電気刺激に対するサメ類の反応実験

誌名	西海区水産研究所研究報告
ISSN	0582415X
著者	矢野, 和成 森, 秀樹 南川, 清 上野, 照剛 内田, 詮三 長井, 健生 戸田, 実 増田, 元保
巻/号	78号
掲載ページ	p. 13-30
発行年月	2000年6月

Behavioral Response of Sharks to Electric Stimulation

Kazunari Yano*, Hideki Mori**, Kiyoshi Minamikawa**,
Shoogo Ueno***, Senzo Uchida****, Kensho Nagai*****,
Minoru Toda**** and Motoyasu Masuda*****

ABSTRACT

The behavioral responses of sharks to electric stimulation were studied. We used two methods of electric stimulation, one is the Electric Field Experiment (EFE) and the other is the Partial Electric Field Experiment (PEF). The responses of three species of sharks, *Carcharhinus falciformis* (60 cm TL), *Triaenodon obesus* (119 cm TL), and *Stegostoma fasciatum* (220 cm TL), to the EFE electric stimulation were studied. The captive sharks swam in a circular tank (7 m in diameter, 1.2 m in depth). The source unit consisted of a signal generator, which produced the wave form, frequency, and voltage, and a power amplifier. Electrodes were 5 cm×10 cm copper plates, separated by a distance of 3.5 m. A 60 Hz sine wave and DC pulse electric fields were chosen. The 60 Hz sine wave was 1 V to 10 V (r.m.s) and the DC pulse period was either 1 sec or 5 sec (duty ratio is 10%). All sharks swam close to the side of the tank when the signal generator was off. When the 60 Hz sine wave and DC pulse electric field were being produced, two species, *C. falciformis* and *T. obesus*, immediately turned around. The sharks were demonstrated a high rate of turning when exposed to the DC pulse electric fields. Conversely, *S. fasciatum* did not change its swimming patterns when the signal generator was on.

The PEF was conducted for eight species; three species were same the individuals tested in the EFE plus five additional species: *Galeocerdo cuvier* (218 cm TL),

---

Received January 14, 2000（平成12年1月14日受理）
Contribution from Seikai National Fisheries Research Institute, No. 597（西海区水産研究所業績第597号）

*西海区水産研究所石垣支所　〒907-0451　石垣市桴海大田148-446（Seikai National Fisheries Research Institute, Ishigaki Tropical Station, Fisheries Agency of Japan, 148-446 Fukai Ota, Ishigaki, Okinawa 907-0451, Japan）
**中部電力電気利用技術研究所　〒459-8001　名古屋市緑区大高町北関山20-1（Chubu Electric Power Co. Inc., Electrotechnology Applications R&D Center, 20-1 Kitasekiyama, Oodaka-cho, Midori-ku, Nagoya, Aichi 459-8001, Japan）
***東京大学医学部医用電子研究施設　〒113-0033　文京区本郷7-3-1（Institute of Medical Electronics, Faculty of Medicine, University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan）
****国営沖縄記念公園水族館　〒905-0206　本部町石川424（Okinawa Expo Aquarium, 424 Ishikawa, Motobu, Okinawa 905-0206, Japan）
*****碧南海浜水族館　〒447-0853　碧南市浜町2-3（Hekinan Seaside Aquarium, 2-4 Hamamachi, Hekinan, Aichi 447-0853, Japan）

Carcharhinus melanopterus (65 cm TL), *Triakis scyllium* (64 cm TL), *Cephaloscyllium isabellum* (53 cm TL), and *Scyliorhinus torazame* (42 cm TL). Electrodes were separated by a distance of 30 cm or 2 cm. Four species, *C. melanopterus, C. falciformis, T. obesus*, and *T. scyllium*, gave a strong response to the electric field, two species, *C. isabellum* and *S. torazame*, gave a weak response to the electric field, but two other species, *G. cuvier* and *S. fasciatum*, did not show a response to the electric field. Hence, the behavioral response patterns were different among the species.

Objectives of the study include the results of the behavioral responses of sharks to electric stimulation and examination of the possibility of electric fields for repellence from shark attacks and protection from shark depredation of fisheries.

