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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

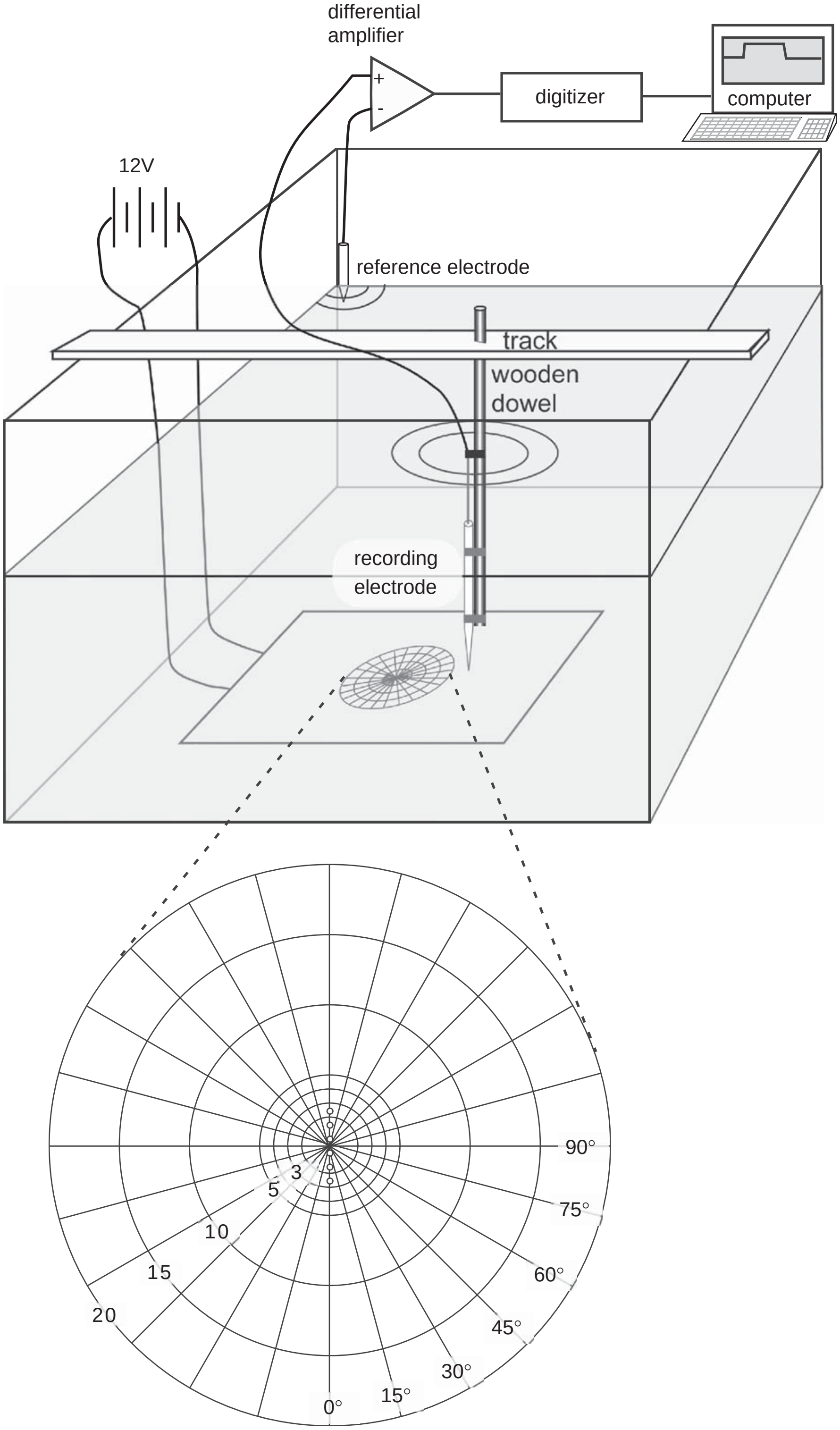

Fig. 1. Experimental apparatus used to measure voltage in a controlled environment. A 12 V marine battery produced a dipole electric field in the seawater through a pair of electrodes in the acrylic plate on the floor of the tank. The voltage was measured differentially with a recording electrode that was moved to various positions around the dipole. Concentric circles of 2, 3, 4, 5, 10, 15 and 20 cm radius were drawn around the center of the dipole and lines radiated from the dipole axis at 15° increments from 0° to 90° (expanded view at bottom). These landmarks served as reference points to position the recording electrode relative to the center of the dipole. Output from the differential amplifier was digitized and stored on computer.

