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Electroreception in neonatal bonnethead sharks, *Sphyrna tiburo*

Abstract The ability of sharks to orient to weak electric fields is well documented, but a detailed analysis of orientation pathways is lacking. Digital video analysis was used to quantify the behavioral response of naïve neonatal bonnethead sharks, *Sphyrna tiburo*, to prey-simulating weak electric fields. Sharks less than 24 h post-parturition failed to demonstrate a positive feeding response to the electrodes whereas vigorous biting at the electrodes was observed in all sharks greater than 32 h post-parturition. Orientation behaviors were classified as one of five types: "straight" approach, "single turn," "overshoot," "spiral tracking," and "orient without biting." One-third of all orientations were elicited at stimulus intensities of less than 20 nV cm^{-1}. The median electric stimulus threshold for initiation of orientation was 47 nV cm^{-1} and the minimum was less than 1 nV cm^{-1}. Most orientations to the dipole were from a distance of less than 10 cm with a maximum orientation distance of 22 cm. The innate feeding response to electric stimuli is demonstrated for the first time in a chondrichthyan fish.

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Introduction

The ability of elasmobranch fishes to detect and orient to weak electric fields is well documented (summarized in Kajiura and Holland 2002). Experiments are typically conducted by introducing an odor stimulus to arouse searching behavior in the sharks, which are then presented with a prey-simulating dipole electric field (Kalmijn 1971, 1978, 1982; Kajiura and Holland 2002). Aroused sharks that swim within detection range of the dipole field usually respond by turning sharply toward the electrodes and biting at them as if they were a natural prey item. Although previous work has demonstrated that sharks orient to and bite at electric dipoles, a detailed analysis of orientation behavior is available for only two species, juvenile scalloped hammerhead and sandbar sharks (Kajiura and Holland 2002).

The bonnethead shark, *Sphyrna tiburo*, is a small, coastal shark found in warm temperate waters of the western Atlantic and eastern tropical Pacific (Castro 1983). Adults reach a maximum size of 110 cm and pups are born at a total length of 30–32 cm. Litters of 8–12 pups are born annually in the summer and the pups emerge as fully formed miniature versions of the adults. The pre-branchial head is shovel shaped with a broadly rounded anterior margin and electrosensory pores distributed across the width of the head on dorsal and ventral surfaces (Compagno 1984). The bonnethead shark has a greater number of electrosensory pores than some carcharhinid species (the dusky shark *Carcharhinus obscurus* and the gray reef shark *C. amblyrhynchos*; Raschi 1984 and Daniels 1967, respectively) but has fewer pores than others (the sandbar shark *C. plumbeus* and the blacktip shark *C. limbatus*; Kajiura 2001). Bonnethead sharks are abundant and keep well in captivity, and their small size facilitates handling. These factors combine to make bonnethead sharks an ideal study animal for tests of electroreceptive response.

This article describes and quantifies the orientation responses of neonatal bonnethead sharks to prey-

simulating electric stimuli to test the predictions of the orientation algorithms hypothesized by Kalmijn (1988, 1997) and modeled by Brown (2002). Neonatal sharks were chosen as they have not had a chance to learn a wide variety of orientation patterns and are most likely to demonstrate the simplest algorithm for location of an electric dipole.

Materials and methods

Capture and holding facilities

Pregnant female bonnethead sharks, *Sphyrna tiburo*, were captured by rod and reel fishing on the seagrass flats of Florida Bay around Marathon, Florida. Sharks were quickly transported to the laboratory in a 1-m circular holding tank on a small skiff. Transport time was less than 15 min. The sharks were maintained in either a 4.9-m square tank (1997) or a 7.6-m diameter circular tank (1998) with flow-through seawater supplemented with aeration. Sharks were fed to satiation daily on a diet of cut squid. Females gave birth in the tanks and the neonates were immediately moved to one of three adjacent experimental tanks. The adult females were released within 24 h of giving birth. The experimental tanks were 2.4×4.9-m concrete tanks with a water depth of approximately 0.6 m. Water temperature ranged from 29.4 to 31.5°C and salinity ranged from 31.0 to 31.5 ppt.

All neonates were offered food (cut squid) within 12–16 h of birth but did not eat until at least 24–32 h post-parturition. Qualitative observations were made of sharks between 1 and 5 days post-parturition and data were collected on sharks between 5 and 32 days post-parturition. Up to 25 individuals were maintained in each of the three tanks and no effort was made to test sharks individually.