INTRODUCTION

Elasmobranch fishes respond to weak electrical voltage gradients, which they detect with the ampullae of Lorenzini (Kalmijin, 1978). Dijkgraaf and Kalmijin (1962) found that skates could detect voltage gradients as low as 0.01 microvolts per centimeter. Kalmijin (1971) reported that the shark, *Scyliorhinus canicula*, and the skate, *Raja clavata*, are extremely sensitive to weak electric fields and they can be stimulated by the bioelectric fields emanating from the flatfish. Kalmijin (1978) demonstrated that the bottom dwelling, shallow-water shark, *Mustelus canis*, the common smooth dogfish, can detect minute electrical voltage gradients as small as five thousandths of a microvolt (=5 nanovolts) per centimeter. Understanding the shark's mechanoreceptive sense is easy compared with grasping the nature of their "sixth sense", the ability to sense weak electric fields (Hueter and Gilbert, 1990). Sharks not only sense these fields but also rely upon them to locate prey and perhaps navigate through the ocean (Hueter and Gilbert, 1990). Tricas et al. (1995) reported that the weak stimulus is used in the field by reproductively active male stingrays to locate mates, and also by female rays to locate buried consexuals. Sisneros et al. (1998) stated that reproductively active adult clearnose skates discharge their electric organs at rates near the peak frequency sensitivity of the adult electrosensory system, which facilitates electric communication during social behavior.

In addition to feeding and reproductive studies, electric fields have been studied as a methods of repellence from shark attack. The electric dart is an experimental weapon that can instantly paralyze a large shark (Nelson, 1983). The expendable dart (which remains on the shark) is delivered by spear and produces a pulsed electric field between the inside of the shark and the outside water (Baldridge, 1974; Nelson, 1983). Electric shark barriers were arranged around beaches in South Africa to prevent sharks from entering thus protecting bathers (Smith, 1991). The Natal Sharks Board, South Africa, developed the "Shark POD" (Shark Protective Oceanic Device) in 1992 (Taylor, 1998). The Shark POD used an electric field to protect divers and not injure the shark (Taylor, 1998). However, differences in behavioral response of several shark species to the electric field are not clearly described.

A fatal shark attack on a shell diver occurred in Aichi Prefecture on 9 April 1995 (Yano, 1996a, b). The Aichi Prefecture Government started a shark research project to study attacks and the behavior of sharks. Our project team studied the behavioral response of sharks to several electric stimuli. We used two methods of electric stimulation, one is the Electric Field Experiment (EFE) and the other is the Partial Electric Field Experiment (PEF).

Objectives of the study include 1) the results of the behavioral responses of sharks to electric stimulation and 2) examination of the possibility of electric fields for repellence from shark attacks and protection from shark depredation of fisheries.

MATERIALS AND METHODS

Electric Field Experiment (EFE)

The sharks used in the electric field experiment are listed in Table 1. We tested the behavioral response of three species; the silky shark, *Carcharhinus*

Table 1. The sharks used in the Electric Field Experiment (EFE), Partial Electric Field Experiment with electrodes separated by a distance of 30 cm (PEF-30), and PEF with electrodes separated by a distance of 2 cm (PEF-2).

Species name	Total length (cm)	Sex	Number of experiment		
			EFE	PEF-30	PEF-2
Carcharhinus falciformis	60	female	23	5	0
Triaenodon obesus	119	male	7	5	0
Stegostoma fasciatum	220	female	3	5	0
Galeocerdo cuvier	218	female	0	6	0
Carcharhinus melanopterus	65	male	0	0	5
Triakis scyllium	64	female	0	0	5
Cepahloscyllium isabellum	53	female	0	0	5
Scyliorhinus torazame	42	male	0	0	5

falciformis, the whitetip reef shark, *Triaenodon obesus*, and the zebra shark, *Stegostoma fasciatum*. One individual swam in the tank during each experiment. The number of experiments ranged from three to 23 for each species (Table 1).