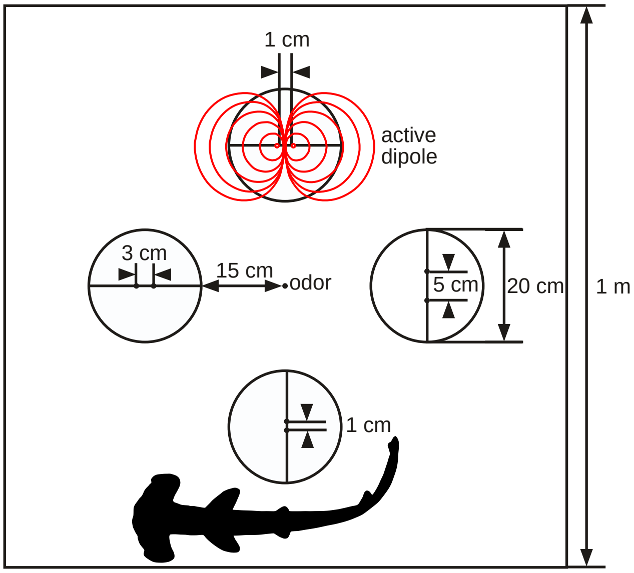

Fig. 2. Electrode array used to study the response of juvenile scalloped hammerhead sharks to prey-simulating dipole electric fields. In each trial, one of the four electrode pairs was activated with a weak electric current which generated a dipole electric field around the electrodes. Electrodes were spaced 1, 3 or 5 cm apart and each electrode pair was equidistant from an odor delivery tube in the center of the plate. The electrodes were spaced symmetrically on the plate, and around the center of each electrode pair a 10 cm radius circle was drawn as a frame-of-reference for subsequent video analysis. A line drawn on the plate through the dipole axis was also used during video analysis to determine orientation angle of the shark with respect to the dipole axis. An outline of a shark is included for scale.

experimentation. A total of 19 sharks were tested (13 females, 6 males) ranging in size from 46.0 cm total length (TL) to 58.5 cm TL with a mean of 53.29 ± 0.90 standard error of the mean (s.e.m.) cm TL.

A 1 m^2 clear acrylic plate was outfitted with four pairs of electrodes arranged equidistant around a center hole through which odor was introduced (Fig. 2). Two electrode pairs had a 1 cm separation distance and one pair each had a 3 and 5 cm separation distance. Fifty centimeter lengths of seawater-filled tygon tubing connected each electrode to a gold-plated stainless steel underwater connector. The underwater cables were the same as those used in the electric field measurement experiments. A battery-powered stimulator on the surface could activate any one of the four electrode pairs and vary the amount of electric current applied across the electrodes. To closely approximate the electric field emanating from the prey, the applied current for the behavioral trials was much lower (5–50 μA) than the current applied for the electric field measurement experiments (600–800 mA). A digital video camera mounted on a sliding track above the pen recorded the response of the sharks as they oriented toward the electric fields.

Two variables were manipulated in the experiments. In one set of experiments, a constant current of 5.0 μA was applied across a variety of electrode separation distances (1, 3, 5 cm). The other manipulation varied the amount of electric current (5.0, 25.0, 50.0 μA) across a fixed, 1 cm electrode separation distance. The range of generated electric fields was within the range measured from prey (Kalmijn, 1972, 1974) and was chosen based upon literature values that had successfully elicited feeding behavior in other elasmobranch species (Kalmijn, 1971, 1978, 1982a). The manipulation of electrode separation distance and applied current strength produced a range of DC dipole moments. For example, 5 μA of electric current applied across a 1 cm electrode separation distance results in a dipole moment of 5 μA cm, whereas the same 5 μA current applied across a 5 cm electrode separation distance results in a dipole moment of 25 μA cm.

To initiate a trial, a barrier net was used to separate an individual test subject within the shallow (<0.5 m) part of the pen from the other sharks that swam freely throughout the deeper part of the pen. The test shark was allowed to acclimate for several minutes within the testing arena. Approximately 20–60 ml of food odor (squid rinse) was then slowly introduced through the odor delivery tube in the center of the electrode array and allowed to dissipate throughout the pen. The odor was introduced only at the start of an experiment to initially arouse the shark and cause it to start searching for food. Once the shark became aroused by the odor, the odor delivery was terminated and one of the electrode pairs was activated. The response of the shark was recorded with the overhead video camera at 30 frames per second.

To quantify the orientation to the electric field, the video footage was analyzed frame-by-frame to determine in which frame the shark initiated its orientation toward the active dipole. This frame was extracted and a deinterlace filter applied with the image analysis program NIH ImageJ. The ImageJ software was then calibrated with a known frame of reference (20 cm diameter circle drawn on the plate) and used to measure the distance from the center of the dipole to the closest edge of the shark's head. The angle described from the point on the shark's head to the center of the dipole, then along the dipole axis was also measured and used in conjunction with the distance to calculate the voltage gradient (V cm^{-1}) at the point where the shark initiated its turn (cf. Kajiura and Holland, 2002, Fig. 3). This provided a more conservative estimate of orientation distance than measuring to the center of the head which would add several cm to the maximum orientation distance. This technique has been used by previous investigators to estimate the minimum voltage gradient that elicits a response by elasmobranchs (Kalmijn, 1971, 1978, 1982a; Johnson et al., 1984; Kajiura and Holland, 2002; Kajiura, 2003).

