

Electroreception in juvenile scalloped hammerhead and sandbar sharks

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Summary

The unique head morphology of sphyrnid sharks might have evolved to enhance electrosensory capabilities. The ‘enhanced electroreception’ hypothesis was tested by comparing the behavioral responses of similarly sized carcharhinid and sphyrnid sharks to prey-simulating electric stimuli. Juvenile scalloped hammerhead sharks *Sphyrna lewini* and sandbar sharks *Carcharhinus plumbeus* oriented to dipole electric fields from the same maximum distance (approximately 30 cm) and thus demonstrated comparable behavioral-response thresholds ($<1 \text{ nV cm}^{-1}$). Despite the similarity of response threshold, the orientation pathways and behaviors differed for the two species. Scalloped hammerheads typically demonstrated a pivot orientation in which the edge of the cephalofoil closest to the dipole remained stationary while the shark bent its trunk to orient to the center of the dipole. By contrast, sandbars swam in a broader arc towards the center of the dipole. The different orientation

patterns are attributed to the hydrodynamic properties of the cephalofoil, which enables the hammerheads to execute sharp turns at high speed. The greater trunk width of the sandbar sharks prevented them from demonstrating the same degree of flexibility. Therefore, although the sphyrnid head morphology does not appear to confer a greater sensitivity to prey-simulating dipole electric fields, it does provide (1) a greater lateral search area, which may increase the probability of prey encounter, and (2) enhanced maneuverability, which may aid in prey capture.

Movies available on-line

Key words: ampullae of Lorenzini, Carcharhinidae, elasmobranch, enhanced electroreception hypothesis, Sphyrnidae, *Carcharhinus plumbeus*, *Sphyrna lewini*.

Introduction

All chondrichthyan fishes can detect electric fields with their electroreceptors, the ampullae of Lorenzini. This electrosense enables them to locate potential prey items that might otherwise be obscured from their other sensory systems, for example if the prey is buried in the substratum. Although elasmobranch orientation to prey bioelectric fields was first documented over 35 years ago (Kalmijn, 1966), surprisingly few studies since have examined the behavioral responses of elasmobranchs to potential prey items.

Of more than 380 shark species (Compagno, 1999), only nine species have been examined for electroreceptive response (Table 1). Of those, the minimum voltage gradients that elicit a feeding response have been determined for the smooth dogfish *Mustelus canis* (Kalmijn, 1982), the nurse shark *Ginglymostoma cirratum* (Johnson et al., 1984) and the reef blacktip shark *Carcharhinus melanopterus* (Haine et al., 2001). No studies have examined the electrosensory-mediated behavioral response of sphyrnid sharks, even though it is hypothesized that enhanced electroreceptive capabilities might have driven evolution of the sphyrnid head morphology (Compagno, 1984).

The ‘enhanced electroreception’ hypothesis proposes that the sphyrnid head morphology provides a greater electrosensory search area compared with similar sized carcharhinid sharks (Kajiura, 2001a). The consequent greater head area is accompanied by a greater number of electrosensory pores, which provide sphyrnids with a pore density (pores cm^{-2}) comparable with other species. Because the pore density remains comparable, there is no loss of spatial resolution over the width of the head. Although there is supporting morphological evidence, a comparison of behavioral responses to electrosensory stimuli between carcharhinid and sphyrnid sharks is lacking.

The present study describes and quantifies the behavioral responses of a sphyrnid shark and a carcharhinid shark to test the predictions of the enhanced electroreception hypothesis. The responses of juvenile scalloped hammerhead sharks *Sphyrna lewini* and sandbar sharks *Carcharhinus plumbeus* to prey-simulating electric fields were compared to determine if scalloped hammerhead sharks sampled a greater area of the substratum than similarly sized sandbar sharks. The sensitivity

Table 1. *Shark species tested for electroreceptive response*

Order	Species	Reference
Squaliformes	<i>Mustelus canis</i>	Kalmijn, 1978
Orectolobiformes	<i>Ginglymostoma cirratum</i>	Johnson et al., 1984
Lamniformes	<i>Carcharodon carcharias</i>	Tricas and McCosker, 1984
Carcharhiniformes	<i>Scyliorhinus canicula</i>	Kalmijn, 1971
	<i>Cephaloscyllium ventriosum</i>	Tricas, 1982
	<i>Prionace glauca</i>	Kalmijn, 1978
	<i>Triakis semifasciata</i>	Kalmijn, 1978
	<i>Negaprion brevirostris</i>	Kalmijn, 1978
	<i>Carcharhinus melanopterus</i>	Haine et al., 2001

Although six carcharhiniform sharks have been tested for their response to electric stimuli, no studies have examined any species within the family Sphyrnidae.

of both species to dipole electric fields was also compared. These two species were chosen to represent typical sphyrnid and carcharhinid head morphologies, respectively.

Comparative behavioral studies of feeding response should test species that share a similar feeding behavior. Juvenile scalloped hammerhead sharks feed primarily on benthic fishes and crustaceans (Clarke, 1971). Juvenile sandbar sharks also feed primarily on benthic fishes and crustaceans but also feed on small fishes in the water column (Medved et al., 1985). In addition, the size of juveniles of both species is comparable (Compagno, 1984). Thus, a comparison can be made between two comparably sized species with somewhat similar feeding habits that differ in head morphology.

Methods

Facilities

Thirteen juvenile scalloped hammerhead sharks *Sphyrna lewini* (Griffith and Smith 1834) were caught in Kaneohe Bay, Oahu, HI, USA by hand-line fishing with barbless hooks, which minimized damage to the mouth area. Immediately after being brought to the surface, the sharks were dehooked, placed in a 1 m-diameter, seawater-filled, fiberglass hemisphere and quickly transported to the outdoor shark pens at the Hawaii Institute of Marine Biology (HIMB), Coconut Island, HI, USA. Twelve juvenile sandbar sharks *Carcharhinus plumbeus* (Nardo 1827) were caught by long-line fishing outside Kaneohe Bay (approximately 21° 29.9'N, 157° 46.3'W). Transport of the sandbar sharks to HIMB was *via* a covered 1.2 m-diameter, fiberglass holding tank, and the sandbars were maintained in the same outdoor pens as the hammerheads. For both species, sharks were measured, sexed and marked with identifying fin clips prior to being placed in the pen. The sharks were fed to satiation on a diet of cut squid and fish every other

day and were allowed to acclimate to the pen for a minimum of one week prior to testing.

The pen in which experiments were conducted was approximately 10 m × 20 m, with a maximum depth of 2.4 m. The pen was bounded by fences at both ends that enclosed the sharks but allowed tidal flushing of water and small reef fish to move through freely into the pen. Because the pen was merely an enclosure of part of the natural reef, the habitat in the pen was representative of the reef habitat in Kaneohe Bay and included live coral, various reef fishes and invertebrates. Thus, the pen represented a semi-natural habitat complete with typical reef fauna.

The shallow (<0.5 m) part of the experimental pen was used as the test arena. This area was chosen because at low tide the shallow depth facilitated videotaping of the sharks with an overhead camera. A barrier net was deployed across the width of the pen to isolate the shark being tested from others in the deeper part of the pen. Individually testing each shark eliminated interaction effects from other individuals that might also attempt to bite at the electrodes.

Experimental apparatus

A stimulus generator was designed to apply prey-simulating dipole electric fields to the seawater. The stimulus generator was comprised of a battery-powered circuit that passed electric current through the seawater, which acted as a series resistor in the circuit (Fig. 1). The stimulus generator enabled the experimenter to vary the strength of the applied stimulus current and to switch between any of the four dipole pairs. An ammeter in series allowed the experimenter to monitor the amount of current being applied through the circuit. Although the stimulus generator was designed to be able to deliver a wide range of electric stimuli, only a single stimulus type, a 1 cm dipole-separation distance with an applied current of 6.0 μA, was used for the trials. This stimulus was chosen based on the parameters that elicited the best response from juvenile scalloped hammerhead sharks (Kajiura, 2001b).