Experimental apparatus and protocol

The experimental apparatus was identical to that described by Kajiura and Holland (2002). Four pairs of electrodes were evenly distributed around a 1-m^2 acrylic plate that was placed on the bottom of the tank (Fig. 1). The dipole separation distance was 1 cm for all electrode pairs. Salt-bridge electrodes, which consisted of seawater-filled 1-m lengths of Tygon tubing, were pressed through the acrylic plate from the underside so that the tubes opened flush with the surface of the plate. The opposite ends of the tubes were tightly sealed to gold-plated stainless steel underwater connectors at the end of underwater cables (cf. Kalmijn 1978). A stimulus generator on the surface enabled the operator to activate any pair of electrodes and control the amount of applied electric current. Only one electrode pair was activated at any time while the other three served as controls. The current that passed between the active pair of electrodes was monitored constantly with a digital multimeter and was initially regulated in 0.5-µA increments from 5.5 to 8.0 µA. In a subsequent experimental series the current was held constant at 6.0 ± 0.1 µA for all experiments. In the center of the acrylic plate, a single hole, placed equidistant from all the electrode pairs, led to an odor delivery tube that was used to introduce food odor (squid rinse) to the test arena. Odor delivery was precisely controlled through a large syringe and three-way valve. Squid rinse was used as an attractive odorant because sharks were fed on a diet that consisted exclusively of cut squid.

A Chinon SV-8 wide-angle submersible video camera eye was positioned at the surface directly over the active dipole and the lens was submerged to ensure a clear image. No metal parts contacted the seawater thereby eliminating the possibility of generating galvanic fields. The video signal was recorded on Hi8 videotape at 30 frames per second (fps).

To begin an experiment, the acrylic plate was placed on the bottom of the tank with all electrode pairs turned off. A single electrode pair was activated and approximately 50 cm^3 of squid rinse was introduced through the odor delivery tube. The latency

Fig. 1 Experimental apparatus used to test the behavioral response of neonatal bonnethead sharks to electric stimuli. An acrylic plate on the bottom of the tank housed four pairs of electric dipoles that were randomly activated to generate a prey-simulating electric field. Electric current applied across an electrode pair was monitored constantly with a digital multimeter and regulated to within 0.1 µA of the target intensity. An odor delivery tube in the center of the plate allowed introduction of squid rinse to the tank from a syringe and reservoir on the surface. The response of the sharks to the electric fields was imaged with a video eye positioned over the active dipole and recorded on Hi8 videotape for subsequent analysis
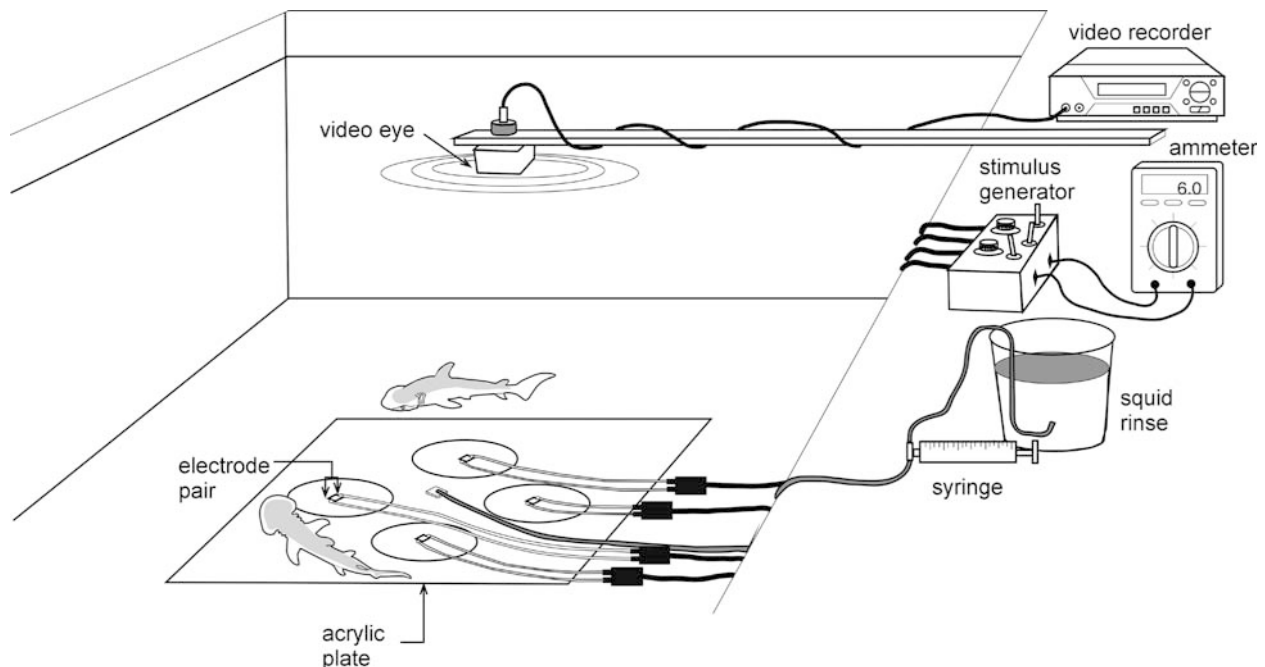
time from odor introduction until detection by a shark was very short (< 1 min). The video camera recorded the response of the sharks to the active dipole. A trial lasted until the arousal level of the sharks declined, usually about 6 to 8 min. At the end of a trial, the active dipole was turned off and sharks were fed to satiation with cut squid. After feeding had stopped, excess squid was removed from the tank and discarded, the electrode array was removed, and sharks were not re-tested for a minimum of 24 h. Sharks were fed to satiation once daily and were tested immediately prior to being fed. Hunger, and hence, motivational state of the sharks, was thus controlled by testing sharks that were uniformly deprived of food for about 24 h. Experiments were conducted under University of Hawaii IACUC-approved protocols.