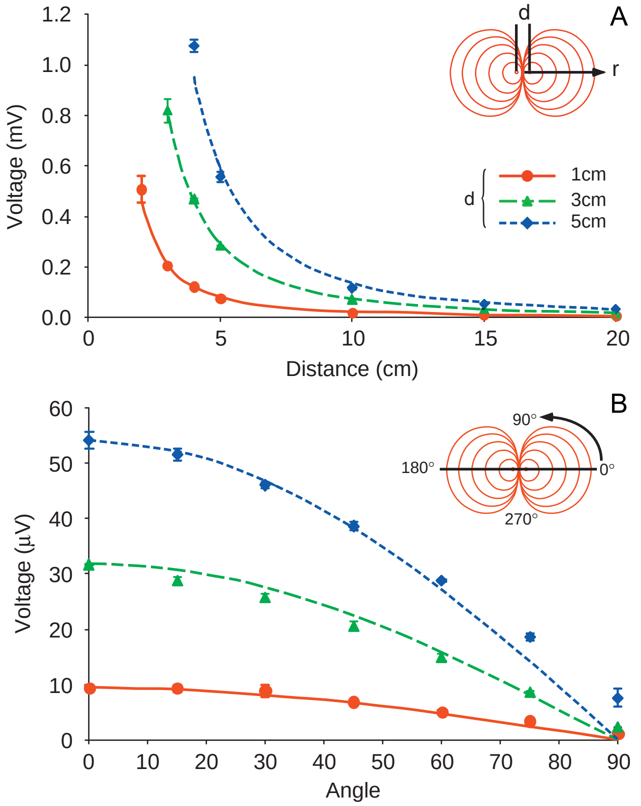

Fig. 3. Measured values (mean ± SD) of the voltage plotted with the calculated theoretical values. (A) The voltage decreases as a square of distance and (B) it also decreases as a cosine function from a maximum at 0° to a minimum at 90°. The measured values (symbols) closely fit the modeled values (lines) for both parameters. For (A), the measurements were taken along the dipole axis at 0°. For (B), the measurements were taken at a radius of 15 cm from the center of the dipole.

For each individual, the maximum orientation distance was selected for analysis which resulted in a maximum of 19 values with no replication. For some individuals, a response to a particular stimulus was not recorded which resulted in a smaller sample size for some treatments. The orientation distance data were tested for normality and homoscedasticity and log transformed if necessary prior to analysis with individual 1-way ANOVA tests using dipole separation and applied current strength as separate treatments.

Results

Electric field measurement

The voltages were measured for 1, 3 and 5 cm dipoles and the measured voltages closely matched the modeled values for an ideal dipole charge distribution in half space (Griffiths, 1989; Kalmijn, 1982a). For all three dipole sizes the voltage decreased as a square of distance, and the standard deviation error bars enclosed the modeled values (Fig. 3A). The inverse square relationship was maintained even though the actual magnitude of the voltage increased proportionally with dipole size (Fig. 3A). This resulted in a given voltage being present at a greater distance with correspondingly larger dipole sizes.

The voltage also varied as a cosine function of angle around the dipole axis. The voltage was greatest in the plane of the dipole axis (0°) and decreased to zero in the perpendicular plane (90°) (Fig. 3B). Although not shown, when the angle exceeded 90°, there was a predictable change in sign from positive to negative. The close match between measured and modeled voltages indicates that the electric field intensity can be accurately interpolated for any position around the dipole.

Behavioral response

As the relatively small volume of odor stimulus dissipated through the large testing arena, the experimental shark would become aroused and dramatically change its swimming behavior. The sharks would swim at an increased velocity close to the bottom and demonstrate apparently exaggerated head yaw. Because the odor was so diffuse, and the odor delivery was stopped well before the sharks approached the acrylic plate, they did not orient toward or bite at the odor source, but bit only at the electric stimulus. Feeding responses (bites) were obtained for all dipole sizes and applied current strengths. Sharks oriented to the center of the dipole by turning sharply (defined by Kajiura and Holland, 2002 as $>20°$ change in trajectory), swimming toward the center of the dipole and biting at the electrodes. This behavior was initiated from a maximum distance of 46.1 cm. Sharks that were motivated to search for food always bit at the active dipole when they passed within the 10 cm radius frame-of-reference circle drawn around each electrode pair. Sharks never bit at the non-active (control) electrodes. Multiple bites at the active dipole were sometimes observed. Sharks would bite once then immediately swim away, turn back and bite at the dipole again, often repeatedly. In these instances, only the initial orientation was included in the analysis as subsequent orientations might have derived from the shark knowing the location of the dipole from the initial interaction.