Current from the stimulus generator was delivered to the target dipoles *via* underwater cables and seawater-filled polyethylene tube (Tygon, Akron, USA) salt bridges. Four pairs of shielded 18AWG SO underwater cables (Impulse Enterprise, San Diego, USA) were plugged into the stimulus generator. The cables passed current to seawater-filled polyethylene tubes *via* underwater connectors with gold-plated stainless steel pins (see Kalmijn, 1978). One end of a 50 cm length of polyethylene tubing was fitted snugly over the rubber sleeves that partially encased the pins of the underwater connectors. The seawater-filled polyethylene tubing formed a salt bridge between the underwater connector and the electrode array. The electrode array consisted of a 1 m² clear acrylic plate that was divided from the corners into four quadrants of equal area (Fig. 1). Within each quadrant, a pair of holes was drilled with a separation of 1 cm. This reflected the size of naturally occurring prey items in the stomach of juvenile scalloped hammerhead sharks (A. C. Bush, personal communication). The salt bridges were inserted through the holes from the

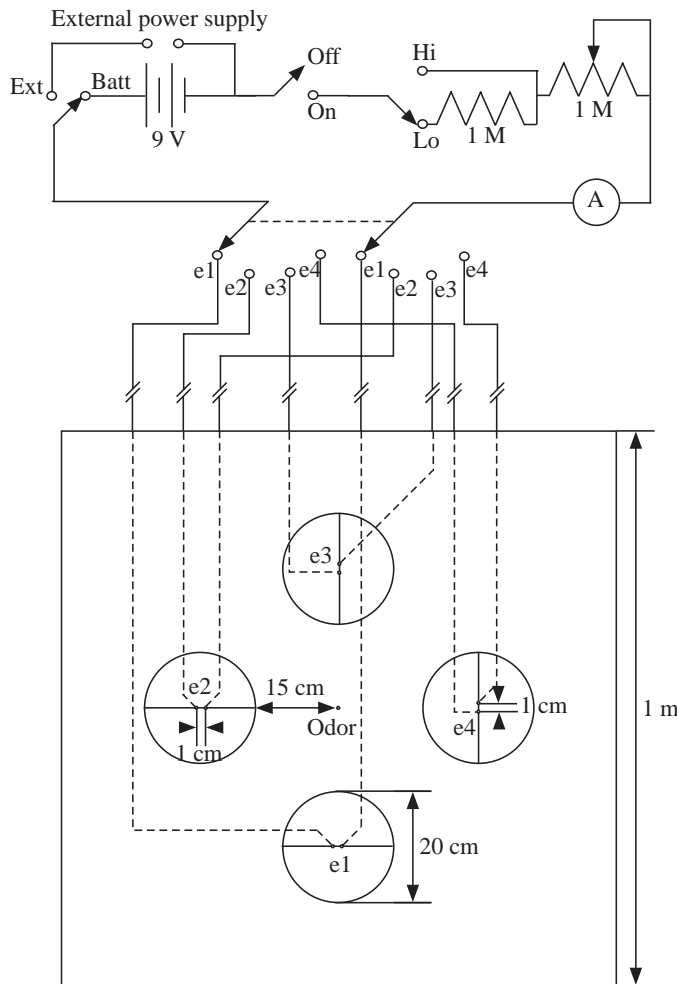


Fig. 1. Circuit diagram and electrode array used to study the response of scalloped hammerhead and sandbar sharks to prey-simulating dipole electric fields. During each trial, one of the four electrode pairs (e1–e4) was activated with a weak electric current ($6\ \mu\text{A}$), which generated a dipole electric field around the electrodes. Electrodes were spaced 1 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 a 10 cm radius circle was drawn around the center of each electrode pair to serve as a frame of reference for subsequent video analysis. A line drawn on the plate through the dipole axis of each electrode pair was also used in video analysis to reference the orientation angle of the shark with respect to the dipole axis. Batt, internal 9 V battery; Ext, external power supply; Hi, high current pathway through the circuit; Lo, low current pathway through the circuit.

bottom of the plate and were flush with the upper surface. In the center of the plate and equidistant (25 cm) from the center of each electrode pair was a single hole that was used to introduce an odor stimulus to the testing arena. An odor-delivery tube was flush-mounted to the surface of the plate from the bottom and extended from the hole in the center of the plate to a syringe above water. The syringe was fitted with a three-way valve that allowed the experimenter to draw an odor stimulus (squid rinse) from a bucket on the surface and

remotely introduce the odor to the center of the electrode array. Although the clear acrylic plate could be seen by the sharks, its primary function was to mask extraneous electric fields in the immediate vicinity of the dipoles. Therefore, any bite responses were attributable to the electrodes and not natural prey items nearby.

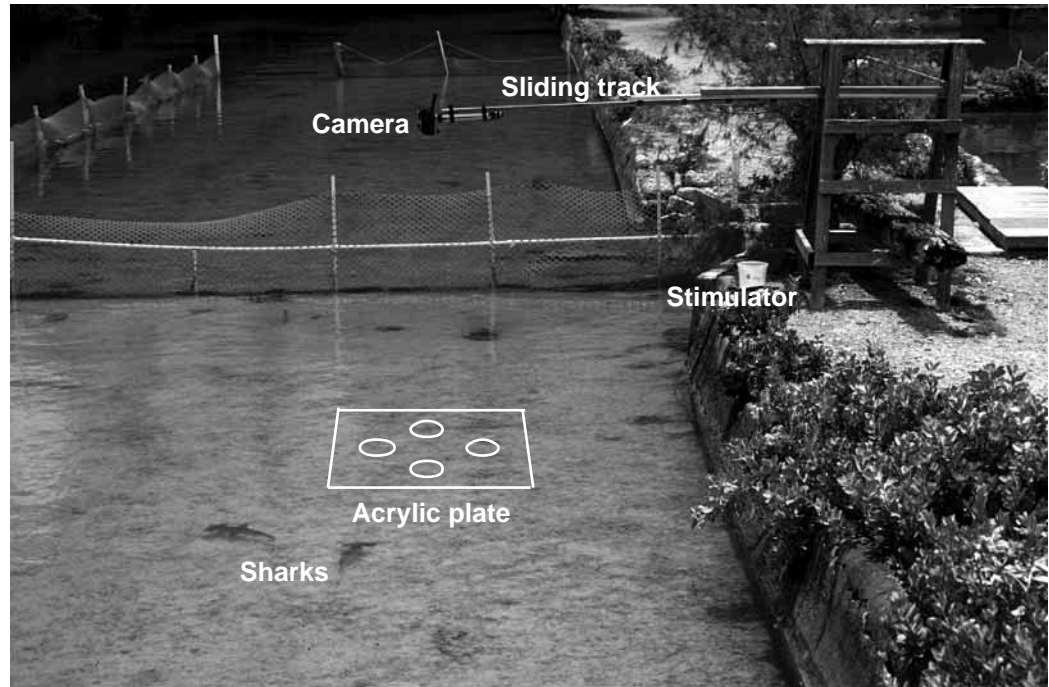
A Sony TR101 Hi8 video camera mounted on a moveable track approximately 2 m above the surface of the water was positioned directly over the plate (Fig. 2). The camera 'record' and 'stop' functions were operated by remote control, which minimized extraneous experimenter movements during an experimental trial. Experiments were conducted primarily at low tide to minimize water distortion of the video image, and the camera was fitted with a polarizing filter that reduced surface glare.

Experimental protocol

At the beginning of each trial, a single shark was introduced to the testing arena and allowed to acclimate for several minutes. A well-acclimated shark would swim throughout the entire pen and not limit itself to swimming along the edge of the pen or along the barrier net. To stimulate the shark to start to search for food, an olfactory cue (squid rinse) was introduced to the pen *via* the odor-delivery tube. During each trial, only one of the four dipoles on the acrylic plate was active at any given time, while the other three served as controls. When the shark detected the odor and began to demonstrate searching behavior (as indicated by increased tail beat frequency, increased frequency of turning and swimming close to the bottom), the video camera was activated and the response of the shark to the electric field was recorded on Hi8 videotape at $30\ \text{frames sec}^{-1}$. A continuous audio commentary of the shark's movements and behavior was recorded on the audio track of the videotape. Once a shark had bitten at a dipole, that dipole was turned off and another dipole was activated. Trials were brief because the shark would become unresponsive (as indicated by decreased tail beat frequency, decreased frequency of turning and swimming throughout the water column) after a couple of minutes. At the end of each trial, the shark was fed to satiation and allowed to rejoin the others on the opposite side of the barrier net. Any excess food was removed from the pen prior to introduction of the next individual to the testing arena. The protocol was repeated for up to eight individuals per day.

