PAPER

Behavioral Responses of Two Species of Sharks to Pulsed, Direct Current Electrical Fields: Testing a Potential Shark Deterrent

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ABSTRACT

To describe and contrast the behavioral responses of two species of sharks to an electrical deterrent, sharks were baited to a food odor source within a strong pulsed, direct current electrical field. A head twitch behavior was elicited in scalloped hammerhead (*Sphyrna lewini*) and leopard sharks (*Triakis semifasciata*) at mean voltage gradient thresholds of 4.16 ± 0.59 V/m ($\overline{X} \pm SD$) and 4.30 ± 0.78 V/m, respectively, and did not differ significantly. A shimmy behavioral response was elicited in some hammerhead sharks at a mean threshold of 5.54 ± 1.55 V/m. A retreat behavioral response occurred in hammerhead and leopard sharks at a mean, maximum threshold of 18.50 ± 13.27 V/m and 9.64 ± 10.28 V/m, respectively. The hammerhead sharks retreated at significantly stronger field strengths than the leopard sharks, suggesting that some species may require stronger electrical fields for effective deterrence. Both species of shark remained significantly further away and spent less time near the food odor source when the electrical field was on versus off. The maximum voltage gradient threshold required to cause the sharks to retreat was much higher than previously reported, and the electrical field was not 100% effective at excluding sharks. The sharks only retreated after involuntary muscle contractions were induced by the electrical field.

Keywords: ampullae of Lorenzini, elasmobranch, electrical deterrent, *Sphyrna lewini, Triakis semifasciata*

1. Introduction

Electrical shark deterrents have been developed and studied since the 1960s in an effort to protect humans and equipment (Gilbert and Gilbert, 1973), despite the relatively low incidence of sharks attacks on humans (Klimley and Curtis, 2006). Nevertheless with the increased popularity of sport diving, and the growing need to protect marine equipment and commercial divers, interest in shark deterrents has not waned. Electrical deterrents have been considered more promising than chemical or olfactory deterrents because the latter disperse over time in water. However, very little has been published on electrical deterrents, the behavioral responses they elicit, and the thresholds required to deter sharks.

Smith (1974, 1991) reported that sharks would not cross a voltage gradient greater than 5.5 V/m. However, Charter et al. (1996) stated in a patent that the effective voltage gradient for the most common use of the deterrent ranges from 1-10 V/m. The wide range of voltage gradients reported and the lack of behavioral information indicate the need for more rigorous study. Another study ambitiously tested the effectiveness of an electrical shark deterrent on great white sharks, *Carcharodon carcharias*, in the field. Smit and Peddemors (2003) attracted white sharks with bait and quantified the number of attacks on a target when a shark deterrent (the previously commercially available SharkPOD, Natal Sharks Board) was off or on. When the deterrent was powered on the probability of the shark taking the bait dropped from about 0.70 to 0.08 and 0.90 to 0.16 in five and ten minute test periods, respectively. While study of this species is important for human safety, neither the voltage gradients required to deter the sharks, nor associated behaviors (other than approaches and feeding occurrences), were reported. It was also unclear how many sharks were tested. Therefore a systematic investigation of the mechanisms involved in inducing deterrent responses is necessary.

To more rigorously test the effectiveness of a pulsed, direct current electrical field as a shark deterrent, and to describe what behavioral responses are elicited, we motivated captive sharks to voluntarily penetrate a strong electrical field using food scent. Similarly sized, juvenile scalloped hammerhead sharks, *Sphyrna lewini*, and leopard sharks, *Triakis semifasciata*, were chosen due to their ease of capture, different swimming behaviors, and body morphologies. It has been suggested that larger fish may respond more vigorously to strong electric fields (Vibert, 1967; Reynolds, 1996; Dolan and Miranda, 2003), but the effect of size on susceptibility to the electrical field becomes minor or negligible after fish reach sizes greater than 15-25 cm in total length (Taylor et al., 1957; Anderson, 1995; Dolan and Miranda, 2003), heavier than 50 g (Zalewski, 1985), or larger than 75-100 cm^3 in volume (Dolan and Miranda, 2003). Because the hammerhead and leopard sharks in this study easily surpassed the size, mass, and volume limits, the effect of size on their responses can therefore be assumed as negligible. In addition, scalloped hammerhead and leopard sharks were tested to

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determine if their responses to the electrical field differed, as is the case for different fish species (Lamarque, 1967, 1990).

Trials were done in a captive setting so we could test individual animals and perform paired comparisons with the same sharks with the electrical field off and on. We tested each shark with the electrical field both off and on, to: (1) describe the reactions induced by the electrical field, (2) quantify any consistent, stereotyped responses that were observed, (3) compare the thresholds and behaviors between the two species of sharks, (4) determine if the electrical field affected how closely they approached a food odor source, and (5) determine where they chose to spend their time in the tank.