Video digitization and analysis

Video footage from the Hi8 tape was digitized on a computer at 640×480 pixels, 30 fps and stored on disk. Deinterlaced digital movies were constructed of each bite at the dipole. A movie would start with the frame in which a shark entered the field of view and would end when the focal shark had bitten the dipole and swam out of the field of view. The response of the sharks to the electric field was quantified using frame-by-frame analysis of the digitized movies (Fig. 2). The frame in which a shark first initiated a turn toward the active dipole was copied into an image analysis program (NIH Image v. 1.61). From this frame, the distance from the center
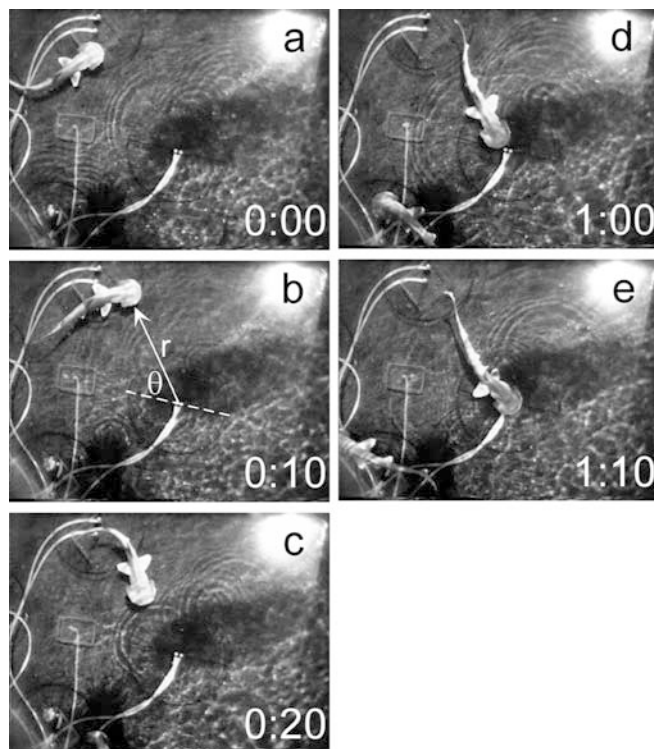
of the dipole at which the shark initiated the turn and the angle of the shark with respect to the dipole axis were measured (Fig. 2b). For all orientations, the distance from the edge of the head closest to the center of the dipole was used as the most conservative measure of orientation distance. The electric field intensity at the point where the shark initiated its turn toward the center of the dipole was calculated using the ideal dipole field equation from Kalmijn (1982). A circle of 10 cm radius drawn on the acrylic plate around the dipole served as a frame of reference to calibrate the image analysis software. Only responses in which no other sharks were present within a 10 cm radius of the dipole were included. If an individual shark bit at the dipole multiple times without swimming out of frame, only the first orientation was analyzed.

Results

Age at first response

Neonatal sharks less than 24 h post-parturition were not aroused by the odor of cut squid and failed to demonstrate a feeding response either to active electric dipoles or cut squid. These sharks swam with a jerky anguilliform locomotion that changed within the 1st day to more closely resemble the smoother swimming pattern of the older neonates. Approximately one-third of the sharks between 24 and 32 h post-parturition were aroused by the squid odor and all sharks greater than 32 h post-parturition were aroused by the squid odor. Arousal was clearly indicated by an increased tail beat frequency, increased swimming velocity, increased frequency of turning, and exaggerated head yaw. Whereas non-aroused sharks swam throughout the entire water column, aroused sharks typically swam close to the bottom. Once within the detectable range of the electric field, the aroused sharks demonstrated a feeding response and bit vigorously at the active dipole. Sharks never bit at the non-active control dipoles and would immediately stop biting at the active dipole when the current was switched off. Behavioral response remained the same with age for all sharks greater than 2 days post-parturition.