The motivational state of individual sharks was assessed by quantification of their swimming behavior (i.e. tail beat frequency). The number of tail beats in one minute was counted in sharks that were not aroused by food odor and was counted again after introduction of food odor when the sharks were aroused to search for food. Tail beat frequency of food-odor-aroused and non-aroused sharks of both species were compared using analysis of variance (ANOVA). The scalloped hammerhead sharks were starved for 2 days between trials, whereas it was necessary to starve the sandbar sharks for 4–6 days between trials in order to elicit a comparable increase in tail beat frequency when exposed to a food odor stimulus.

Fig. 2. Experimental apparatus used to study the response of scalloped hammerhead and sandbar sharks to prey-simulating dipole electric fields. One of the four electrode pairs (circles on the acrylic plate) was activated with a weak electric current, which generated a dipole electric field around the electrodes. The response of the sharks was recorded with a video camera mounted onto the end of a sliding track and positioned directly above the center of the electrode array.



Experiments were conducted with relatively naive sharks that were exposed to the activated dipoles for a maximum of three trials. After a maximum of three experimental trials (over 1–2 weeks), sharks were released back into the wild. All experiments were conducted under University of Hawaii IACUC-approved protocol.

Analysis

The Hi8 video footage was digitized on a computer equipped with a video digitization board that captured a high-resolution image (640 pixels \times 480 pixels) of each frame at 30 frames sec^{-1} . Digital movies of 320 pixels \times 240 pixels and 30 frames sec^{-1} were constructed of each bite at the dipole. The reduced size was necessary to allow the video to play from a CD-ROM at full motion 30 frames sec^{-1} . Each sequence would start with the frame in which the shark entered the field of view and would end when the shark bit the dipole and swam out of the field of view. The criteria used to define biting behavior were deliberately conservative, and bites were considered to have occurred only if the shark clearly snapped its lower jaw in an attempt to bite at the electrodes. Biting behavior could be reliably detected on the video record by observing the shark positioning its head directly over the electrodes and the gill flaps flaring as water was passed through the mouth and over the gills.

Frame-by-frame analysis of the video footage allowed detailed observation of the orientation pathways of the sharks and enabled the quantification of orientation distance to the dipole and the position of the shark relative to the dipole axis (Fig. 3). An orientation towards a dipole was defined as a deviation of $>20^\circ$ from the preceding course trajectory. The resulting change in trajectory would result in any portion of the

shark's head passing directly over the active dipole. The frame in which the shark initiated its orientation to the dipole was copied to an image-analysis program (NIH Image v1.6.1, US National Institutes of Health, <http://rsb.info.nih.gov/nih-image/>). The 20-cm diameter frame-of-reference circle drawn around each dipole was used to calibrate the image-analysis software. The orientation distance was measured from the center of the dipole to the closest side of the shark's head. In addition to the orientation distance, the initial angle of the shark with respect to the dipole axis was also measured (Fig. 3). From these data (distance and angle with respect to the dipole axis), the electric-field intensity (i.e. voltage gradient, V cm^{-1}) at the position where the shark initiated a turn towards the electrodes was calculated using the 'ideal dipole field' equation from Kalmijn (1982). This electric-field intensity value was taken as the behavioral-response threshold of the sharks to the electric stimulus. The calculated field intensity values were log transformed to allow application of general linear models and compared between the two species.

Search area

Search area was defined as the swath of substratum that passed immediately under the head of the shark over unit time. The search area was quantified by analyzing the swimming path of sharks as they swam in the absence of introduced olfactory stimuli. Ten of the 13 hammerheads and 10 of the 12 sandbar sharks were randomly selected for quantification of search area. The sharks were videotaped as they swam in a slow, steady, straight trajectory under the camera mount. Digital movies were created of each pass and analyzed on the computer by marking points over each eye for every other frame of a 1 s sequence (Fig. 4). A polygon was created by

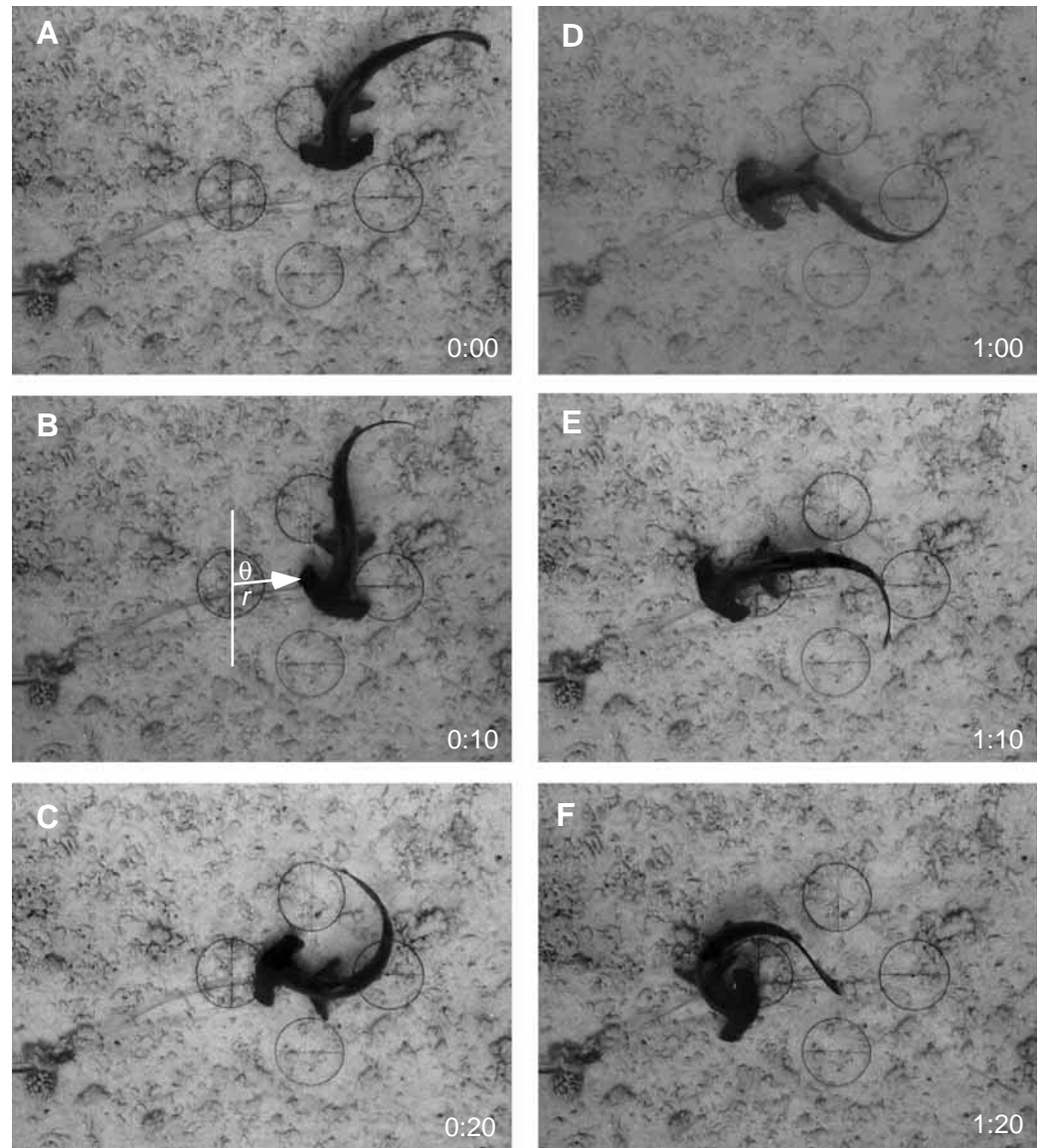


Fig. 3. Representative sample of a scalloped hammerhead shark orientation to a dipole electric field. (A) The shark is swimming within frame prior to orientation to the electric field. (B) The shark initiates an orientation to the dipole, and the distance (r) of the shark with respect to the center of the dipole is measured, as well as the angle (θ) with respect to the dipole axis. (C) The shark swims towards the electrodes and (D) bites at the electrodes. After biting, the shark (E) swims away and (F) promptly turns back towards the electrodes. The counter in the lower right of each frame denotes the time in seconds followed by the frame number.

connecting each point, and the area of the polygon was calculated by calibration of the image-analysis software to a known measurement within the field of view. The area sampled by the head of the shark could thus be quantified and was compared between the two species using a t -test for unequal variances.