2. Methods

2.1. Animal Collection and Maintenance

Experiments with juvenile scalloped hammerhead (total lengths of 51.2-57.5 cm) and leopard sharks (total lengths of 39.3-58.2 cm) were conducted at Coconut Island, Oahu, Hawaii and Long Beach, California, respectively. Experiments were conducted in a laboratory setting to control for electrical field distortions caused by other fishes, rocks, plants, and water flow.

Scalloped hammerhead sharks were captured, using hand-lines with barbless hooks, in Kaneohe Bay, Hawaii. Sharks were considered to be adjusted to their new surroundings when they swam normally and displayed even coloration; this usually only took a few hours. Because the sharks had been caught with bait, we assumed they were motivated to feed. In addition, previous studies of scalloped hammerhead pups maintained in similar settings usually accepted food within 24 h of capture (Lowe, 1996, 2001). The hammerhead sharks were tested on the day of capture or the following day. After being tested, the sharks were immediately released back into the bay after notching the trailing edge of the shark's pectoral fin for identification and to prevent reuse of previously tested sharks.

Leopard sharks were acquired from local aquaria in southern California. Animals were maintained in cylindrical, polyurethane holding tanks until they were feeding. The sharks were fed anchovies, squid, and mussels *ad libitum* three times per week. Kao (2000) found that leopard sharks between 70-120 cm and greater than 120 cm total length had empty stomachs 32 and 28 h after feeding, respectively. As a result, sharks were fed until satiation and then fasted from 48-72 h prior to being tested, at which point it was assumed they would be motivated to feed.

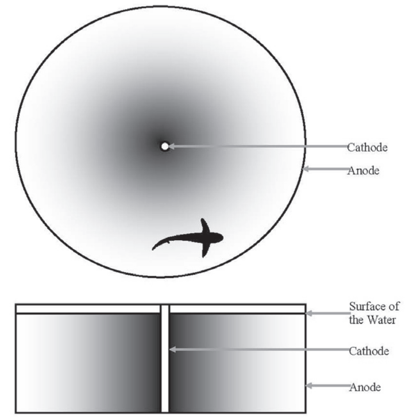
2.2. Electrode Design

The electrical field producing electrodes were constructed from galvanized hardware cloth (16-ga) with 6 x 6-mm mesh. Electrodes were cylindrical in shape, with the cathode being a much smaller cylinder and placed in the center of the anode (Figure 1). The cathode had a 6-cm radius and was supported by wrapping it tightly around a 91-cm-tall, 12-cm-diameter PVC pipe glued to an acrylic base. The anodes were approximately 10-cm smaller in diameter than the testing tanks and were self-supporting. Due to differences in testing tank size between Hawaii and California, the electrodes were also differently sized. The anodes were 296 cm in diameter for the hammerhead shark trials and 220 cm in diameter for the leopard shark trials. Although ideally the testing apparatuses would have been identically sized, a larger set up was used with the hammerhead sharks because unlike leopard sharks they are obligate swimmers and it is easier for them to continually swim in a larger space. The electrodes were immersed in seawater for two days prior to their first use to allow the hardware cloth to accumulate chloride ions. Circuitry was designed to produce a pulsed, direct current electrical field similar to that used by Smith (1974, 1991), with 5 pulses/s, and a pulse duration of 0.8 ms (Smith 1974, 1991). A square pulse shape, which switched off or on virtually instantaneously, was chosen to minimize the damaging effects of the electrical field to the fish (Sharber and Corothers, 1988; Sharber et al., 1994). The field was powered by three, 12-V, 12-Ah gel cell batteries. During the experiments, the water level was kept below the tops of the electrodes to prevent the sharks from swimming over them and to allow for a dry place to attach the wire leads. This resulted in a functional electrode height of 54.2 cm for all hammerhead shark trials and 78.3 ± 1.4 cm ($\overline{X}$ ± *SD*) for all leopard shark trials. The input voltages were measured every minute from the field producing electrodes with a digital oscilloscope (TDS210, Tektronix, Texas) with a high voltage differential probe (P5200, Tektronix, Texas).

The smaller, central electrode was always used as the cathode during all experiments to help ensure the safety of the shark and to try to deter sharks from the odor source. If elicited, the behavior electrotaxis causes fish to lose control of their swimming muscles and the fish cannot leave the field of their own volition and the responses of the fish depend on its orientation in the field (Vibert, 1967). If a fish is facing the anode, the fish will swim involuntary towards the anode (anodic electrotaxis) and be tetanized at the anode (Vibert, 1967); meaning that if the central electrode in our study were the anode, the sharks would be drawn to the odor source, and the area of the tank with the highest voltage gradients,

FIGURE 1

Diagram of the experimental tank from above and from the side to show the trends in voltage gradient strength. The field is strongest near the cathode (darker color), and weakest near the anode (lighter color).



and tetanized. However, if a fish is facing the cathode, cathodic electrotaxis would result in the shark being drawn towards the cathode and then towards the anode (Vibert, 1967). Because our goal was to deter sharks without necessarily harming them, we chose to have the cathode as the central electrode so that if electrotaxis was induced, the shark would swim away from the bait into an area of the tank with lower voltage gradients (due to the geometry of the electrodes) where they could recover voluntary control.

