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Response of juvenile scalloped hammerhead sharks to electric stimuli

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Abstract

Sharks can use their electrosensory system to detect electric fields in their environment. Measurements of their electrosensitivity are often derived by calculating the voltage gradient from a model of the charge distribution for an ideal dipole. This study measures the charge distribution around a dipole in seawater and confirms the close correspondence with the model. From this, it is possible to predict how the sharks will respond to dipolar electric fields comprised of differing parameters. We tested these predictions by exposing sharks to different sized dipoles and levels of applied current that simulated the bioelectric fields of their natural prey items. The sharks initiated responses from a significantly greater distance with larger dipole sizes and also from a significantly greater distance with increasing levels of electric current. This study is the first to provide empirical evidence supporting a popular theoretical model and test predictions about how sharks will respond to a variety of different electric stimuli.

Keywords: Dipole; Electroreception; *Sphyrna lewini*; Sphyrnidae; Elasmobranch

Introduction

The ability of elasmobranch fishes to orient to electric fields is well documented. They have been demonstrated to use their electrosense to detect prey (Kalmijn, 1971; Tricas, 1982), mates (Tricas et al., 1995) and potential predators (Sisneros et al., 1998). They have also been hypothesized to use their electrosense to navigate within the earth's magnetic field (Kalmijn, 1974, 1981, 1982b; Paulin, 1995). The majority of research on elasmobranch electroreception has focused on how it is employed in prey detection. To elicit a feeding response, a pair of electrodes is typically used to generate a dipole electric field in the seawater that approximates the standing direct current (DC) field that surrounds living organisms (Kalmijn, 1972, 1974, 1978). The response of the fish is then recorded as it orients toward and bites at the electrodes (Kalmijn, 1971, 1978, 1982a; Tricas, 1982; Johnson et al., 1984; Kajiura and Holland, 2002; Kajiura, 2003). Using a model for the charge distribution of an ideal dipole (Kalmijn, 1982a; Griffiths, 1989; Denny 1993; Benedek and Villars, 2000), the electric field intensity is then calculated for the point at which the fish initiates its orientation toward the dipole. That electric field intensity provides a measure of the sensitivity of the fish. However, despite the ubiquitous use of a mathematical model to calculate the electric field intensity (Kalmijn, 1982a; Johnson et al., 1984; Kalmijn, 1997; Kajiura and Holland, 2002; Kajiura, 2003; Camperi et al., 2007), there are no published accounts of the actual charges surrounding a dipole in seawater being empirically measured to validate the theoretical field characteristics. To address this

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shortcoming, this study measured and mapped the charge distribution in seawater and compared it to the modeled distribution of electric charges for an ideal dipole.

Given the ability to model the charge distribution, predictions can then be made about how the sharks will respond to a variety of prey-simulating dipole electric fields. By manipulating parameters such as the separation distance of the electrodes on the dipole and the magnitude of the electric current passed between the electrodes, various electric field sizes and intensities can be generated. It was predicted that the sharks would orient from a greater distance when exposed to larger electrode separations because a larger separation will establish a proportionally larger electric field. Similarly, sharks should also orient from a greater distance when exposed to a dipole with a greater applied current strength. Implicit in these predictions is the assumption that the electric field parameters remain sufficiently naturalistic that the sharks will demonstrate normal feeding behavior. It was further predicted that the sharks would be best attuned (i.e. demonstrate the greatest sensitivity) to electric stimuli that most closely resembled their natural prey. These predictions were tested by quantifying the response distance of the sharks to various stimuli and subsequently calculating the minimum voltage gradient that elicited a response (i.e. their threshold sensitivity).

Methods

Electric field measurement

To verify that the literature model of electric field intensity values (Kalmijn, 1982a; Griffiths, 1989; Denny, 1993; Benedek and Villars, 2000) matched actual values experienced by the sharks, a dipole electric field was measured in a controlled tank environment. The experimental apparatus used is illustrated in Fig. 1. A fiberglass tank (122 cm × 243 cm × 76 cm) was filled to a depth of 48 cm with seawater at a temperature of 27.5 °C and a resistivity of 18.0 Ω cm. Two 1 mm diameter holes separated by 1 cm were drilled through the center of a 61.0 cm × 41.9 cm acrylic plate. The acrylic plate was marked with concentric circles of 2, 3, 4, 5, 10, 15 and 20 cm radius around the center of the 1 cm dipole. Radiating from the center of the dipole were lines drawn at 15° increments from 0° to 90° with respect to the dipole axis. On the underside of the acrylic plate was glued a machined acrylic block that connected the holes on the plate to individual screw-in hose barbs. Fifty cm lengths of seawater-filled tygon tubing were press-fitted snugly on the hose barbs and the plate was then centered on the bottom of the tank. The opposite end of each length of tubing was tightly sealed to gold-plated stainless steel pins at the end of a shielded underwater cable. A 12 V marine deep cycle battery was used to apply a 600–800 mA DC current between the electrodes which generated an electric field of sufficient magnitude to be easily measured.

The voltage at various locations around the dipole was measured with chlorided silver wire electrodes (10 T Medwire; Mount Vernon, NY, USA) encased in glass pipettes filled with seawater agar to provide mechanical stability. The reference electrode was affixed to the side of the tank near the surface of the water as far as possible (approximately 145 cm) from the center of the dipole. The recording electrode was vertically offset 5 mm from the surface of the acrylic plate and was affixed to a vertical wooden dowel secured to a sliding track on the lip of the tank. By positioning the sliding track around the lip of the tank, the recording electrode sampled the voltage at various points around the acrylic plate. For each measurement, the wooden dowel was positioned away from the center of the dipole to minimize any distortion of the electric field. The output from the electrodes was filtered (low pass: 0.1 kHz, high pass: 300 Hz) and amplified differentially at 10000 × with a Warner DP304 amplifier (Hamden, CT, USA). The data were digitized with a PowerLab model 16/30 (Colorado Springs, CO, USA) sampling at 1 kHz using Chart software and a 1 mV calibration pulse was provided at the start and end of each recording session. Measurements were made of the voltage at 2, 3, 4, 5, 10, 15 and 20 cm radius and at angles from 0° to 90° at 15° increments with respect to the dipole axis. The order in which the points were sampled was randomized and a complete data set was collected three times. The measurements were repeated for dipole separation distances of 3 cm and 5 cm. For the 3 cm dipole, measurements started at 3 cm from the center of the dipole (1.5 cm from the closest pole) and for the 5 cm dipole measurements started at 4 cm from the center of the dipole (1.5 cm from the closest pole).

Behavioral assays

The behavioral trials were conducted in the large outdoor holding pens at the Hawaii Institute of Marine Biology (HIMB), Coconut Island, Oahu. The experimental apparatus, protocol and analysis methodology have been previously described (Kajiura and Holland, 2002) and all experiments were conducted under University of Hawaii IACUC protocol 99-028-3. Briefly, juvenile scalloped hammerhead sharks, *Sphyrna lewini* (Griffith and Smith, 1834), were caught with barbless hooks and quickly transported to the outdoor holding pens at HIMB where they were allowed to acclimate for a minimum of one week prior to the start of