A similar technique was used to quantify the velocity of the sharks. The linear distance traveled by the shark in a 1 s period was measured and compared between the two species using a t -test.

Torso flexibility

The maximum lateral flexure demonstrated by scalloped hammerhead and sandbar sharks as they turned towards a dipole electric field was measured by digital video analysis. The video frame in which the shark demonstrated the greatest body flexure towards the dipole was analyzed for six individuals of each species. Lines were drawn from the center

of the snout to the origin of the first dorsal fin and then to the dorsal precaudal notch on the caudal peduncle. The resulting angle was measured for each individual, and the data were pooled within the two species and analyzed using ANOVA.

The degree of flexibility is at least partly attributable to the cross-sectional area of the trunk. Cross-sectional area was quantified from sharks that became incidental mortalities as a result of long-line fishing or other research projects. To measure cross-sectional area, the heads of 14 scalloped hammerhead and 13 sandbar shark individuals of a wide range of sizes were severed in the transverse plane at the posterior edge of the lower jaw. The severed trunk of each head was placed on a piece of paper and the trunk area was traced. The traced area was digitized and measured using image-analysis software (NIH Image v1.61), and the data were analyzed using analysis of covariance (ANCOVA).

Results

Thirteen scalloped hammerhead and 12 sandbar sharks were tested for their response to prey-simulating dipole electric fields. The size range of the sharks is listed in Table 2 and the mean total length of the sharks did not differ significantly

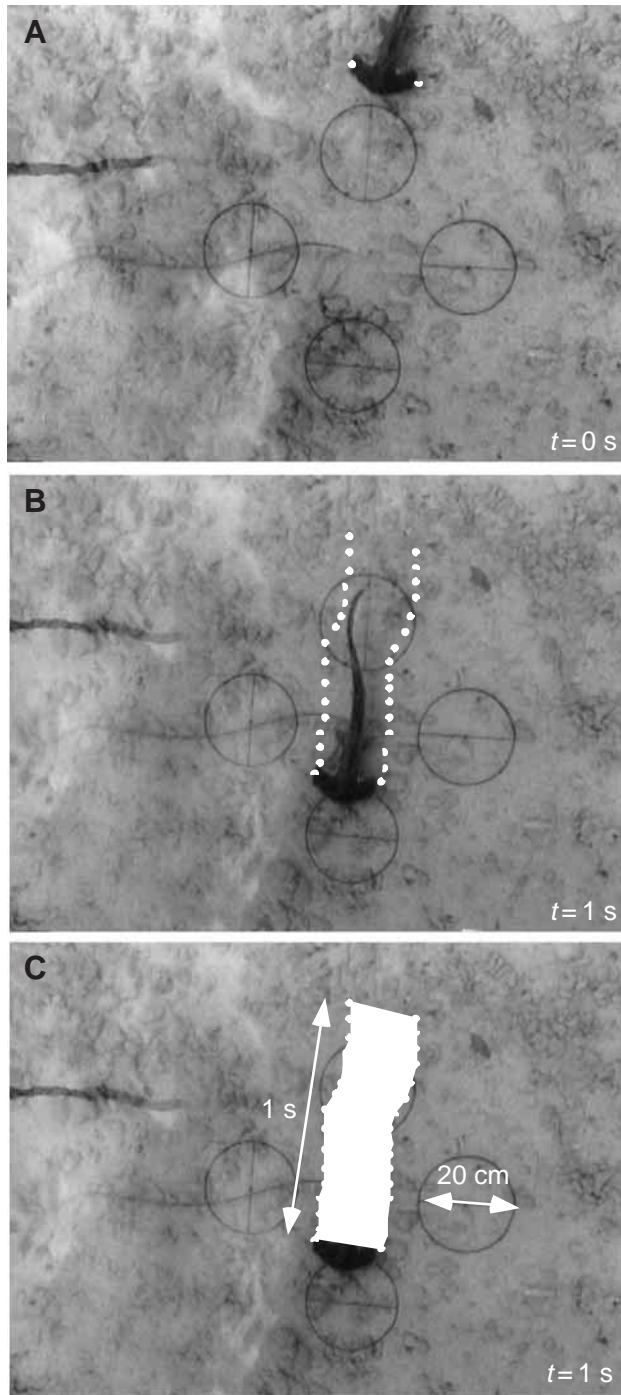


Fig. 4. Quantification of the search area of a scalloped hammerhead shark. (A, B) The positions of the distal extremes of the head were marked on every other frame for a 1 s period. (C) The area that the head had covered in that 1 s period was measured by reference to a known area; a 20 cm diameter circle drawn on the electrode array.

between the species (ANOVA; $F_{1,23}=3.598$, $P=0.0705$). When aroused by the food odor stimulus, both species demonstrated a marked change in swimming behavior. The sharks increased their swimming velocity and swam close to the bottom, with the ventral surface of the head <2 cm above the substratum. Both species demonstrated a feeding response by biting at the active dipole and ignoring the non-active dipoles. Sharks sometimes bit repeatedly at an active dipole but immediately stopped biting when the electric current was turned off. Although the hammerhead sharks always responded by biting at the active dipole, the sandbar sharks occasionally did not bite even when they passed within 10 cm of the electrodes. These 'no bite' responses accounted for 13.3% of the total passes. Only responses in which a clear orientation ($>20^\circ$ change in course trajectory) or bite were seen were included in subsequent analyses.

Orientation distance and angle

The primary variate in all behavioral studies of electroreception is the distance from the center of the dipole at which a shark initiates its orientation. Both species initiated orientations from the same range of distances (Fig. 5). The scalloped hammerhead sharks demonstrated the greatest number of orientations from distances of <5 cm, with a maximum orientation distance of 30.6 cm. The sandbar sharks demonstrated the greatest number of orientations from distances of <10 cm and orientated from a maximum distance of 31.6 cm.

If taken in isolation, the distance from the electrodes at which the orientation was initiated is an insufficient indicator of the electric-field intensity to which the shark responds. Because the electric-field intensity decreases as a cube with increasing distance from the electrodes, orientations initiated at a greater distance from the center of the dipole are at a lower electric-field intensity. The electric-field intensity not only decreases as a cube with increasing distance but also varies as a cosine function with respect to the dipole axis (Kajiura, 2001b). The electric-field intensity is greatest in the plane parallel to the dipole axis and decreases to a theoretical null in the perpendicular plane. It was hypothesized that sharks would initiate orientations at a greater distance from small axis angles where the electric-field intensity is greatest. This hypothesis was supported by the data. Both species demonstrated a significant inverse relationship between orientation distance and angle with respect to the dipole axis (Fig. 6; regression; S .

Table 2. Mean shark total length and size range for scalloped hammerhead and sandbar sharks used in these experiments

Species	N	Mean length \pm S.E.M. (cm)	Range (cm)
<i>Sphyrna lewini</i>	13	62.7 \pm 2.60	53.3–79.5
<i>Carcharhinus plumbeus</i>	12	68.7 \pm 1.68	62.0–79.0

There was no significant difference in mean size between the two species.

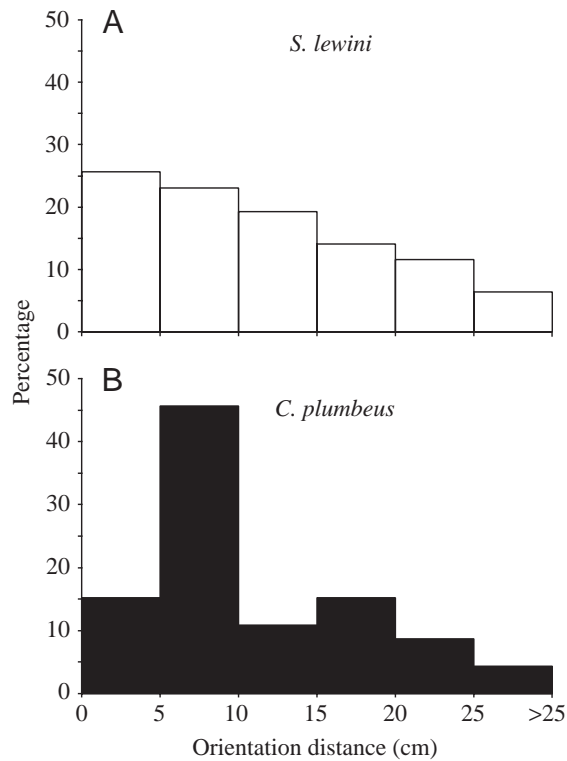


Fig. 5. Histogram of the percentage of orientations throughout the range of orientation distances. Whereas the scalloped hammerhead sharks *Sphyrna lewini* (A) demonstrated a uniform decrease in number of orientations with increasing distance, the sandbar sharks *Carcharhinus plumbeus* (B) demonstrated a greater number of orientations from distances between 5 cm and 10 cm.