2.3. Electrical Field Calculations and Measurements

The voltage gradients were strongest near the cathode and weakest near the anode due to the geometry of the electrodes (Figure 1). The voltage gradient isopotentials took the shape of expanding concentric rings. Because of the differing sizes of the electrodes, it was possible to create voltage gradients higher than the voltage supplied by the batteries, due to the increased charge density around smaller-sized cathode.

Because measurement equipment would have interfered with the sharks' movements during the experiments, it was necessary to predict the voltage gradients for the behavioral analysis. To calculate the voltage gradient at a radial distance in the tank, the following equation was used (D. Novotny, Pers. Comm.):

$$E = V / ((ln\ (r_o/r_i))*r)$$

where E is the voltage gradient (V/m), V is the input voltage (V), r_o is the anode radius (m), r_i is the cathode radius (m), and r (m) is the radial distance of the point in question. For comparison, systematic measurements were made with silver-silver chloride recording electrodes for each electrode pair, set at three depths, at four or five radial distances on three separate days. Silver-silver chloride wires were used in the recording electrodes because they are small, compact, and are resistant to the formation of junction potentials which can cause measurement errors. To make a recording electrode a 1.5 cm long piece of silver-silver chloride wire was soldered to the inner conductor of an insulated coaxial cable. The grounding shield in the coaxial wire was connected to ground on the oscilloscope to eliminate noise. The set up was then waterproofed with aquarium sealant, leaving only 1 cm of silver-silver chloride wire exposed to the seawater. In Hawaii, the recording electrodes were connected to a differential oscilloscope with an amplifier set at ten times (Oscilloscope 2120B, B+K Precision Instruments, California). In California, an amplifier system (MacLab 4e and Scope software v3.6.5, AD Instruments, Colorado) and a computer (MacIntosh Power Book, Apple, California) were used to record the signal from the recording electrodes. In California, the recording electrodes were recessed in aquarium tubing to reduce the polarization of the recording electrodes as a precautionary measure, although there were no observable difficulties with the previous set-up. Additionally, to determine if the relationship between the predicted and measured voltage gradients was stable over the 30-min trial period, the voltage gradient was measured at a fixed position once every 5 min.

Because the water conductivity was subject to change for each trial and does affect the efficiency of the power transfer into the fishes, the power densities that elicited behaviors were also calculated:

$$D = c_w * E^2$$

where D is the power density (W/m^3), c_w is the conductivity (mho/m or S/m), and E is the voltage gradient (V/m) (Kolz and Reynolds, 1989).

2.4. Experimental Procedure

Temperature, conductivity, and salinity of the seawater were measured before each experiment. Temperature was measured to the nearest 0.1°C and water temperature was maintained at approximately 20°C in the leopard shark experimental tank with heaters. Conductivity was measured to the nearest 0.01 mho/m. On days when it was not possible to measure the conductivity of the seawater, the conductivity measurement of another trial day with the closest temperature and salinity was substituted. Salinity was measured to the nearest 0.5 ppt.

Shark behavioral responses to the electrical field were recorded with a video camera mounted above the tanks. Reference markings placed on the bottom of the tanks were used to determine at what distance from the center of the tank behavioral responses occurred. Each shark was tested individually and was subjected to one control and one treatment trial on the same day with a 30-min break between trials; the trial order was randomly determined for each shark. Sharks were considered adjusted to the experimental tank when they were swimming normally and had normal coloration; this usually took 2-3 h. In both trials, squid scent was introduced into the cathode through aquarium tubing every 5 min. Squid scent was prepared by placing cut squid pieces in approximately 250 mL of seawater. The seawater then contained fluids and odors from the squid and worked as an attractant to the sharks. During the trials, water flow was turned off to reduce the distortion of the electrical field. Between trials, water flow was restored for 30-min to aerate the water and disperse the squid odor. The radial distance from the center of the tank was used to calculate the voltage gradient that elicited a behavioral response from the sharks. In addition, the closest each shark approached the odor source was noted for both control and treatment trials. Finally, the tanks were divided into concentric zones to determine where in the tank the sharks spent time with the electrical field off and on. The first zone extended from the cathode (6 cm) to a radial distance of 50 cm. The second zone went from 50 cm to 100 cm (hammerhead shark trial) or 110 cm and the anode (leopard shark trial). Finally, the third zone in hammerhead shark trial was from 100 to 150 cm and the anode (Figure 2a and 2b). The time spent in each zone was divided by the volume of the zone to control for the effects of volume. For the treatment trials, while the shark was present in the testing tank and near the tank's edge where the electrical field is weakest, the electrical field was turned on and slowly increased over a period of approximately 30 s until set at a strength that initiated the head twitch response at a radial distance of approximately 50 cm. The input voltage ranges used in hammerhead and leopard shark trials were 10-11 V and 8-11.25 V respectively.