The electric field is strongly influenced by the environmental parameters of temperature and salinity. Throughout the course of the behavioral trials, temperature ranged from 26.8 to 27.7 °C and the salinity ranged from 34.90 to 35.27 ppt. These values yielded seawater resistivities of 17.69–18.22 Ω cm. Because the size of the electric field increases proportionally with

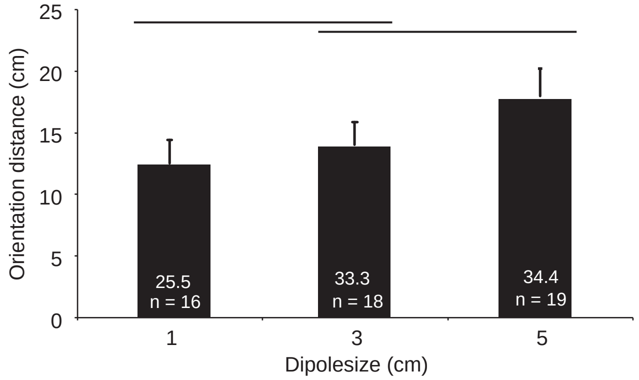

Fig. 4. Mean orientation distance + s.e.m. for three dipole separations. Sharks oriented from greater distances at greater dipole separations. The difference was significant between the 1 and 5 cm dipoles. Distance was measured from the closest edge of the shark's head to the center of the dipole. The maximum orientation distance (cm) for each treatment is included within each bar along with the sample size.

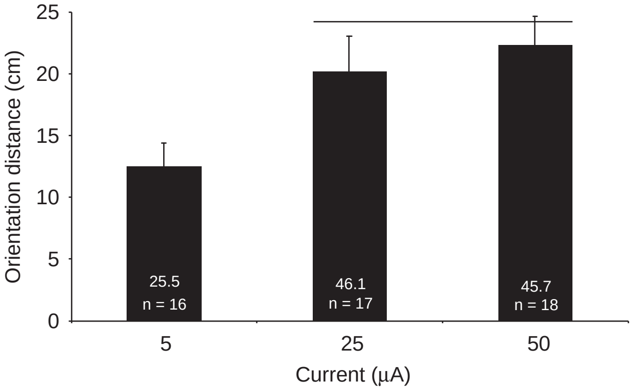

Fig. 5. Mean orientation distance + s.e.m. for three levels of applied electric current. Sharks initiated orientations from a greater distance with increased applied current. The orientation distances were significantly greater for both 25 and 50 μA compared to 5 μA. Distance was measured from the closest edge of the shark's head to the center of the dipole. The maximum orientation distance (cm) for each treatment is included within each bar along with the sample size.

electrode separation distance, it was predicted that the sharks would orient from farther away as the electrode separation increased from 1 to 5 cm. Consequently, response distances were compared for the three electrode separation distances (1, 3, 5 cm) that approximated typical prey sizes for these sharks. The orientation distance data failed the test of normality so were log transformed to achieve normality and homoscedasticity. The sharks demonstrated a significant difference in orientation distance with increased electrode separation (Fig. 4, ANOVA, $F_{2,\ 56} = 3.630$, $p = 0.033$). Sharks oriented to the 5 cm dipole from a greater distance than they did to the 1 cm dipole (Tukey's test, $p = 0.025$). The mean orientation distance for the 1 cm dipole was 11.9 ± 1.86 s.e.m. cm and for the 5 cm dipole was 17.9 ± 2.25 s.e.m. cm. The mean orientation distance for the 3 cm dipole was intermediate at 14.0 ± 1.84 s.e.m. cm and did not significantly differ from either the 1 cm or 5 cm dipoles (Tukey's test, $p = 0.397$ and $p = 0.355$, respectively).

The size of the electric field also increases proportionally with the applied electric current and the sharks oriented from a significantly greater distance with increased current (Fig. 5, ANOVA, $F_{2,\ 51} = 5.322$, $p = 0.008$). The sharks oriented from a significantly greater distance for the 25 μA compared to the 5 μA treatment (Tukey's test, $p = 0.049$) and for the 50 μA compared to the 5 μA treatment (Tukey's test, $p = 0.009$). The orientation distances for the 25 and 50 μA treatments did not differ significantly (Tukey's test, $p = 0.795$). These data were both normal and homoscedastic so no transformation was required. The mean orientation distances for the three treatments were: 5 μA: 11.9 ± 1.86 s.e.m.; 25 μA: 20.1 ± 2.88 s.e.m.; 50 μA: 22.3 ± 2.29 s.e.m. cm.

Threshold sensitivity

The minimum voltage gradient that elicits a response is a measure of the sensitivity of the sharks. Approximately 37.5% of all responses were elicited at voltage gradients of less than $10\,\mathrm{nV\,cm^{-1}}$, and 4.5% of responses were elicited at voltage gradients of less than $1\,\mathrm{nV\,cm^{-1}}$. The median voltage gradient that resulted in the initiation of a response to a 1 cm dipole was $11.0\,\mathrm{nV\,cm^{-1}}$. For the 3 cm dipole the median voltage gradient was $25.2\,\mathrm{nV\,cm^{-1}}$ and for the 5 cm dipole the median voltage gradient was $35.9\,\mathrm{nV\,cm^{-1}}$. These values did not differ significantly from each other (Kruskal–Wallis, $H = 0.861$, $p = 0.650$) which indicates that the sharks responded similarly to all dipole separation sizes.