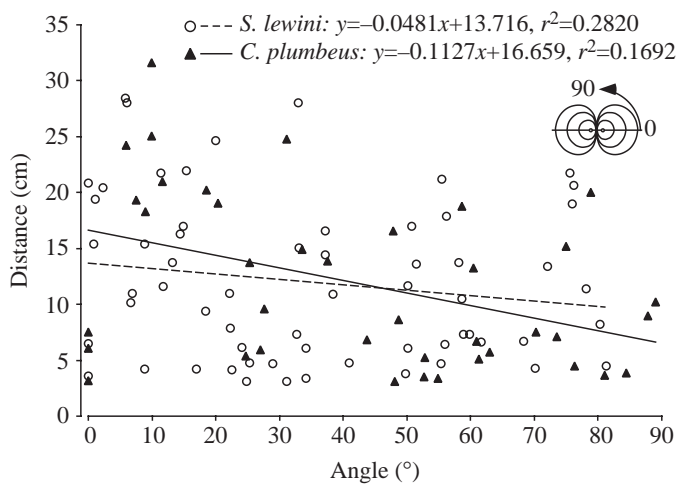


Fig. 6. Orientation distance plotted against angle with respect to the dipole axis. Both scalloped hammerhead sharks *Sphyrna lewini* and sandbar sharks *Carcharhinus plumbeus* oriented from a significantly greater distance at smaller axis angles where the electric-field intensity is greatest. A model dipole in the corner shows voltage equipotentials around the dipole axis.

lewini $F_{1,57} = 4.715$, $P = 0.0342$, $r^2 = 0.2820$, $N = 13$; *C. plumbeus* $F_{1,35} = 20.376$, $P < 0.0001$, $r^2 = 0.1692$, $N = 12$). In other words, both species initiated orientations from a greater distance at small axis angles. To detect the same electric-field intensity, the sharks needed to be closer to the dipole when they encountered the field at angles of approximately 90° . The initial angle of encounter with respect to the dipole axis did not differ from a random distribution for either species (regression; *S. lewini* $F_{1,8} = 3.329$, $P = 0.1108$, $N = 13$; *C. plumbeus* $F_{1,8} = 0.615$, $P = 0.4587$, $N = 12$). In other words, the sharks initiated orientations from any point around the center of the dipole. Therefore, although the sharks initiated orientations from all around the dipole, they oriented from a greater distance when they initiated orientations from small axis angles.

Behavioral-response threshold

The electric-field intensity was calculated from the position at which the shark initiated its orientation to the dipole. This electric-field intensity value was defined as the behavioral-response threshold. Both species initiated approximately 70% of orientations at an electric-field intensity of $< 0.1 \mu\text{V cm}^{-1}$ (Fig. 7). The percentage of orientations at higher electric-field intensities decreased markedly for both species. Data from

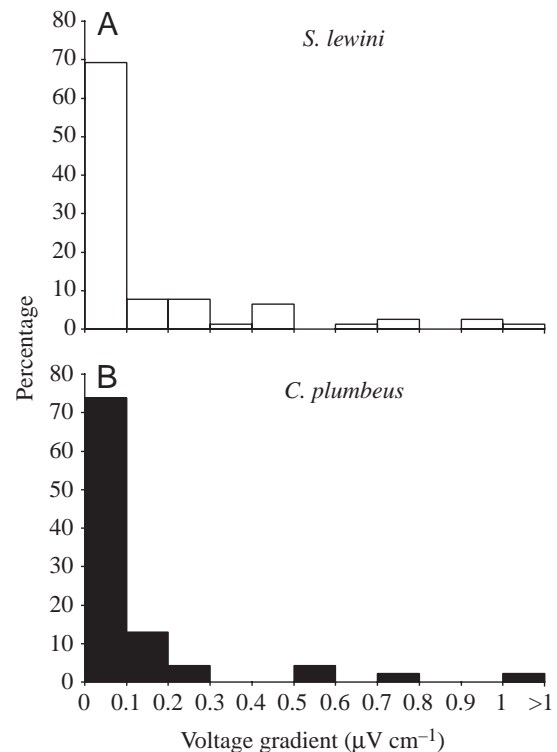


Fig. 7. Histogram of the percentage of orientations at electric-field intensities of $< 1 \mu\text{V cm}^{-1}$. Scalloped hammerhead sharks *Sphyrna lewini* (A) and sandbar sharks *Carcharhinus plumbeus* (B) demonstrate similar distributions across the entire range of field intensities. Approximately 70% of orientations were initiated to stimuli of $< 0.1 \mu\text{V cm}^{-1}$ for both species, with few orientations requiring a higher field intensity to initiate a response.

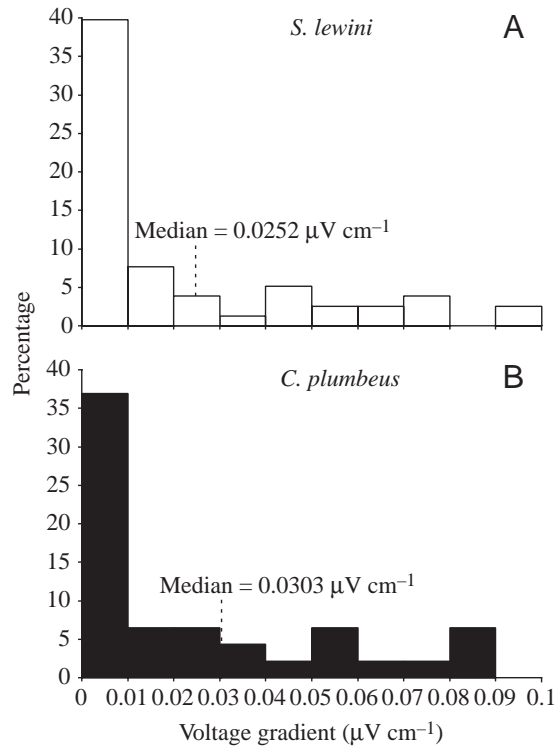


Fig. 8. Histogram of the percentage of orientations at electric-field intensities of $<0.1 \mu\text{V cm}^{-1}$. Scalloped hammerhead sharks *Sphyrna lewini* (A) and sandbar sharks *Carcharhinus plumbeus* (B) demonstrate similar distributions across the entire range of field intensities. Both species initiated approximately 35–40% of orientations to stimuli of $<0.01 \mu\text{V cm}^{-1}$.

orientations to an electric-field intensity of $<0.1 \mu\text{V cm}^{-1}$ are shown in Fig. 8. The frequency distribution of orientations was remarkably similar for the two species, with both species initiating approximately 35–40% of all orientations to an electric-field intensity of $<0.01 \mu\text{V cm}^{-1}$. Because of the strongly skewed distribution of the behavioral-response threshold values, median values rather than means were compared between the two species (Sokal and Rohlf, 1981). The median behavioral-response threshold for the scalloped hammerhead sharks was $0.0252 \mu\text{V cm}^{-1}$ and for the sandbar sharks was $0.0303 \mu\text{V cm}^{-1}$. The log-transformed median values did not differ between the species (ANOVA; $F_{1,119}=0.014$, $P=0.9064$), which indicates that the scalloped hammerhead sharks did not demonstrate greater behavioral sensitivity to dipole electric fields than did the sandbar sharks. The minimum electric-field intensity that elicited a response was 0.4 nV cm^{-1} for the scalloped hammerhead sharks and 0.5 nV cm^{-1} for the sandbar sharks.