3. Results

3.1. Water Temperature, Conductivity, and Salinity

Water temperatures in hammerhead shark trials ranged from 26.8-28.2°C with a mean of 27.2 ± 0.3°C ($\overline{X} \pm SD$). The conductivity of the seawater ranged from 5.28-5.42 mho/m with a mean of 5.35 ± 0.05 mho/m. Water salinities from south Kaneohe Bay ranged from 34.25-35.00 ppt during the study period (University of Hawaii School of Environmental Science and Technology). The water temperatures in leopard shark trials ranged from 15.6-23.0°C with a mean of 20.1 ± 2.5°C. The conductivity of the seawater in leopard shark trials ranged from 4.64-5.21 mho/m with a mean of 4.83 ± 0.18 mho/m and the salinity ranged from 30.5-32.5 ppt with a mean of 31.0 ± 0.5 ppt.

3.2. Electrical Field Measurements

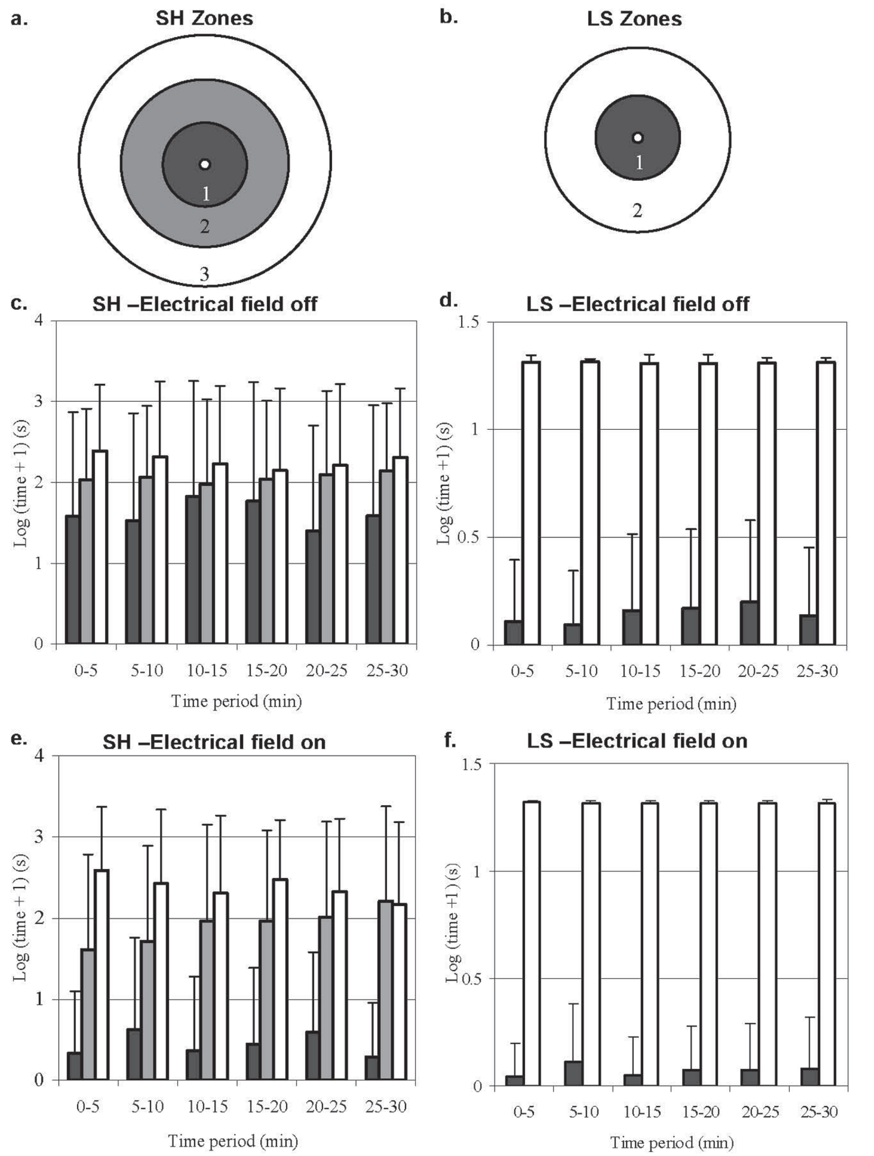
The electrical fields produced were measured to determine if the resulting voltage gradients corresponded to values predicted by the equation for each electrode set. The measured voltage gradients were 33-45 % less than the predicted voltage gradients for all field-producing electrode sets. However, linear regressions of the calculated versus measured voltage gradients for each electrode set were significant and accounted for 94-97 % of the variability in the data (linear regression: hammerhead shark trials: $F = 4383.03$, $df = 1$, $p < 0.0001$, $R2 = 0.94$; leopard shark trials set 1: $F = 2689.38$, $df = 1$, $p < 0.0001$, $R2 = 0.95$; leopard shark trials set 2: $F = 7777.07$, $df = 1$, $p < 0.0001$, $R2 = 0.97$). As a result, the regression equation for each electrode set was used to correct for the differences between the measured and calculated voltage gradients. In addition, no significant difference was found between the corrected, predicted values from the measured voltage gradients (paired t-test: $t = 2.02$, $df = 20$, $p = 0.057$). The difference between the corrected, predicted values and measured values was always less than 2 %. Finally, no significant difference was found with time between the corrected predicted values and measured values (linear regression: $F < 0.01$, $df = 1$, $p = 0.97$, $R2 < 0.01$).