Discussion

This study is the first to measure the charge distribution of a dipole in seawater and compare the measured values to modeled values for an ideal dipole charge distribution. The close correspondence verified that the actual field intensities were accurately represented by the model. Furthermore, the parameters of the dipole were manipulated to generate a suite of prey-simulating electric fields that were used to test predictions about the behavioral responses of the sharks.

Electric field measurement

The charge distribution of a dipole electric field in half space is modeled by the equation: $V = (\rho I d \cos\theta / \pi r^2)$

(Griffiths, 1989; Kalmijn, 1982a). The variables include: ρ is the resistivity of the seawater (Ω cm), I is the applied electric current (A), d is the electrode separation distance (i.e. distance between positive and negative poles of the dipole) (cm), r is the radius (i.e. distance from the center of the dipole to the position in space for which the potential is being calculated) (cm) and θ is the angle from the position in space to the center of the dipole with respect to the dipole axis. This equation describes the voltage in half space, with the electrodes mounted to the base of an insulating plate such that the conducting medium is a hemisphere above the electrodes (Kalmijn, 1982a). From this equation, it is apparent that the voltage (V) varies as an inverse square of distance (r). The voltage also varies as a function of angle with respect to the dipole axis, being maximal in the plane of the dipole axis (0°) and decreasing as a cosine function to a theoretical null in the perpendicular plane (90°). The empirically measured values closely matched the calculated ideal values for both components (Fig. 3).

Although it was the *voltage* that was directly measured in these experiments, it is thought that elasmobranch electroreceptors act as *voltage gradient* detectors (Kalmijn, 1971, 1974, 1978, 1988). The voltage gradient, or electric field (E), is the spatial derivative of the voltage and hence has the units $\mathrm{V\,m^{-1}}$. For an ideal dipole, the voltage gradient varies not as an inverse square, but as an inverse cube with distance. A cosine angular dependency is retained granting the greatest electric field intensity in the plane parallel to the dipole axis with a minimal field strength in the perpendicular plane (Griffiths, 1989; Denny, 1993). For each experimental trial, the appropriate values of distance (r) and angle (θ) were used to determine the electric field intensity at the point where the shark initiated its orientation to the dipole. The close concordance between the measured and calculated values confirms that the response thresholds calculated for the sharks based upon distance (r) and angle (θ) accurately represent the actual field intensities encountered by the sharks. There is also behavioral evidence to support that the electric field intensity is greatest in the plane parallel to the dipole axis. Both scalloped hammerhead and sandbar sharks initiate orientations from a greater distance at small axis angles and need to be closer to the dipole to demonstrate a response when they are in the orthogonal plane (Kajiura and Holland, 2002).

The equation used to model the electric field intensity assumes that the orientation distance exceeds that of the electrode separation distance ($r > d$) (Kalmijn, 1982a; Denny, 1993; Benedek and Villars, 2000). This assumption has been accepted in other studies of elasmobranch electroreception (Kalmijn, 1982a; Johnson et al., 1984; Kajiura and Holland, 2002; Kajiura, 2003) and is sufficient for the resolution obtained in this study. That is, since the head of the shark is large with respect to the dipole separation distance, and it is covered with thousands of electroreceptor pores (Kajiura, 2001), there is no single point along the head that can be taken as the detection point. Therefore, the calculated field intensity should be used as an approximation and not a definitive measure of threshold sensitivity. The value of this technique lies in its ability to compare relative field intensities rather than determining the absolute sensory capabilities which would be best addressed by using neurophysiological techniques (Tricas and New, 1998).

This study chose the point along the side of the head that was closest to the center of the dipole as the point used to calculate the electric field intensity. This is particularly important for sphyrnid sharks in which the distance from the lateral margin to the center of the head can be large. Therefore, if the measurement had been taken to the center of the head it would increase the orientation distance by several cm yielding a greater sensitivity value. Ideally, measurements should be taken to the actual location of the electroreceptor ampullae within the head. However, in *S. lewini*, most electroreceptors on the lateral margins of the head converge in the large infraorbital cluster which extends along much of the width of the cephalofoil (Chu and Wen, 1979). This precludes measuring to a single point within the cluster which is why the more conservative estimate of the periphery of the head was chosen.