Behavioral response

The motivational state of the sharks was assessed by counting the tail beat frequency of individuals both prior to and subsequent to the introduction of a food odor stimulus. In the absence of introduced olfactory stimuli, the sharks swam in a

slow, steady, relatively straight trajectory. By contrast, when exposed to a food odor stimulus, both species demonstrated a marked change in swimming behavior characterized by an increased tail beat frequency and more frequent changes in swimming trajectory. The scalloped hammerheads had a significantly higher tail beat frequency than the sandbar sharks in both food-odor-aroused (ANOVA; $F_{1,18}=11.436$, $P=0.0033$) and non-aroused (ANOVA; $F_{1,30}=11.138$, $P=0.0023$) states. However, both species demonstrated a similar and significant relative increase in tail beat frequency from non-aroused to aroused states (*S. lewini* $1.76\times$ non-aroused state, *C. plumbeus* $1.61\times$ non-aroused state).

Although both species bit at the dipole, the characteristic orientations to a stimulus differed. The scalloped hammerheads typically responded by swimming within detection range of the dipole, then turning sharply towards the dipole. A subset of 25 randomly selected orientation events demonstrated a mean turn angle of $101.0^\circ \pm 4.56\text{SE}$ with a minimum of 41.1° and a maximum of 137.3° for the scalloped hammerhead sharks. The sandbar sharks demonstrated a mean turn angle of $68.5^\circ \pm 4.97\text{SE}$ with a minimum of 23.9° and a maximum of 120.7° . In the process of executing a turn, the scalloped hammerheads appeared to pivot in position, with the side of the head that was closest to the dipole remaining nearly stationary relative to the center of the dipole while the body bent into a C shape. By contrast, the sandbar sharks oriented towards the dipole by swimming in a broader arc that eventually brought them to the center of the dipole. Several distinguishable orientation patterns were recognized in both species (Fig. 9).

Single turn

The ‘single turn’ was by far the most common type of orientation and accounted for over half of all orientations for both species. As the shark was swimming within the field of view of the video camera, it made an abrupt turn ($>20^\circ$ change in course trajectory) and changed course to bring its head directly to the center of the dipole, which it then bit. The distance of orientation was measured from the center of the dipole to the point at which the shark initiated its turn towards the dipole. The edge of the head closest to the electrodes was chosen as the point of reference on the shark. No part of the shark’s body was over the electrodes when the shark initiated its turn. A single turn was, by definition, only one change in trajectory with no subsequent course correction required to position the shark’s head over the center of the dipole.

Straight

A ‘straight’ approach was described as the shark swimming into the field of view of the video camera on a trajectory that brought any part of its head directly over the active dipole. The shark would abruptly stop and bite at the active dipole. Because there was no overt response, no value could be ascribed to the electric-field intensity that initiated a response. Thus, a straight approach was characterized by a trajectory that brought the shark from out of frame over the center of the dipole with

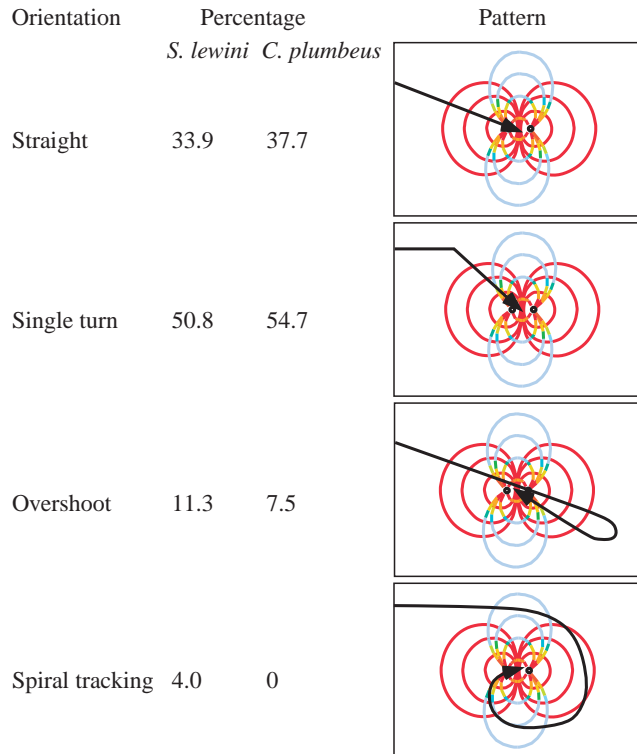


Fig. 9. Orientation pathways demonstrated by scalloped hammerhead sharks *Sphyrna lewini* and sandbar sharks *Carcharhinus plumbeus* with frequency of occurrence of each type. Solid red lines indicate voltage equipotentials around the dipole, and black arrows indicate the path taken by the sharks. Current flow is indicated by the colored lines, with highest intensity (red) nearest the center of the dipole and lowest intensity (blue) furthest away. Whereas the scalloped hammerhead sharks demonstrated a greater variety of orientation pathways, the sandbar sharks were unable to exhibit the same repertoire of behaviors owing to their stiffer bodies.

no change in course. Straight approaches were seen in approximately one-third of all passes in both species.

Overshoot

'Overshoot' was sometimes seen in rapidly swimming sharks. Sharks would swim straight over the electrodes without biting then quickly double back and bite at the electrodes. The shark would experience increasing electric-field intensity as it swam over the dipole, and the field intensity would decrease as the shark moved past the dipole. It was presumed that the shark turned back towards the electrodes at the point where it failed to detect the electric field. The maximum distance of the head past the electrodes was quantified for the overshoot response. This response was seen in 11.3% of orientations for the scalloped hammerhead sharks and 7.5% of orientations for the sandbar sharks.

Spiral tracking

A 'spiral tracking' orientation occurred when the shark made a series of turns in the same direction that brought it to the

center of the dipole through a spiral pattern. This is distinct from the 'single turn' orientation in which only one turn was made to bring the shark directly to the center of the dipole. The distance of orientation was measured from the point at which the shark first turned towards the electrodes. The spiral tracking orientation typically described a path that followed the curvature of the electric field lines to the center of the dipole. Spiral tracking was seen in only 4.0% of orientations for the scalloped hammerhead sharks and was not seen in the sandbar sharks.

Search area

The area of the substratum sampled by the head in 1 s was quantified for 10 individuals of each species; a subset of the original sample. The area searched over unit time did not differ significantly with size of the individual for either species (regression; *S. lewini* $F_{1,9}=1.359$, $P=0.2774$; *C. plumbeus* $F_{1,9}=1.995$, $P=0.1955$). Because there was no difference in area searched across the size range of tested sharks, the data were pooled and compared between the species using a *t*-test. The mean search area per second for the scalloped hammerhead sharks was $677.8\text{ cm}^2\text{ s}^{-1}$ and for the sandbar sharks was $298.0\text{ cm}^2\text{ s}^{-1}$. Although the tested scalloped hammerhead individuals were significantly smaller than the sandbar (*t*-test; $t_{18}=5.392$, $P<0.0001$), they sampled a greater area of the substratum per unit time than did the sandbar sharks (*t*-test for unequal variances; $t_{18}=8.619$, $P<0.0001$).

The velocity of the sharks was quantified concurrently with the search area. The scalloped hammerhead sharks demonstrated a mean velocity of 37.6 cm s^{-1} , and the sandbar sharks demonstrated a mean velocity of 38.5 cm s^{-1} . There was no difference in velocity between the two species (*t*-test; $t_{14}=-0.348$, $P=0.7316$).

Flexibility

The maximum body flexure was quantified for individuals of both species as they turned towards an active dipole. Scalloped hammerhead sharks displayed a mean maximum flexure angle of 85.9° , whereas sandbar sharks displayed a mean maximum angle of 113.3° (Fig. 10). Scalloped hammerhead sharks were able to bend at a significantly more-acute angle than the sandbar sharks (*t*-test; $t_{43}=7.083$, $P<0.0001$, $N=6$). This difference in flexibility is partially attributed to the cross-sectional area of the trunk. The sandbar sharks had a significantly greater trunk cross-sectional area than the scalloped hammerhead sharks across a wide range of sizes (Fig. 11; ANCOVA; $F_{1,23}=14.134$, $P=0.001$).