3.3. Description and Analysis of Behavioral Responses

Four graded, stereotyped behavioral responses to the electrical field were characterized. The first response elicited in both species of shark was termed the 'startle' response because it was similar to the star-

FIGURE 2

Comparison of preferred zones over time with the electrical field off and on. The experimental tanks were divided into three zones for scalloped hammerhead sharks (SH) and two zones for leopard sharks (LS) because of differences in tank size (a, b respectively). The darker the shading of the zone, the higher the voltage gradient ranges in that zone. Data are presented as the average time spent in each zone calculated from the first 45 s of each min (+ 1 SD), the times were normalized by volume of the zone, and transformed (log (time + 1)) to make the variances equal.



tle response of teleost fishes (Lamarque, 1990). This behavior was characterized by rapid changes in swimming direction and greatly increased swimming speed for several seconds when the electrical field was turned on. However, because a startle response often causes an animal to leave the area of the stimulus, and the animals in these experiments were unable to leave, this response was not quantified.

If the sharks moved into areas of the tank with even higher voltage gradients, a 'head twitch' response was elicited. The head twitch was characterized by bouts of twitches of the sharks' gill slits and lateral head twitches. In scalloped hammerhead sharks there were 1-27 bouts of head twitches elicited in each shark per 30-min trial at voltage gradients ranging from 3.13-7.01 V/m, with a mean of 4.16 ± 0.59 V/m ($\overline{X} \pm SD$) and power densities ranging from 51.81-260.14 W/m^3, with a mean of 94.68 ± 29.09 W/m^3. In leopard sharks, 0-41 bouts of head twitch were induced per 30-min trial at voltage gradients ranging from 3.05-6.82 V/m, with a mean of 4.30 ± 0.78 V/m, and power densities ranging from 43.45-216.68 W/m^3, with a mean of 92.37 ± 32.05 W/m^3. The voltage gradient and power density thresholds required to elicit this behavior did not differ significantly between hammerhead and leopard sharks (two sample t'-test: voltage gradient: $t' = -1.25$, $df = 206$, $p = 0.11$; power density: $t' = 0.62$, $df = 206$, $p = 0.538$).

