise, all cathode-conditioned stingrays also consumed 20 pieces of shrimp per session, within 22 sessions. For descriptive purposes, we employed a least-square method to fit learning curves for the per-tank average of animals trained to the anode and cathode (Fig. 3). The exponents of the power-function learning curves were 0.491 and 0.315 for anode- and cathode-trained groups, respectively.

For the anode- and cathode-trained groups, the proportion of correct experimental bites was normally distributed, allowing use of a *t*-test. The anode-trained rays performed significantly better than chance ($t = 9.0731$, $P = 0.0004$, DF = 4), as did the cathode-trained rays ($t = 6.9333$, $P = 0.0005$, DF = 5).

The average number of experimental bites for each individual throughout the six sessions was also tested (Table 1; Fig. 4). For 7 of 11 individuals, the number of correct experimental bites was normally distributed, allowing use of a *t*-test. For the four individuals whose distribution was not normal, a nonparametric Wilcoxon signed rank test was used. All 11 individuals performed significantly better than chance over their six experimental sessions. Throughout all conditioning and experimental sessions, rays bit only at the active dipole, and never bit at the non-active, control dipole.

Discussion

Yellow stingrays can discriminate between the anode and cathode of an electric dipole. Using a conditioning para-
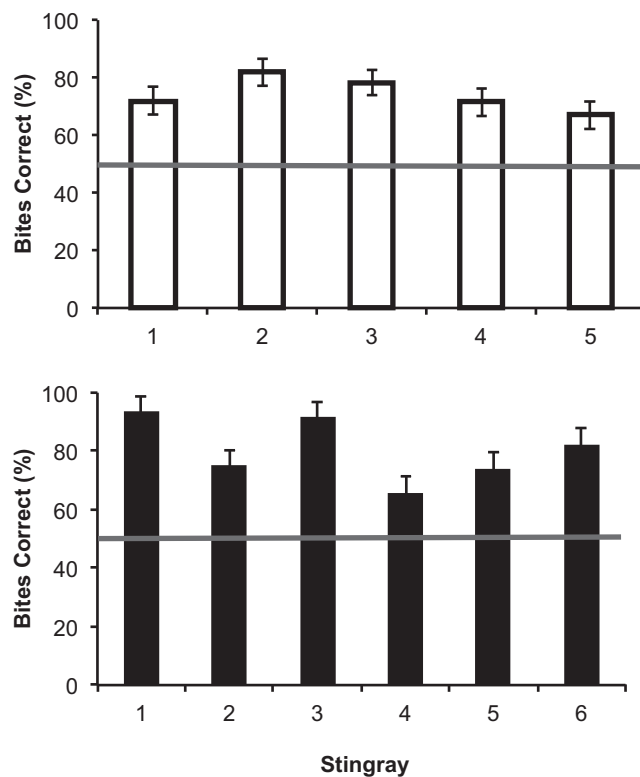

Figure 4. Mean percentage of correct bites per individual (+1 S.D.), from six experimental sessions. White bars are rays conditioned to bite at the anode, and black bars are rays conditioned to bite at the cathode. The mean percentage of correct experimental bites was significantly different from chance (50%, gray line) for all 11 stingrays (Table 1).

digm previously used to study perception, we conditioned 11 yellow stingrays, *Urobatis jamaicensis,* to associate either the anode or cathode of an electric dipole with a food reward. Individuals bit preferentially at the correct pole to which they were conditioned. To our knowledge, this is the first time that this behavioral ability has been demonstrated in elasmobranch fishes.

Electroreception is traditionally thought of as a close-range sensory system employed to detect weak bioelectric fields from cryptic prey, potential mates, and predators at distances of tens of centimeters away from the source (Kalmijn, 1971, 1974; Bedore and Kajiura, 2013). In this application, discrimination of individual poles of an electric dipole may provide additional spatial information on the location or orientation of the stimulus (Brown, 2002; Camperi *et al*., 2007). For example, discriminating an anodal head and cathodal tail stimulus may enable a predatory elasmobranch to direct its attack to the more vulnerable head of its prey. Likewise, a stationary stingray could utilize this ability to differentiate the head and tail of an approaching predator, which would provide information on its orientation and movement direction.

All bioelectric sources present a complete dipole or higher level source (quadrapole, octopole) with poles in close physical proximity to each other. This creates a complex three-dimensional charge distribution in space, which also incorporates a temporal component due to ventilation, limb movement, or swimming (Bedore and Kajiura, 2013). The large number of electroreceptors and their broad spatial distribution over the head of sharks (Kajiura, 2001; Kajiura *et al.*, 2009) and body of batoids (Bedore, 2013) likely confers the ability to generate a spatial map of charge distribution around the animal. The ability to discriminate polarity contributes to the resolution of such charge distribution.

Numerous other species across the vertebrate clade have demonstrated the ability to localize prey and conspecifics using only their electroreceptors (Bullock, 1982; Wilkens and Hoffman, 2005). Electrolocation has been documented among agnathans (Bodznick and Northcutt, 1981), amphibians (Himstedt *et al.*, 1982), chondrosteans (Wilkens *et al.*, 1997), mammals (Scheich *et al.*, 1986; Czech-Damal *et al.*, 2012), sarcopterygians (Northcutt, 1980), and teleosts (Alves-Gomes, 2001). The electrogenic teleosts in particular can use their electric organs and associated tuberous electroreceptors to effectively image their environment (Caputi and Budelli, 2006; von der Emde, 2006). Although other species use electroreceptors for target detection, to our knowledge, this is the first documentation of polarity discrimination using ampullary electroreceptors.

In addition to detecting bioelectric fields, electroreception has also been suggested as a mechanism to facilitate navigation within the earth's dipole magnetic field (Kalmijn, 1974). It is hypothesized that as a shark swims through the Earth's magnetic field, it induces a detectable electric field around its head (Johnsen and Lohmann, 2005). The intensity of the induced electric field varies as a function of swimming velocity and also as the direction in which the animal is swimming with respect to the geomagnetic field (Kalmijn, 1974; Paulin, 1995). Alterations in orientation can provide the shark with directional information; in order for it to maintain a constant heading relative to the geomagnetic field, it need only maintain a constant electrosensory "chord" (Molteno and Kennedy, 2009). This induction-based magnetoreception would allow an individual to utilize the Earth's dipole magnetic field as a constant source for directional information, thus providing it with a compass sense (Montgomery and Walker, 2001). The ability to differentiate polarity of the Earth's dipole magnetic field is critical to elimination of directional ambiguity.

Although electroreception is relatively well studied, even fundamental questions remain unanswered. The capacity to differentiate between poles of an electric dipole is not surprising, but the fact that it is only now being addressed, after half a century of electroreception research, is truly astonishing.

Acknowledgments

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