Discussion

This study is the first to compare behavioral responses to prey-simulating bioelectric fields in two shark species in order to test the predictions of the enhanced electroreception hypothesis. The enhanced electroreception hypothesis predicts that hammerhead sharks will sample a greater area of the substratum than comparably sized carcharhinid sharks with no

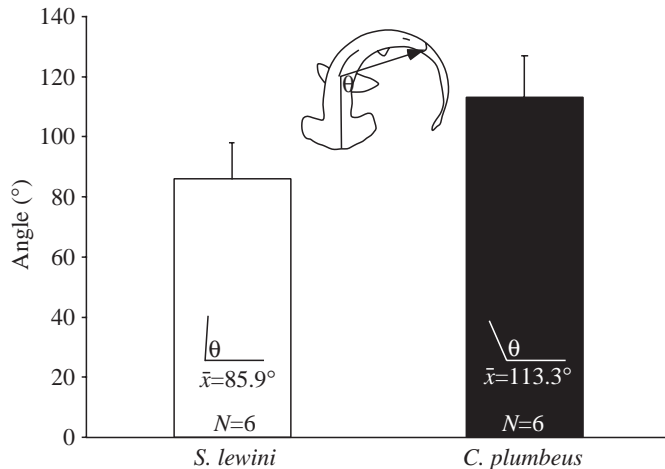


Fig. 10. Histogram of maximum body flexure of scalloped hammerhead sharks *Sphyrna lewini* and sandbar sharks *Carcharhinus plumbeus*. Scalloped hammerhead sharks demonstrated a greater degree of flexibility, with a mean maximum flexure (\bar{x}) of 85.9°, whereas the \bar{x} of sandbar sharks was 113.3°.

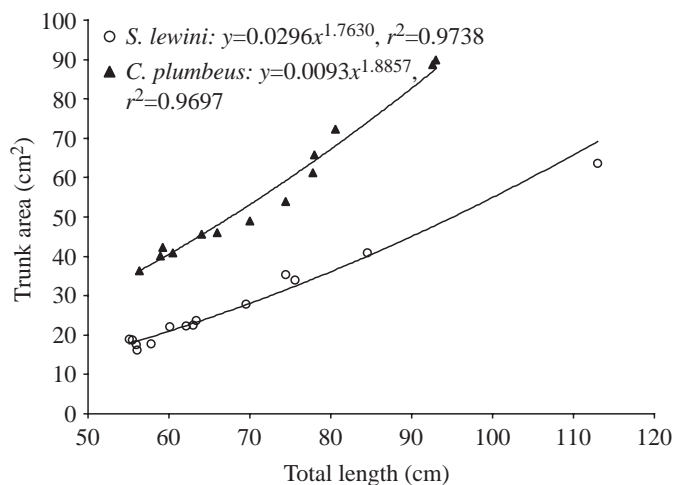


Fig. 11. Cross-sectional area of the trunk (cm²) of scalloped hammerhead sharks *Sphyrna lewini* and sandbar sharks *Carcharhinus plumbeus*. Sandbar sharks have a significantly greater cross-sectional trunk area than the scalloped hammerhead sharks across a wide range of sizes.

loss in sensitivity to electric fields. These predictions were tested under electrically noisy semi-natural conditions to best determine the natural response of sharks in the wild.

Sensitivity

The first prediction of the enhanced electroreception hypothesis is that the scalloped hammerhead sharks should demonstrate equivalent or greater sensitivity to electric fields than similar sized sandbar sharks. This prediction is based on the morphology of the electrosensory system within the laterally expanded sphyrnid cephalofoil. Scalloped hammerhead sharks possess a greater number of electrosensory

pores than sandbar sharks, and these electroreceptors are spread over a greater surface area, thus providing both species with an equivalent pore density (Kajiura, 2001a). The wider head also allows sphyrnids to possess longer ampullary tubules (see Chu and Wen, 1979), which will confer greater sensitivity to uniform electric fields but not necessarily to dipole fields (Murray, 1974; Bennett and Clusin, 1978; Tricas, 2001). Although it was not possible to determine directly what the sharks were capable of detecting (i.e. sensitivity), their behavior was used as an indicator that they had detected and were responding to the stimulus. The present study determined a behavioral-response threshold by calculation of the minimum electric-field intensity that elicited a behavioral response by the sharks. Both species demonstrated similar behavioral-response thresholds, with median responses from 0.025–0.030 $\mu\text{V cm}^{-1}$.

Over 40% of the orientations for both species were to very low electric-field intensities ($<20\text{nV cm}^{-1}$), which indicates that both species detect and respond to extremely weak electric fields. The minimum electric-field intensity that elicited a response was also remarkably similar for the two species ($<1.0\text{nV cm}^{-1}$).

Although the enhanced electroreception hypothesis predicts that hammerhead sharks will demonstrate greater sensitivity to electric fields than carcharhinid sharks, this prediction was not supported by the data. There are several explanations as to why a difference was not seen. A shark might well be able to detect an electric field but not exhibit an overt reaction until the electric field intensity exceeds a behavioral-response threshold, and that threshold may differ between the two species. Perhaps the scalloped hammerhead sharks are indeed more sensitive than the sandbar sharks but also have a greater behavioral inhibition that prevents them from responding immediately upon detection of a stimulus. Thus, two sharks with different sensitivities could have the same behavioral-response threshold, which would superficially make it appear that there was no difference in sensitivity between the species.

Even if the sharks possessed the same sensitivity, the behavioral-response threshold may differ as a function of motivational state. A highly motivated shark may demonstrate a lower response threshold (i.e. apparently greater sensitivity) than a shark that is not aroused or hungry. Because the swimming velocity was the most obvious change in behavior after introduction of food odor, tail beat frequency was used as a measure of motivation. For both species, the tail beat frequency of sharks aroused by food odor was approximately 1.6–1.7 \times the tail beat frequency of non-aroused sharks. The sandbar sharks had to be starved for much longer than the scalloped hammerhead sharks to achieve a similar increase in tail beat frequency. If the tail beat frequency is not a comparable measure of motivation between the species, one species might have been more highly motivated than the other. If the sandbar sharks were more highly motivated, they might have responded to lower electric-field intensities and thus appeared to demonstrate equal sensitivity to the scalloped hammerhead sharks.

Although there was no apparent difference in minimum

response threshold between the two species, those data were based only on clear orientations and bites at the dipoles. Approximately 13% of the sandbar shark passes within 10 cm of the electrodes failed to elicit a bite response, whereas the scalloped hammerheads always bit. The failure to initiate a bite was probably not due to an inability to detect the stimulus but due to a lower motivational state. Alternatively, although the stimulus used in this experiment ($6\mu\text{A}\times 1\text{ cm}$) was the best for eliciting a response from scalloped hammerhead sharks (Kajiura, 2001b), it might have been a sub-optimal stimulus for eliciting a response from the sandbar sharks. A different combination of parameters might have caused the sandbars to bite more readily rather than ignore the dipoles in >10% of the passes. Nonetheless, the comparative behavioral response of the two species to the same stimulus remains valid, and the fact that the scalloped hammerheads always bit may indicate that they are functionally more sensitive than the sandbars.

Orientation pathways

The diversity of orientation pathways indicates that the response of the sharks to electric fields is more varied than previously reported and is not simply a reflex or fixed-action pattern. Previous work simply states that sharks respond with a turn towards the active dipole (Kalmijn, 1971, 1978, 1982; Johnson et al., 1984). The ability to analyze responses frame-by-frame provides greater temporal resolution to the analysis of orientation pathways, thus contributing additional details.

Approximately one-third of all bites at the dipoles were the result of straight approaches from outside the field of view of the video camera. Given the approximate dimensions of the field of view (approximately $99\text{ cm}\times 132\text{ cm}$) and the width of a scalloped hammerhead shark cephalofoil (15 cm), the maximum probability of encountering a given dipole along a straight trajectory is 0.2325. The disproportionate number of straight approaches (*S. lewini*, 0.339; *C. plumbeus*, 0.377) may indicate that the sharks initiated orientations from outside the field of view of the video camera and swam in a straight trajectory towards the center of the dipole. Attempts were made to eliminate this problem by having a large field of view (approximately $99\text{ cm}\times 132\text{ cm}$) with respect to the maximum orientation distance (approximately 30 cm). Nonetheless, because the field of view of the video camera was somewhat variable (depending on the extent of zoom), and because the electrode array was not always centered in the field of view, it is conceivable that some orientations might have been initiated from outside the field of view.