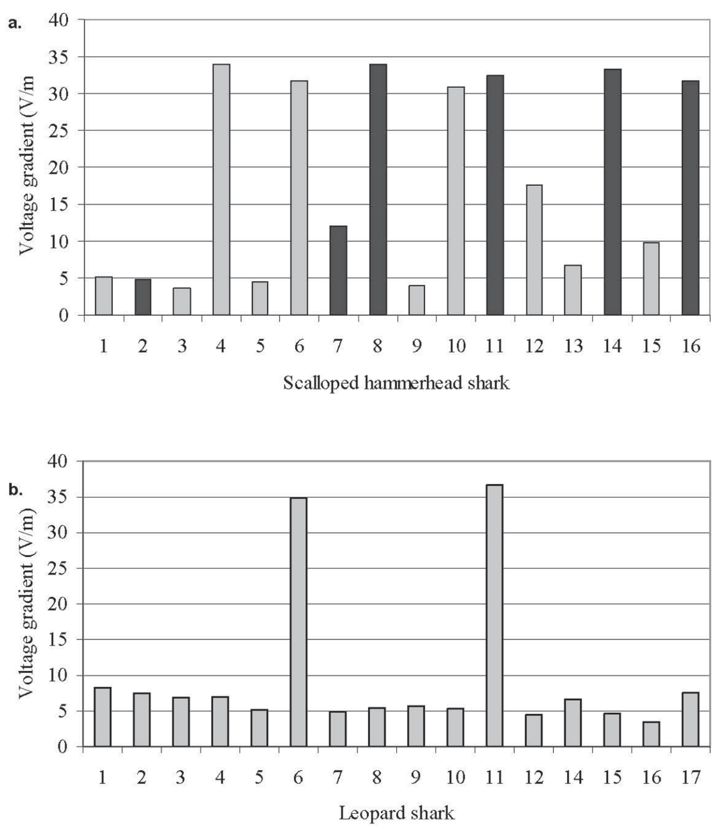
Both species of shark spent less time in the area of the tanks where the head twitch behavior would be displayed (Zone 1), and the amount of time spent in that portion of the tank increased significantly when the electrical field was off (Figure 2). The application of the electrical field and the length of time for which the field had been applied significantly affected the preferred zones of the hammerhead sharks (three-factor ANOVA: $F = 3.78$, $df = 10$, $p < 0.0001$). The hammerhead sharks spent the greatest amount of time in Zone 3 whether the electrical field was off or on (Figure 2c and 2e), but spent significantly less time in Zone 1 when the electrical field was on versus when it was off (Tukey's pairwise comparison: $p < 0.0001$ for all 6 time periods/trial). During half of the time periods, the sharks were spending more time in Zone 3 than in Zone 2, but the time spent in Zone 2 increased with each time period (Figure 2e). The leopard sharks zone preferences were not significantly different over time during the trial; however, the time spent in each zone was significantly affected by whether the field was off or on (two-factor ANOVA: $F = 24.35$, $df = 1$, $p < 0.0001$). The leopard sharks spent the greatest amount of time in Zone 2 regardless if the electrical field was off or on, but also spent significantly less time in Zone 1 when the electrical field was applied (Figure 2d and 2f) (Tukey's pairwise comparison: $p < 0.0001$).

The 'shimmy' behavioral response was characterized by whole body twitches and swimming while rotated 90º from its normal attitude; this behavioral response was only observed in some of the hammerhead sharks. Quite frequently, the shark would also swim quickly on its side repeatedly between the two electrodes. This response was more sustained than the head twitch and could last for over one minute. The shimmy was only observed 1-3 times in six of the 16 scalloped hammerhead sharks, and it occurred at a mean voltage gradient threshold of 5.54 ± 1.55 V/m and power density threshold of 170.66 ± 117.98 W/m^3. The sharks that displayed the shimmy response were not larger or heavier than those that did not (ANCOVA slope: $F = 1.50$, $df = 1$, $p = 0.24$; y-intercept: $F = 1.52$, df = 1, $p = 0.24$).

After swimming into a voltage gradient that was strong enough to induce the head twitch or shimmy responses, the shark would quickly turn and swim to an area of the tank where the voltage gradient was not as strong. Both hammerhead and leopard sharks displayed this behavior, which was

FIGURE 3

Maximum voltage gradient thresholds at which the retreat behavior was elicited in the scalloped hammerhead sharks (a) and leopard sharks (b). The dark gray colored bars indicate the sharks that performed the shimmy behavior while the light grey color indicates those that did not.



defined as the 'retreat' behavior. The maximum voltage gradient required to trigger the retreat behavior, i.e. the maximum voltage strengths the sharks would tolerate, for each shark during the 30-min trial ranged from 3.58-33.96 V/m with a mean of 18.50 ± 13.27 V/m in the hammerhead sharks, and ranged from 3.46-36.65 with a mean of 9.64 ± 10.28 V/m in the leopard sharks (Figure 3). The maximum power densities tolerated by the hammerhead sharks ranged from 69.46-6250.79 W/m^3 with a mean of 2718.037 ± 2742.19 W/m^3. The maximum power densities tolerated by the leopard sharks ranged from 62.37-6255.39 W/m^3 with a mean of 899.75 ± 1974.36 W/m^3. In addition, the hammerhead sharks tolerated significantly higher voltage gradients and power densities than the leopard sharks (two sample t´-test: voltage gradient: $t' = -2.19$, $df = 27$, $p = 0.037$; power density: $t' = 2.15$, $df = 27$, $p = 0.040$).

Additionally, seven of the hammerhead sharks and two of the leopard sharks were successful in reaching the food scent source when the electrical field was on. Nevertheless, when the electrical field was on, the sharks stayed significantly further away from the food scent source than when it was off (hammerhead sharks: randomized block ANOVA: $F = 36.05$, $df = 1$, $p < 0.0001$;leopard sharks: paired *t*-test: $t = -3.87$, $df = 16$, p = 0.0007). The closest approaches of the hammerhead and leopard sharks to the scent source with the electrical field off ranged from 0-60 and 0-39 cm with averages of 24.1 ± 10.6 and 16.6 ± 12.1 cm ($\overline{X} \pm SD$), respectively. However, with the electrical field on, the hammerhead and leopard sharks approached within 0-79 and 0-54 cm of the odor source, with average closest approaches of 36.9 ± 21.4 cm and 28.9 ± 13.2 cm, respectively.