Orientation patterns

Shark orientations to the electrodes ($n = 340$) were categorized into five identifiable patterns (Fig. 3). Four of these patterns have been previously described for another sphyrnid species, the scalloped hammerhead shark, *Sphyrna lewini* (Kajiura and Holland 2002). Examples of neonatal bonnethead shark orientations to prey-simulating dipole electric fields are presented in the electronic supplementary material. Representative samples of the five orientation pathways illustrated in Fig. 3 are shown at full speed and in slow motion. Note that the shark turns back toward the electrodes very quickly in the "overshoot" orientation. Whereas a single example of the orientation types is typically shown, the "spiral tracking" orientation is represented twice. In addition, an example of a multiple bite is shown in which

Fig. 2a–e Typical response sequence of a neonatal bonnethead shark upon encountering a prey-simulating electric field. As the shark (**a**) swims outside of the detection range it encounters the electric field and (**b**) makes a sudden turn toward the electrodes. The shark (**c, d**) swims directly toward the electrodes and (**e**) repeatedly bites at them. From panel **b**, the distance of the shark (r) and its location with respect to the dipole axis (θ) are used to calculate the electric field intensity at the position where the shark initiates its orientation. Time between panels is 0.33 s (10 frames) and the counter in the lower right corner depicts time in seconds:frames

Orientation	Percent	Pattern
straight	21.2	
single turn	51.1	
overshoot	12.3	
spiral tracking	7.8	
orient without biting	7.6	

Fig. 3 Frequency of expression and diagrammatic representation for each of five orientation pathways exhibited by neonatal bonnethead sharks upon encountering a prey-simulating dipole electric field. The "single turn" orientation was the most common and accounted for approximately half of all orientations to the dipole. See text for full descriptions of the various orientation patterns

the shark reorients and bites repeatedly at the electrodes without moving out of frame. Multiple bites followed from any of the orientation pathways and only the initial orientation to the dipole was included in analysis as subsequent orientations could have derived from the shark knowing the location of the dipole from the initial encounter.

A "straight" approach was defined as the shark swimming from out of frame along a straight trajectory that brought its head directly over the center of the dipole. The shark would abruptly stop and bite at the electrodes. Sharks would rotate the posterior edge of their pectoral fins antero-ventrally so that the posterior edge would nearly touch the substratum as they attempted to decelerate and position themselves over the electrodes. "Straight" approaches were seen in 21.2% of all passes.

A "single turn" orientation occurred when the shark made a single, directed turn toward the active dipole. This change in trajectory brought the shark directly to the electrodes without additional course correction. A typical "single turn" sequence is shown in Fig. 2. The "single turn" was the most common type of orientation and accounted for 51.1% of all orientations.

An "overshoot" orientation would appear initially as a "straight" approach with any part of the shark's head passing directly over the active dipole without initiating a bite. Once the shark had swum past the electrodes, it would then turn sharply and double back to bite the active dipole. The maximum distance of the head past the dipole was quantified for the "overshoot" response

on the assumption that the shark turned back toward the dipole at the point where it failed to detect the electric field. This response was seen in 12.3% of orientations.

The "spiral tracking" orientation differed from that described for scalloped hammerhead sharks (Kajiura and Holland 2002). Whereas the scalloped hammerhead sharks seemed to follow the lines of current flow in an arc toward the center of the dipole, the bonnethead trajectory more closely followed the voltage equipotentials. In both instances, however, the orientation was characterized by the shark making a series of turns in the same direction to bring it to the center of the dipole through a spiral pattern. "Spiral tracking" was seen in only 7.8% of orientations.

"Orient without biting" was seen in 7.6% of the passes and is described as the shark demonstrating a clear orientation (usually a head jerk) toward the active dipole but not a bite at the dipole. The shark would often show an alteration of course trajectory that would bring it closer to the dipole. This response was seen mostly toward the end of an experimental session when previously aroused sharks were presumably no longer sufficiently motivated to bite.

Multiple bites at the dipole were observed regardless of approach pattern. Sharks would bite once then swim away, turn back, and bite at the dipole again, often repeatedly. In these instances, only the initial orientation was included in analyses as subsequent orientations might have derived from the shark knowing the location of the dipole from the initial interaction.

Orientation distance and electric field intensity

At the point where the shark initiated its orientation to the dipole, two parameters were measured. The distance from the edge of the head to the center of the dipole was measured along with the corresponding angle formed with respect to the dipole axis (Fig. 2b). Approximately 40% of orientations were initiated at a distance of 5–10 cm from the center of the dipole and the number of orientations from greater distances decreased exponentially (Fig. 4). Fewer than 5% of orientations were initiated from a distance of 20–25 cm and the maximum orientation distance was 22 cm. The angle with respect to the dipole axis at which the sharks initiated their orientations was not randomly distributed ($\chi^2_8 = 71.358$, $P < 0.001$). Sharks initiated orientations more often from smaller axis angles (i.e., parallel with the dipole axis; $y = -0.491x + 13.566$, $R^2 = 0.203$). However, there was no relationship between distance of orientation and angle with respect to the dipole axis (ANOVA: $F_{1,368} = 0.336$, $P = 0.563$). That is, sharks did not orient from a greater distance when they initiated orientations from smaller axis angles.