The straight approach was unable to provide information about the point at which the shark detected the electric field. The shark could have detected the field at any point along its path, but, as there was no obvious change in trajectory or other overt response, the point at which the shark detected the field remains unknown. In fact, none of the orientation pathways provides direct information on the stimulus intensity the shark is capable of detecting, only on the stimulus intensity to which the shark actually responds.

In the overshoot orientation, the shark moved past the

stimulus until it was presumably outside the detection range, then abruptly turned, doubled back to the dipole and bit at it. Why the sharks passed over the stimulus without stopping is unclear. It might be that the sharks were simply moving at such a great velocity that their pliant pectoral fins were unable to provide sufficient deceleration to allow them to stop directly over the stimulus. Alternatively, perhaps the sharks were unable to determine the position of the center of the dipole until they had moved past it and detected the inverse field polarity. Although the scalloped hammerheads were able to reverse direction very quickly and return to the center of the dipole along nearly the same path, the sandbars required a broader arc to double back on an overshoot orientation.

Spiral tracking is perhaps the most interesting orientation pathway, as the scalloped hammerhead sharks appeared to follow the direction of current flow towards the center of the dipole. Freshwater electric fishes align their bodies parallel to lines of current flow and, by maintaining this alignment, swim to the center of an electric dipole (Schluger and Hopkins, 1987; Davis and Hopkins, 1988). Similar orientation behavior is seen in the sculpin (*Cottus bairdi*), in which the lateral line is used to orient to and follow dipole pressure flow lines of a vibrating sphere (Coombs and Conley, 1997). In each of these examples, the orientation path follows along current (or pressure) flow lines, and it is reasonable to suggest that sharks are capable of the same type of orientation.

Orientation mechanisms

Two mechanisms have been proposed to explain the ability of sharks to orient accurately to the center of an electric dipole (Kalmijn, 1997). Once a shark detects an electric field, it could orient to the source by following changes in the direction of the field or by analysis of the field configuration. The sharks may use both methods to localize the source of the electric field. If the sharks respond only to changes in the direction of the field and swim to maintain a constant angle with respect to the field, they would arrive at the center of the dipole (Kalmijn, 1997). Although this is not the most direct path, it does describe the spiral tracking pattern of orientation exhibited by the scalloped hammerhead sharks. Alternatively, the sharks might analyze the field configuration to derive the location of the dipole source (Kalmijn, 1997). This would necessitate the shark being able to sample the field differentially across its head. If differential sampling is utilized, the electroreceptors spaced over a greater area on the laterally expanded sphyrnid cephalofoil may provide increased spatial resolution compared with that of similar sized sharks of other families. Whereas a sphyrnid shark would be better able to detect a voltage gradient across the width of the cephalofoil, a carcharhinid shark, with an electroreceptor distribution that is laterally constrained by its head morphology, would not be able to sample as great a gradient. Regardless of head morphology, spatial analysis of an electric field is feasible only when the shark is well within detectable range of the dipole and might be a secondary approach strategy after the shark initially orients based on the direction of the field (Kalmijn, 1997). Although the single turn

orientation is best explained by the shark deriving the location of the dipole by differential sampling across the head, the spiral tracking can be explained by the shark following the direction of the field to arrive at the center of the dipole. Therefore, the results of this study provide partial support for both mechanisms hypothesized by Kalmijn (1988, 1997). However, sharks may possess multiple techniques for localization of electric dipole sources, including algorithms not yet elucidated.

Flexibility and maneuverability

Although both species demonstrated similar responses to the dipole electric field, the sandbar sharks exhibited a more limited repertoire of orientation pathways. Whereas the scalloped hammerheads demonstrated four different orientation pathways to a dipole (Fig. 9), the sandbars failed to demonstrate the spiral tracking orientation. The absence of this orientation pathway may be attributed to the morphology of the two species. The hydrodynamic properties of the sphyrnid cephalofoil confer greater maneuverability by decreasing stability (Nakaya, 1995). The cephalofoil thus enables sphyrnids to turn more quickly and sharply than is possible for a carcharhinid shark.

A second factor that might limit the maneuverability of a sandbar compared with that of a hammerhead shark is the cross-sectional area of the trunk. Whereas scalloped hammerheads have a greater head width than comparably sized sandbar sharks (Kajiura, 2001a), they also have a smaller trunk cross-sectional area (Fig. 11). This small trunk area may enable the scalloped hammerhead sharks to bend laterally more easily, which will manifest itself in greater maneuverability and thus a potentially larger repertoire of orientation behaviors.

The scalloped hammerhead sharks demonstrated a smooth gradation of decreasing frequency of orientations at increasing distances (Fig. 5). However, the sandbar sharks demonstrated a distinct peak at a distance of 5–10 cm. This peak might be attributable to the differences in trunk flexibility of the two species. The smaller cross-sectional trunk area and greater flexibility of the scalloped hammerhead sharks enabled them to achieve an acute angle of flexure that was significantly different from the obtuse angle demonstrated by the sandbar sharks (Fig. 10). This flexibility, coupled with the hydrodynamic properties of the cephalofoil, allowed the scalloped hammerhead sharks to orient to a stimulus even from very close range. By contrast, the stiffer-bodied sandbar sharks were unable to orient as well from close distances because they were unable to bend with the same degree of flexibility as the scalloped hammerhead sharks. This difference in flexibility would account for the smaller number of orientations from very close range for the sandbar sharks (Fig. 5).

Search area

The second prediction of the enhanced electroreception hypothesis is that sphyrnid sharks will sample a greater area with their electroreceptors than similar sized carcharhinids. This prediction was tested by quantifying the swath of substratum covered by the head of the sharks as they swam

slowly under the video camera. Because the velocity of the two species did not differ, differences in search area can be attributed to the greater head width of the scalloped hammerhead sharks. Although the scalloped hammerheads selected for the subsample were significantly smaller than the sandbar sharks, they sampled a significantly greater area of the substratum per unit time. Therefore, the wider head of the scalloped hammerhead shark greatly increases the amount of substratum sampled, thus increasing the probability of prey encounter. The second prediction of the enhanced electroreception hypothesis is thus supported.

Although the area searched per unit time was quantified as the area immediately under the head of the shark (Fig. 4), the current data indicate that the actual detection range of a prey-simulating electric dipole extends for up to 30 cm laterally from the edge of the head for both species (Fig. 5). Therefore, the effective area sampled is much greater than the conservative value calculated for the two species.

Additional future study

The present study examined electroreception in juveniles of both species. For both species, individuals were free living in the natural environment for an undetermined period before being captured and tested. They had thus been exposed to a variety of naturally occurring bioelectric fields and had no doubt used detection of these fields in their feeding behavior. Future studies could examine the electrosensory response of neonatal sharks born in a captive environment in which they were not exposed to any exogenous bioelectric fields prior to testing. Their response to prey-simulating fields could then be examined to determine if the bite response is innate or part of a learning process in which they learn to associate electric fields with prey.

Additional studies could also examine the response of other sphyrnid species with different head morphologies. The slightly expanded head of the bonnethead shark *Sphyrna tiburo*, combined with the wider trunk and presumably stiffer body, would cause it to respond in a manner intermediate between the scalloped hammerhead and the sandbar shark. At the other morphological extreme within the family Sphyrnidae is the winghead shark *Eusphyra blochii*, which possesses a greatly laterally expanded cephalofoil. It is predicted that the morphology of this species will enable it to sample the greatest area and demonstrate the highest level of flexibility and maneuverability of all the sphyrnids.

The present study tested only a single type of prey-simulating electric stimulus (6.0 μ A \times 1 cm). However, sharks are capable of detecting a variety of prey-simulating electric stimuli as well as non-prey electric fields. Sharks respond to the electric fields of conspecifics (Tricas et al., 1995) and predators (Sisneros et al., 1998) and can theoretically detect induced electric fields caused by swimming through the earth's magnetic field (Kalmijn, 1974; Paulin, 1995) or near geomagnetic anomalies (Klimley, 1993). Therefore, there is a wide range of detectable electric stimuli that remains to be tested.

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