4. Discussion

4.1. Electrical Field Measurements

Although there was a strong, significant relationship between the measured and predicted voltage gradients, the measured values were always less than the predicted values, which was likely attributable to the accumulation of charged particles on the production electrodes. A layer of charged molecules would effectively reduce the amount of current that flowed between the two electrodes (Chandler, 1985). By using the regressions to compensate for this phenomenon, we were able to improve the voltage gradient predictions by 20-40 %.

To test for battery drain over the 30-min period, we compared the measured versus corrected predicted voltage gradients over time and found that they did not differ significantly from each other. In addition, there was no trend with time and the difference between the measured and predicted (corrected) voltage gradients. This indicates that we could accurately predict the voltage gradient anywhere in the experimental tanks and the voltage gradients were predictable over time.

4.2. Description and Analysis of Behaviors

Several graded, stereotyped behavioral responses to the pulsed, electrical fields were described for scalloped hammerhead and leopard sharks. The first response elicited in both species of shark was similar to the startle response of teleost fishes (Lamarque, 1990). All of the sharks rapidly changed direction and greatly increased their swimming speed immediately when the electrical field was turned on, even before the electrical field was turned up to the full input voltage. However, after several seconds of very fast, erratic swimming, they would return to more normal swimming patterns, although they were swimming more rapidly than when the electrical field was off. Unlike the involuntary neuromuscular stimulation that causes the startle response in non-electroreceptive fishes, the startle response in sharks appeared to be triggered by electrosensory stimulation because there were no visible neuromuscular responses (e.g. epaxial muscle twitches). It is likely that in most trials the sharks were above the startle response voltage threshold; however, much larger tanks set-ups would be required to determine the actual voltage threshold for this response. However, because a startle response often causes an animal to leave the area of the stimulus and the sharks in this experiment were unable to leave, the voltage gradient threshold for this response was not quantified.

If sharks moved into areas of the tank with even higher voltage gradients, the head twitch response was elicited. This behavioral response may be homologous with the involuntary muscle contractions described in teleost fishes (Lamarque, 1990). Lamarque (1990) described this response in teleost fishes as the quivering motion of the body or dorsal fin as a result of the fishes' muscles being contracted by the electrical field. The similarity in gradients required to elicit head twitches in the two species was most likely due to the sharks exceeding the thresholds after which size does not or minimally affects the thresholds of behaviors (Rushton, 1927; Taylor et al., 1957; Lamarque and Charlon, 1973; Zalewski, 1985; Anderson, 1995; Dolan and Miranda, 2003).

On one occasion a leopard shark resting on the bottom displayed tail twitches in an area of the tank where the head twitch behavior would have typically been elicited. This suggests that muscle twitches can be elicited in any part of the fish at the same threshold level, but the behavior was mostly manifested around the head of the sharks because they swim head first into the field. This observation is supported by Stewart (1990) who concluded that strong electrical fields act directly on the muscles of marine teleost fishes.

Although there was intraspecific variability in the voltage gradient required to elicit head twitches, both species preferentially stayed out of areas of the tank with voltage above the head twitch threshold when the electrical field was on (Figure 2). This indicated that the electrical field was functioning as a deterrent, likely because of the discomfort caused by the muscle contractions. Smith (1991) proposed that the electrotaxis response, which he observed in only one shark, was the event that caused sharks to leave an electrical field. However, the electrotaxis behavior was never described in Smith's (1991) study. Voltage gradients that caused the head twitch response seemed sufficient to cause sharks to preferentially avoid that area of the tank where it would be elicited.

The shimmy response was elicited in some of the hammerhead sharks and in none of the leopard sharks. Sharks that demonstrated the shimmy response were not longer or more massive than those that did not, and, interestingly, some individuals of both species swam into voltage gradients greater than 30 V/m and still did not display the shimmy response (Figure 3). The shimmy may have only been displayed by only some of the sharks because: (1) they were in a more susceptible physiological state (Vibert, 1967; Sternin and Nikoronov, 1976); (2) have differing body forms (Zalewski, 1983; Dolan and Miranda, 2003); and/or (3) different electrical somatic resistivities (Lamarque, 1990). High intraspecific and interspecific variability has also been observed in contractile responses of electrically-stimulated fish muscle preparations (Bird and Cowx, 1990), which may explain the variability both within the hammerhead shark group and between the two species.