The distance and angle at the point where the shark initiated its orientation were used to calculate the electric field intensity at that location. The equation used was
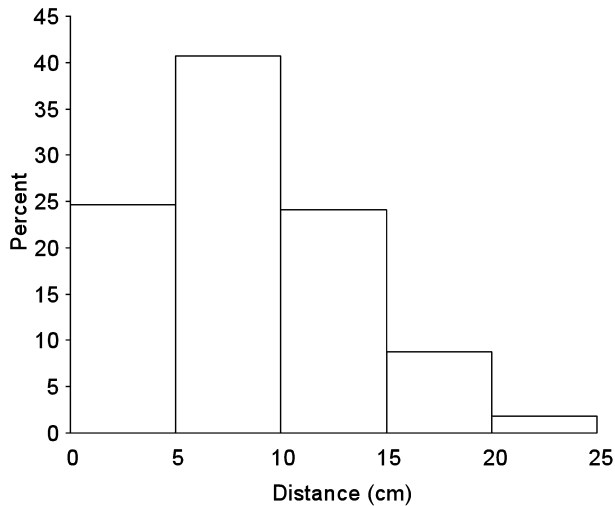
Fig. 4 Distances at which neonatal bonnethead sharks initiated orientations toward the center of a dipole electric field. Most orientations were initiated from a distance of less than 10 cm from the center of the dipole and the maximum orientation distance was 22 cm

modified from Kalmijn (1982) and considers the electrode separation distance, strength of the applied electric current, resistivity of the seawater, distance from the dipole at which the orientation was initiated, and angle with respect to the dipole axis. Although most responses were initiated at low stimulus levels (i.e., low electric field intensities), in some instances a demonstrable behavioral response was not seen until the shark encountered a higher level of stimulus. Approximately two-thirds of all orientations were initiated at a calculated electric field intensity of less than 100 nV cm^{-1} (0.1 μV cm^{-1}). There was a dramatic decline in the number of orientations to stimulus intensities of greater than 100 nV cm^{-1} (Fig. 5a). The percentages of orientations to stimuli of less than 100 nV cm^{-1} are represented at another order of magnitude in Fig. 5b. One-third of all orientations were to a stimulus intensity of less than 20 nV cm^{-1} and the median electric field intensity that elicited a behavioral response was 47 nV cm^{-1}. A large number of orientations were initiated to stimuli of less than 10 nV cm^{-1}, which indicates the high degree of sensitivity to electric fields demonstrated by these sharks.

The minimum electric field intensity that elicited a response did not differ with shark age in the range of 7–32 days post-parturition (ANOVA: $F_{1,205} = 0.770$, $P = 0.654$, 1998 data). That is, older sharks did not demonstrate greater sensitivity by responding to a lower electric field intensity than younger sharks. There was also no difference in orientation distance with age (ANOVA: $F_{1,205} = 0.846$, $P = 0.359$, 1998 data).

Electric field intensity was varied by applying currents from 5.5 to 8.0 μA and there was no difference in behavioral response threshold at the different applied current strengths (ANOVA: $F_{1,387} = 0.995$, $P = 0.735$). At higher applied current strengths, orientations were
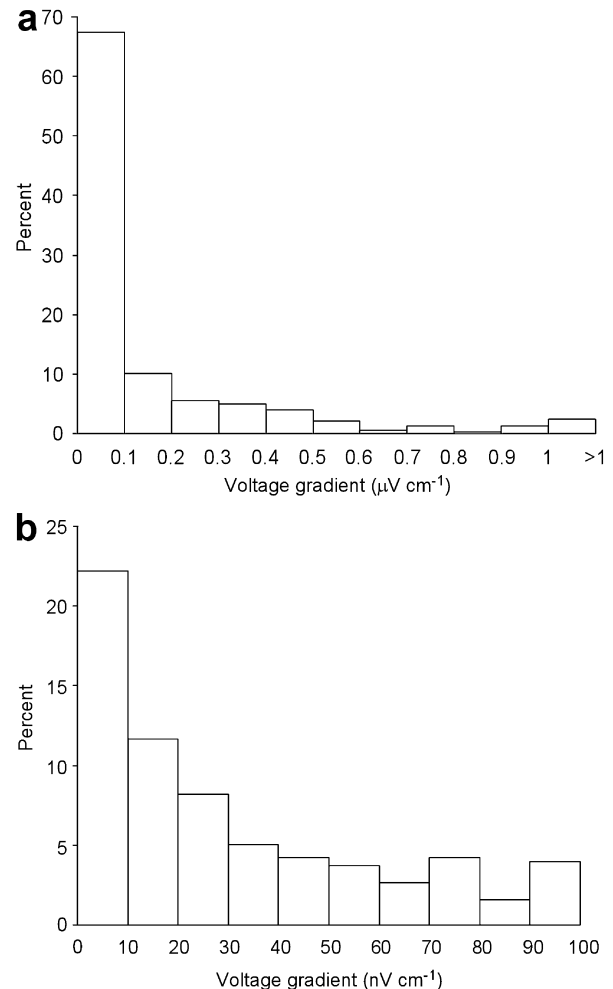