Behavioral response

The fact that the sharks bit at the dipoles attests to the adequacy of the stimulus to represent prey. The sharks initiated orientations from distances in excess of 40 cm and demonstrated their ability to precisely locate the dipole source by biting only when directly over the center of the dipole. The non-active (control) electrodes were never bitten even though they were visually identical to the activated electrodes. In addition, the food odor that diffused throughout the pen served only to arouse the sharks and did not present a point stimulus for orientation. Indeed, the sharks never bit at the odor source on the acrylic plate.

Two parameters, electrode separation distance and applied current strength, were independently manipulated to test for differences in orientation distance to different stimulus conditions. The 1, 3 and 5 cm dipoles simulated small, medium and large prey items for this size of shark and the electric current strengths, from 5.0 to 50.0 μA, were used to generate prey-simulating, weak electric fields similar to the 50–500 μV fields measured around crustaceans and teleosts (Kalmijn, 1974). A given electric field intensity will occur at a greater distance from the center of the dipole when the separation distance between the poles is increased, thus

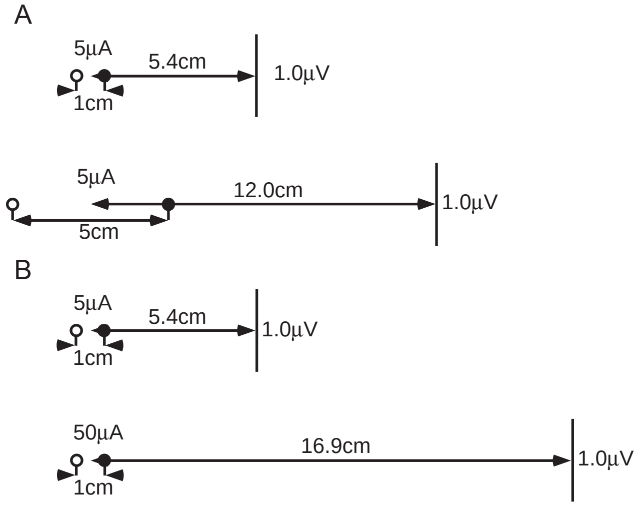

Fig. 6. Diagrammatic representation of how electric field intensity varies with changes in dipole separation and applied current strength. Any given voltage (*V*) will occur at a greater distance from the center of the dipole when (A) dipole separation is increased and current strength is constant; or when (B) current strength is increased and dipole separation is constant. In (A), the applied electric current is held constant at 5 μA for dipole separations of 1 and 5 cm creating DC dipole moments of 5 and 25 μA cm, respectively. A voltage of 1.0 μV is produced at 5.4 cm from the center of a dipole with a 1 cm separation distance. That same voltage (1.0 μV) occurs at a distance of 12.0 cm from the center of a dipole with a 5 cm separation distance. Therefore, increasing the electrode separation from 1 to 5 cm would more than double the possible detection distance in this example. In (B), the dipole separation is held constant at 1 cm for applied current strengths of 5 μA and 50 μA. A voltage of 1.0 μV is produced at 5.4 cm from the center of a dipole that has an applied current strength of 5 μA. That same voltage (1.0 μV) occurs at a distance of 16.9 cm from the center of a dipole that has an applied current strength of 50 μA. Therefore, increasing the current strength from 5.0 to 50.0 μA would provide a three-fold increase in possible detection distance. Both of these examples assume a seawater resistivity of 18.0 Ω cm, and an orientation angle of 0°.

creating a greater DC dipole moment (Fig. 6A). Therefore, it was predicted that for a given electric field intensity (*E*) the sharks would orient to a dipole from a greater distance (*r*) when the separation between the poles (*d*) was increased: (($E \propto (d/r)$). Thus the sharks will encounter a given electric field intensity at a greater distance from the center of the dipole when the electrode separation is increased (Fig. 6A). The prediction of increased orientation distance with increased dipole size was supported by the data. The sharks oriented from a significantly greater distance when exposed to a 5 cm dipole compared to a 1 cm dipole (Fig. 4).

Although the sharks oriented from a significantly greater distance when the electrode separation distance was increased, if the electrode separation distance exceeds the size of a natural prey item the sharks might not interpret the larger electric field as prey (Fitzgerald, 2002). Therefore, the behavior of the sharks may be influenced by their perception of the stimulus and they might not respond as predicted if the parameters are extrapolated beyond certain limits. For instance, if the electrode separation is exceedingly large, the sharks might not bite at the dipole but might actually be repelled. Because this study examined only prey-simulating stimuli, this hypothesis invites further investigation.

A given electric field intensity will also occur at a greater distance from the center of the dipole when the applied current strength is increased (Fig. 6B). Therefore, if sharks respond by orienting to the dipole when they detect some threshold electric field intensity (*E*), it was predicted that the sharks would orient from a greater distance (*r*) when exposed to dipoles of a constant size but with greater applied current strengths (I): ($E \propto (I/r)$). The prediction of increased orientation distance at greater applied current strength was also supported by the data (Fig. 5).