Fishes in pulsed, direct current fields undergo taxes, either anodic or cathodic, but neither type of electrotaxis adequately describes the shimmy response observed in the hammerhead sharks in our study. According to Vibert (1967), anodic electrotaxis involves involuntary movements of a fish to the anode where it may undergo tetanus. However, the electrotaxis and tetanus behaviors are not characterized by the loss of normal swimming attitude seen in our study in the shimmy response nor the repeated movement to both electrodes. If the sharks were displaying the anodic electrotaxis behavior, they should have moved to the anode and remained there in a state of tetanus. Cathodic electrotaxis involves the animals initially swimming toward the cathode and then turning and involuntarily swimming to the anode, where they may undergo tetanus (Vibert, 1967). The response described in the literature that most closely resembles the shimmy is pseudo-forced swimming, which is characterized as unbalanced swimming, often accompanied by tetanus (Vibert, 1967). Although pseudo-forced swimming seems similar to the shimmy, it is not elicited by pulsed, direct current fields (Vibert, 1967).

After experiencing the head twitch or shimmy behaviors, sharks would quickly move to an area of the tank where these behaviors were not elicited. The retreat response was elicited in all the hammerhead sharks, and in 16 out of the 17 leopard sharks. The mean maximum voltage gradients tolerated by the hammerhead and leopard sharks before they displayed the retreat response was 18.50 ± 13.27 V/m and 9.64 ± 10.28 V/m, respectively (Figure 3). These mean retreat voltage gradients were much higher than the previous deterrent thresholds published by Smith (1974, 1991) and those documented in a patent for an electrical shark deterrent system (Charter et al., 1996). Although the higher tolerance of the sharks in our study may be a result of forced acclimation (the sharks could not completely leave the electrical field), it is still important to note the variability in response thresholds of the different shark species.

The hammerhead sharks tolerated significantly higher voltage gradients than the leopard sharks, possibly due to differences in physiology (Vibert, 1967; Sternin and Nikoronov, 1976), body morphology (Zalewski, 1983; Dolan and Miranda, 2003), different swimming activity levels (Lamarque, 1990), and/or somatic resistivities (Lamarque, 1990). Alternatively, the higher tolerance of the hammerhead sharks to the strong electrical field may be a result of their higher swimming speeds, which resulted in them penetrating the field more deeply than the leopard sharks before learning what area of the tank to avoid. As well as the interspecific variation in maximum retreat thresholds, both species in this study exhibited intraspecific variability, it is possible the maximum voltage gradient required to cause some sharks to retreat may be higher than indicated here.

Although hammerhead sharks may have been motivated by the food odor located at the center of the tank, they would seldom venture too close the odor source and would swim around the perimeter of the tank where the head twitch was elicited. During the trials, some hammerhead sharks swam so closely to the head twitch voltage gradient threshold that just the closest tip of their cephalofoil was twitching. On average the sharks spent an increasing amount of time in Zone 2, where the head twitch is elicited, during the experimental trials until the mean time spent in Zone 2 surprisingly exceeded the mean time spent in Zone 3, which contains the lowest voltage gradients in the tank (Figure 3d).

The observations made during this study suggest that the deterrent effects of strong electrical fields are more likely the result of neuromuscular responses rather than electrosensory responses. Elasmobranchs behaviorally respond to pulsed DC fields of 5-500 nV/cm, via detection from ampullae of Lorenzini (Kalmijn, 1982). Additionally, primary and secondary afferent nerves saturate below 1 μV/cm (Tricas and New, 1998) and 10 μV/cm (Montgomery, 1984), respectively. Because the electrical field required to deter the sharks was ten million times stronger than the lowest demonstrated electrosensory sensitivity of elasmobranch fishes (Kalmijn, 1982), this suggests that the sharks were unable to sense the changes in field strength with their ampullae of Lorenzini and were 'feeling out' the head twitch zone, so that they would not inadvertently swim into it again.

The pulsed, DC electrical field tested was successful at reducing the amount of time the sharks spent close to the food scent source and how closely they approached it. Additionally the sharks appeared unharmed by their exposure to the electrical field: captive leopard sharks fed and swam normally after the experiments, and a few of the scalloped hammerhead sharks were recaptured later and appeared healthy and motivated to feed. However, the electrical field did not create an absolute zone of exclusion; some sharks were able to penetrate all the way to the food scent source, meaning that the deterrent was not 100% effective at keeping sharks away. Additionally, different shark species require different voltage gradients to cause the sharks to retreat from the electrical field.

This study significantly increases our understanding of how sharks behaviorally respond to strong electric fields and the voltage and power thresholds that elicit these responses. While the electrical field was successful at reducing how close the sharks approached and remained in the central area of the tank, the energy demands of creating and sustaining an electrical field to protect large areas like beaches may be too costly when the relative rarity of shark attack is considered. Additionally, the potential effects on other wildlife and humans would also need to be considered. Nevertheless, this information may provide engineers and technologists with ideas on how to implement and improve the reliability of electrical shark deterrents that could be developed to protect people and sensitive equipment in the marine environment.

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