Fig. 5a, b Percentage of orientations by neonatal bonnethead sharks to various levels of threshold stimuli. **a** Two-thirds of all orientations were initiated at a stimulus intensity of less than 100 nV cm^{-1} (0.1 μV cm^{-1}). **b** Approximately one-third of all orientations were to a stimulus intensity of less than 20 nV cm^{-1}. The large number of orientations initiated to low levels of stimulus intensity indicates the great sensitivity to electric fields demonstrated by these sharks

initiated from a significantly greater distance (ANOVA: $F_{1,387} = 5.668$, $P = 0.018$) but the higher current and greater distance combined to provide a similar electric field intensity.

Discussion

Ontogeny of response

Although biting at prey-simulating electric fields has been documented for several shark species (Kalmijn 1971, 1978; Tricas 1982; Johnson et al. 1984; Tricas and McCosker 1984; Haine et al. 2001; Kajiura and Holland 2002), no previous studies have examined electroreception in neonatal sharks. The sharks used in these experiments were all born in captivity and raised in

concrete tanks where they were exposed only to their own electric fields and the fields of their conspecific tank mates. From birth, they were fed on a diet of cut squid, which is non-electrogenic; thus, they were not exposed to the bioelectric cues of live prey items. Nevertheless, they responded to the electric dipoles by biting at them as if they were natural prey. All sharks demonstrated this orientation to the electric stimulus and bite response by 32 h post-parturition and approximately one-third responded within 24 h of birth. Prior to that, the sharks did not respond even to the olfactory stimulus of squid rinse. This feeding response, directed to an electric field and demonstrated within hours of birth, in the absence of any possibility of food association, indicates that the sharks possess an innate feeding response to electric stimuli just as they do to olfactory stimuli.

As precocious organisms lacking parental care it is critical that the neonatal bonnetheads are able to feed successfully soon after birth. Successful feeding is dependent upon detection and localization of prey and thus the development of the sensory systems and behavioral responses in neonatal sharks are of particular interest. Because these sharks were born and maintained in an environment devoid of natural electrogenic prey, their innate feeding response to an electric stimulus provides an opportunity to study the early development of sensory biology and behavior in truly naïve animals.

The lack of response to electric stimuli in the first several hours post-parturition is likely due to the sharks not being sufficiently motivated to feed rather than an inability of the sensory system to detect the presented stimuli. The uncoordinated swimming behavior of the sharks in the first 24 h post-parturition makes them especially vulnerable to predation so their immediate motivation may be self-preservation rather than food consumption. Therefore, feeding behavior may be temporarily suppressed in post-parturition pups although the sensory system is likely functional.

The electrosensory system of the clearnose skate, *Raja eglanteria*, is functional in embryos prior to hatching (Sisneros et al. 1998). Thus, it is likely that the electrosensory system of the neonatal bonnetheads is also functional immediately post-parturition if not in utero. This remains to be tested by application of neurophysiological recording techniques to the electrosensory system of embryonic and neonatal sharks.

The present experiments were conducted only with neonatal sharks, mostly less than 1 month old, and any ontogenetic changes over such a short time period would likely be non-detectable. However, the behavioral response to electric stimuli might change throughout ontogeny as the sharks continue to gain experience with electric stimuli and as morphological changes in the sensory system change the electroreceptive capabilities. For example, adults might have a greater number of sensory hair cells in the ampullae proper as an ontogenetic increase in hair cell number is documented for the auditory system of another elasmobranch, the thornback skate, *Raja clavata* (Corwin 1983). A greater number of sensory hair cells would provide a higher signal:noise ratio that would result in greater sensitivity (Raschi 1986). Larger adult sharks possess longer ampullary tubules that would provide a greater voltage difference across the sensory hair cells and allow the sharks to detect smaller potential differences in a uniform electric field (New and Tricas 1997). In addition, the best tuning frequency of the electrosensory system might change throughout ontogeny as demonstrated in the Atlantic stingray, *Dasyatis sabina* (Sisneros and Tricas 2002). Future studies could examine the response of adult sharks to see if changes in morphology and experience create a corresponding change in response to electric stimuli. In particular, it would be interesting to see if the median response threshold decreases to a level comparable to other shark species (i.e., 25–30 nV cm^{-1} for juvenile scalloped hammerhead and sandbar sharks; Kajiura and Holland 2002).