The range of electric currents used in these experiments was chosen based upon literature values that had successfully elicited feeding behavior by various elasmobranch species (Kalmijn, 1971, 1978, 1982a; Johnson et al., 1984; Kajiura and Holland, 2002; Kajiura, 2003). The applied currents were constrained within a range known to be stimulatory to the sharks, therefore it is not surprising that the sharks responded as predicted by initiating feeding orientations at successively greater distances with increased applied current. However, the correlation of orientation distance with applied current must be qualified by recalling that the nature of the response is dependent upon the shark perceiving the stimulus as prey. If the stimulus is not perceived as prey, the shark may detect the electric field but not bite at it. Alternatively, a shark that detects and orients to an electric field at a distance may abandon that orientation once the stimulus strength no longer resembles that of a prey item. Although the sharks would theoretically respond from a greater distance at higher current strengths, their behavior might differ from that predicted by simply scaling the model.

Threshold sensitivity

It was predicted that the sharks would demonstrate the best response to stimuli that most closely matched their natural prey items. Although a variety of prey items of different sizes are found in the stomach of juvenile hammerhead sharks in Kaneohe Bay, the most common prey items are benthic shrimp (Family: Alpheidae) and gobies (Family: Gobiidae) (Clarke, 1971; Bush, 2003). Both of these prey items are most closely approximated in size by the 1 and 3 cm dipoles.

Although the sharks demonstrated the lowest median response threshold (11.0 nV cm^{-1}) when presented with the smallest dipole size (1 cm), the responses did not differ significantly among the different size dipoles. Because the range of tested dipole sizes reflects the size range of their natural prey items, it is perhaps not surprising that there was no difference. However, it is predicted that as the sharks increase in size throughout ontogeny, they will become increasingly attuned to larger dipole sizes that will more accurately represent their correspondingly larger prey.

The behavioral response used as the indicator that the shark had detected the dipole represents a conservative estimate of the position at which the shark actually detected the electric field. The shark may have detected the electric field at a greater distance (i.e. at a lower electric field intensity) but continued to swim along the same trajectory until it reached an electric field intensity that triggered a behavioral response (i.e. a change in direction) (Kim, 2007). This behavioral response threshold is the value quantified in these experiments and is thus a conservative estimate of the sharks' sensory capabilities.

The minimum response thresholds determined in this study are similar to, but slightly lower than, the values previously reported for this species (Kajiura and Holland, 2002). In the study by Kajiura and Holland (2002), a single stimulus (6 μA, 1 cm electrode separation) yielded a median electric field threshold of 25.2 nV cm^{-1} whereas in this study, a 5.0 μA current applied across a 1 cm electrode separation distance yielded a median electric field threshold of 11.0 nV cm^{-1}. These values are much lower than the threshold determined for neonatal bonnethead sharks, *Sphyrna tiburo*, which had a median threshold of 47 nV cm^{-1} (Kajiura, 2003). In this study, 37.5% of orientations by the juvenile scalloped hammerhead sharks were to a stimulus of less than 10 nV cm^{-1} and 4.5% of all orientations were to a stimulus of less than 1 nV cm^{-1}. These values compare favorably with other non-sphyrnid shark species. The smooth dogfish, *Mustelus canis*, demonstrated the ability to detect voltage gradients as low as 5 nV cm^{-1} (Kalmijn, 1978, 1982a). Trained captive nurse sharks, *Ginglymostoma cirratum*, demonstrated minimum threshold sensitivities of 5–10 nV cm^{-1} in the presence of a 20 nV cm^{-1} applied background field (Johnson et al., 1984). The sandbar shark, *Carcharhinus plumbeus*, responded to a minimum voltage gradient of 0.5 nV cm^{-1} and a median voltage gradient of 30.3 nV cm^{-1} which did not differ significantly from the scalloped hammerhead (Kajiura and Holland, 2002). Although the experimental apparatus and stimuli used in this study were similar to those described by Kalmijn (1978, 1982a), differences in analytical methods might not allow the results to be directly compared. For instance, some previous studies merely estimated orientation distance and were unable to analyze footage frame-by-frame to determine precise orientation distance (Kalmijn, 1971, 1978, 1982a). In addition, whereas those previous studies grouped orientation angles as either along the dipole axis, normal to the dipole axis or intermediate, this study was able to accurately measure orientation angle to the nearest degree from the individual video frames. The limitation of different methodologies can be overcome by testing different species under identical conditions and comparing the minimum response thresholds obtained for the different species (cf. Kajiura and Holland, 2002).

These experiments deliberately tested only stimuli that simulated natural prey items. Thus, the range of stimulus size and intensity was limited. However, elasmobranch fishes are capable of detecting non-prey electric fields. Elasmobranchs respond to the electric fields of conspecifics (Tricas et al., 1995), of predators (Sisneros et al., 1998) and can theoretically respond to induced fields caused by swimming through the earth's magnetic field (Kalmijn, 1974; Paulin, 1995) or near geomagnetic anomalies (Klimley, 1993). Therefore, a wide range of detectable electric stimuli remains to be tested.