Orientation patterns

The orientation pathways described for the bonnethead sharks closely follow those previously described for scalloped hammerhead and sandbar sharks (Kajiura and Holland 2002). Like the scalloped hammerhead, the bonnethead sharks also demonstrate "straight," "single turn," "overshoot," and "spiral tracking" orientation patterns. The bonnetheads also demonstrate an additional orientation type, "orient without biting," not seen in the scalloped hammerheads.

As the sharks swam along a "straight" trajectory they would have reached a detection threshold at some point along their path. However, in the absence of an overt behavioral response, the point at which the sensory system first detected the field remains unknown. The video eye covered a field of view of approximately 47×63 cm, which is more than double the maximum response distance observed. Therefore, it is unlikely that the sharks initiated orientations from outside the field of view of the video camera and then swam in a straight trajectory toward the electrodes. Rather, their swimming path happened by chance to bring them directly over the dipole and no additional course correction was required.

Consistent with observations of scalloped hammerhead and sandbar sharks (Kajiura and Holland 2002) the "single turn" was the most common orientation pattern demonstrated by the bonnetheads. The highly directed nature of the orientation and lack of additional course correction indicates that the bonnetheads were likely able to infer the position of the electrodes from the point where they initiated the turn. The non-uniformity of the field across the surface of the cephalofoil could be used to derive the location of the electrodes as proposed by Kalmjin (1988, 1997). An orientation in which the shark made a single turn to bring it directly to the dipole would provide the shark with a larger voltage change across its head than if it followed a curving trajectory (Brown 2002).

In the "overshoot" orientation the sharks initially swam past the electrodes before doubling back to bite at them. Although this may indicate inexperience on the part of the neonates, even more experienced juvenile sharks demonstrate the same "overshoot" orientation pathway (Kajiura and Holland 2002). As the sharks swim past the dipole, the inverse polarity or a change in field direction might be the cues that trigger the initiation of the response. It behooves the sharks to be able to accurately orient to a prey item to maximize predatory efficiency. While orienting to live prey, multiple sensory cues interact to provide the sharks with more information that may enable them to localize the prey item more precisely.

The "spiral tracking" type of orientation has been documented for freshwater electric fishes orienting to an electric dipole (Schluger and Hopkins 1987; Davis and Hopkins 1988), juvenile sharks orienting to an electric dipole (Kajiura and Holland 2002), and mottled sculpin using their lateral line to orient to a vibrating sphere dipole (Coombs and Conley 1997). However, unlike these examples, the bonnethead sharks seem generally to follow along the voltage equipotentials rather than along the current flow lines. Nonetheless, there remains sufficient variation in the orientation pathways that the fit to the voltage equipotentials is not exact.

A mechanism by which sharks use their spiral tracking orientation to localize the center of an electric dipole has been theorized and modeled but not empirically tested (Kalmijn 1988, 1997; Brown 2002). It is hypothesized that sharks can locate the center of a dipole by maintaining a constant angle with respect to the direction of current flow (Kalmijn 1988, 1997). This would bring the shark to the center of the dipole via a curving trajectory (see Kalmijn 1997). The voltage equipotentials are oriented orthogonal to the direction of current flow, and thus, by following along the equipotential lines, the bonnethead sharks do arrive at the center of the dipole. These behavioral observations provide support for the proposed pathway described by Kalmijn (1997) and modeled by Brown (2002).

The neonatal bonnetheads also demonstrated an "orient without biting" response that was the least common type of response. In most instances, when a shark initiated an orientation toward an electric stimulus it would consummate the orientation with a bite at the electrodes. Toward the end of an experimental session, the sharks would be less aroused to bite at the dipole and any responses would be less vigorous. Alternatively, if a shark had bitten at the dipole repeatedly throughout an experimental session without reward, it might have quickly learned to ignore that stimulus. Nonetheless, sharks were repeatedly aroused to bite at the same stimulus 24 h later.

The wide variety of orientation pathways indicates that sharks demonstrate different responses to the same electric stimulus. Different behavioral responses to electric stimuli are also documented for the swell shark, *Cephaloscyllium ventriosum* (Tricas 1982). When presented with the electric field of a prey item, swell sharks would demonstrate either a "yawn" or a "gulp" response depending on the distance of the prey from the snout of the shark. The different behavioral responses found in swell sharks (Tricas 1982), scalloped hammerhead and sandbar sharks (Kajiura and Holland 2002), and the bonnetheads indicate that the response of the sharks to electric stimuli is not expressed as a single fixed action pattern but is dependent upon multiple factors including motivational state, arousal level, and stimulus intensity.