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References

Benedek, G.B., Villars, F., 2000. Physics, with Illustrative Examples from Medicine and Biology. AIP Press, New York.

Bush, A., 2003. Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks, Sphyrna lewini, in Kane'ohe Bay, O'ahu, Hawai'i. Environ. Biol. Fishes 67, 1–11.

Camperi, M., Tricas, T.C., Brown, B.R., 2007. From morphology to neural information: the electric sense of the skate. PLoS Comput. Biol. 3, 1–14.

Chu, Y.T., Wen, M.C., 1979. A study of the lateral-line canals system and that of Lorenzini ampullae and tubules of elasmobranchiate fishes of China. In: Monograph of Fishes of China 2. Shanghai Science and Technology Press, pp. 117–126.

Clarke, T.A., 1971. Ecology of scalloped hammerhead shark, Sphyrna lewini, in Hawaii. Pac. Sci. 25, 133–144.

Denny, M.W., 1993. Air and Water: The Biology and Physics of Life's Media. Princeton University Press, Princeton, NJ.

Fitzgerald, T.P., 2002. Behavioral responses of juvenile sandbar sharks, Carcharhinus plumbeus, to direct current and alternating current stimuli. MS Thesis, University of Hawaii, Honolulu.

Griffiths, D.J., 1989. Introduction to Electrodynamics. Prentice Hall, Englewood Cliffs, NJ.

Johnson, C.S., Scronce, B.L., McManus, M.W., 1984. Detection of DC electric dipoles in background fields by the nurse shark. J. Comp. Physiol. 155, 681–687.

Kajiura, S.M., 2001. Head morphology and electrosensory pore distribution of carcharhinid and sphyrnid sharks. Environ. Biol. Fishes 61, 125–133.

Kajiura, S.M., 2003. Electroreception in neonatal bonnethead sharks, Sphyrna tiburo. Mar. Biol. 143, 603–611.

Kajiura, S.M., Holland, K.N., 2002. Electroreception in juvenile scalloped hammerhead and sandbar sharks. J. Exp. Biol. 205, 3609–3621.

Kalmijn, A.J., 1971. Electric sense of sharks and rays. J. Exp. Biol. 55, 371–383.

Kalmijn, A.J., 1972. Bioelectric fields in sea water and the function of the ampullae of Lorenzini in elasmobranch fishes. SIO Reference Series no. 72–83, pp. 1–21.

Kalmijn, A.J., 1974. The detection of electric fields from inanimate and animate sources other than electric organs. In: Autrum, H. (Ed.), Handbook of Sensory Physiology, vol. 3. Springer, New York, pp. 149–199.

Kalmijn, A.J., 1978. Electric and magnetic sensory world of sharks, skates, and rays. In: Hodgson, E.S., Mathewson, R.F. (Eds.), Sensory Biology of Sharks, Skates and Rays. US Government Printing Office, Washington, DC, pp. 507–528.

Kalmijn, A.J., 1981. Biophysics of geomagnetic-field detection. IEEE Trans. Magn. 17, 1113–1124.

Kalmijn, A.J., 1982a. Electric and magnetic-field detection in elasmobranch fishes. Science 218, 916–918.

Kalmijn, A.J., 1982b. Theory of electromagnetic orientation: a further analysis. In: Bolis, L., Keynes, R.D., Maddrell, S.H.P. (Eds.), Comparative Physiology of Sensory Systems. Cambridge University Press, Cambridge, pp. 525–560.

Kalmijn, A.J., 1988. Detection of weak electric fields. In: Atema, J., Fay, R.R., Popper, A.N., Tavolga, W.N. (Eds.), Sensory Biology of Aquatic Animals. Springer, New York, pp. 151–186.

Kalmijn, A.J., 1997. Electric and near-field acoustic detection, a comparative study. Acta Physiol. Scand. 161, 25–38.

Kim, D., 2007. Prey detection mechanism of elasmobranchs. Biosystems 87, 322–331.

Klimley, A.P., 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Mar. Biol. 117, 1–22.

Paulin, M.G., 1995. Electroreception and the compass sense of sharks. J. Theor. Biol. 174, 325–339.

Sisneros, J.A., Tricas, T.C., Luer, C.A., 1998. Response properties and biological function of the skate electrosensory system during ontogeny. J. Comp. Physiol. A 183, 87–99.

Tricas, T.C., 1982. Bioelectric-mediated predation by swell sharks, *Cephaloscylium ventriosum*. Copeia 1982, 948–952.

Tricas, T.C., New, J.G., 1998. Sensitivity and response dynamics of elasmobranch electrosensory primary afferent neurons to near threshold fields. J. Comp. Physiol. A 182, 89–101.

Tricas, T.C., Michael, S.W., Sisneros, J.A., 1995. Electrosensory optimization to conspecific phasic signals for mating. Neurosci. Lett. 202, 129–132.