Behavioral response threshold

The distance from the center of the dipole and the angle with respect to the dipole axis were used to calculate the electric field intensity at the point where the shark initiated its turn toward the electrodes (Fig. 2b). The distance from the dipole alone is an incomplete indicator of the electric field intensity. The dipole electric field intensity varies as a cosine function with the greatest field intensity in the plane parallel to the dipole axis and the lowest field intensity in the orthogonal plane (Kalmijn 1982). Therefore, it was hypothesized that the sharks would initiate orientations from a greater distance at lower axis angles where the electric field intensity is greatest. Although the bonnethead sharks initiated orientations from all around the dipole, they initiated orientations more frequently from low axis angles. However, the bonnetheads did not orient from a greater distance when they initiated orientations at low axis angles. This is in contrast to the scalloped hammerhead and sandbar sharks, which did initiate orientations from a greater distance at lower axis angles (Kajiura and Holland 2002). For sharks encountering prey randomly oriented in the environment, it is adaptive to be able to localize and orient to a prey item regardless of its electrical orientation with respect to the shark.

It is important to distinguish the detection threshold from the response threshold. The point at which the shark initiated its orientation might not be the point at which the shark's electrosensory system first detected the electric field. The shark could have detected the electric field at a greater distance but continued to swim along the same trajectory until the stimulus was sufficiently strong to elicit a behavioral response. This behavioral response threshold is the stimulus level quantified in these orientations and is thus a conservative estimate of the sharks' sensory capability.

The behavioral response threshold is influenced by the motivational state and arousal level of the shark. An attempt was made to control motivational state by conducting experiments on sharks that had been deprived of food for 24 h. Arousal level was observed qualitatively throughout each trial for the entire population of sharks. There was a strong initial reaction to the introduction of food odor whereby the sharks swam

close to the bottom and increased their tail beat frequency, swimming velocity, and frequency of turning and demonstrated exaggerated head yaw. This level of arousal would continue for the first few minutes then gradually decline, and most of the sharks would return to almost normal swimming after several more minutes. Even if additional odor were introduced, the sharks would not increase their velocity again unless a significant period of time had elapsed.

Some responses were initiated only at high stimulus levels (Fig. 5). The higher behavioral response threshold values derived mostly from orientations that were initiated from very close to the electrodes (< 5 cm) and are not representative of the maximum sensitivity of the sharks. In fact, many of the orientations were to very low stimulus levels (< 20 nV cm^{-1}), which indicates that these sharks detect and respond to extremely weak electric fields. The behavioral response threshold for the neonatal bonnethead sharks closely matches that obtained from recording from the primary afferent neurons in the electrosensory system of the round ray, *Urolophus halleri* (Tricas and New 1998). The primary afferents of the round ray encode electrosensory information down to 20 nV cm^{-1} and approximately one-third of the bonnethead orientations were to stimuli of 20 nV cm^{-1}or less. The minimum electric field intensity that elicited a response was < 1 nV cm^{-1}, which is consistent with other elasmobranch species (Kalmijn 1982, Kajiura and Holland 2002).

There was no difference in the behavioral response of the sharks to various electric currents within the tested range. An increase in current will cause a corresponding increase in the electric field intensity. If sharks respond at a given stimulus threshold, they would encounter that threshold at a greater distance when a higher current was applied. Therefore, it was predicted that sharks would orient from a greater distance at higher current levels and this was supported by the data. The range of electric current tested (5.5–8.0 µA) was based on literature values for stimuli that were successful at eliciting feeding responses in other elasmobranch species (Kalmijn 1971, 1978; Johnson et al. 1984). However, the range of tested currents was not an exhaustive sample of the range of stimuli detectable by the sharks. This study was restricted to prey-simulating stimuli and therefore only small, 1-cm dipoles and weak electric current were used; other combinations of stimuli remain to be tested.

Over 90% of passes within a 10 cm radius around the dipole resulted in a bite at the dipole (Fig. 3). The powerful behavioral releasing stimulus of the electric field was demonstrated in observations of the sharks' response to the simultaneous presentation of the active dipole and pieces of food. Cut squid placed less than 5 cm from the active dipole would sometimes be ignored as sharks swam past the squid to preferentially bite at the electrodes. Similar behavior is documented for the lesser spotted dogfish, *Scyliorhinus canicula*, which also preferentially bit at the dipole rather than food (Kalmijn 1971). These examples indicate that electric stimuli override other sensory modalities in the final phase of the attack.

This study is the first to examine electroreception in neonatal sharks and demonstrates that they bite at electric fields without prior association of electric stimuli with food. The high sensitivity of the neonatal bonnetheads indicates that they possess a well-developed electrosensory system that enables them to detect prey soon after birth. Whether this already high degree of sensitivity increases throughout ontogeny as demonstrated for other elasmobranch species remains to be tested.

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