The methods used in the EFE are outlined in Fig. 1. The captive sharks swam in a circular tank, 7 m in diameter and 1.2 m in depth, at the Okinawa Expo Aquarium. We conducted the electric field experiment from 11 to 13 December, 1996. The electric source unit consisted of a signal generator (Yokokawa Denki FG 120) and power amplifier (NF Kairo 4502). The signal generator produced the wave form, frequency, and voltage. A 60 Hz sine wave and DC pulse electric fields were chosen. The 60 Hz sine wave was 1 V to 10 V (r.m.s) and 0.1 A to 2.5 A, and the DC pulse was 0.2 V to 10 V and 0.1 A to 5 A. The pulse period for experiment No. 9 was 0.5 seconds of stimulation and 4.5 seconds without stimulation (duty ratio is 10%) and experiment No. 19 was 0.1 seconds of stimulation and 1.9 seconds without stimulation (duty ratio is 10%) (Table 2). All other experiments were 0.1 seconds of stimulation and 0.9 seconds without stimulation (duty ratio is 10%), for 10 minutes (Table 2).

Electrodes were 5 cm by 10 cm copper plates, separated by a distance of 3.5 m. We set one of the electrodes at the center of the tank and set the other electrode on the side of the tank (Fig. 1). We observed swimming patterns during normal conditions and while presenting electric stimuli to the sharks for 10 minutes and recorded the patterns with two video cameras from different angles. One camera

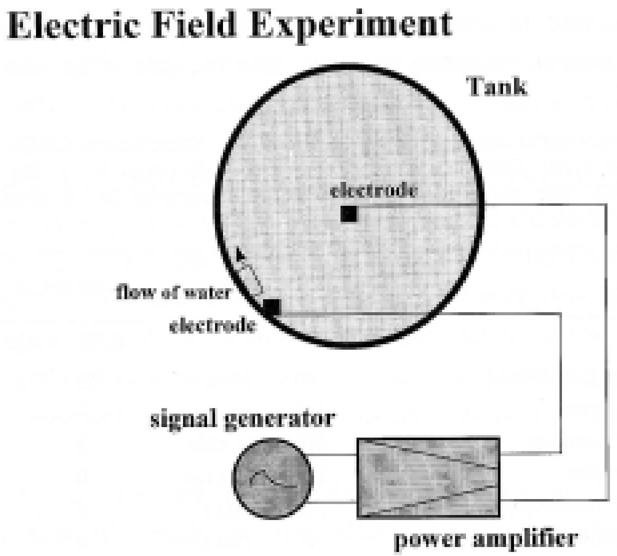

Fig. 1. Outline of the methods for the Electric Field Experiment (EFE).

Table 2. Date and time of experiments, type of stimulation, number of turns, number of passes between electrodes, and behavioral response during EFE of three species of sharks, *Carcharhinus falciformis, Triaenodon obesus*, and *Stegostoma fasciatum*. ⧺ : very strong response ; + : strong response ; − : no response.

Number of experiment	Date of experiment	Time of experiment	Type of stimulation	Electric current (A)	Potential difference (V)	Pulse period for stimulation (sec)	Pulse period for no stimulation (sec)	Number of turns	Number of passes between electrodes	Response
C. faciformis										
1	11 Dec 96	13:20–13:30	No					1	22	−
2	11 Dec 96	13:35–13:45	DC pulse	5	10	0.1	0.9	40	15	⧺
3	11 Dec 96	14:07–14:17	No					2	17	−
4	11 Dec 96	14:20–14:30	60Hz sine	2.5	10			11	13	+
5	11 Dec 96	14:51–15:01	No					1	21	−
6	11 Dec 96	15:05–15:15	DC pulse	5	10	0.1	0.9	41	16	⧺
7	11 Dec 96	15:39–15:49	No					0	22	−
8	11 Dec 96	15:50–16:00	60Hz sine	1.95	3.75			7	20	+
9	11 Dec 96	16:23–16:33	DC pulse	5	10	0.5	4.5	13	25	⧺
10	12 Dec 96	10:38–10:48	No					2	15	−
11	12 Dec 96	10:52–11:02	DC pulse	0.5	1	0.1	0.9	46	3	⧺
12	12 Dec 96	11:37–11:47	No					1	18	−
13	12 Dec 96	11:49–11:59	DC pulse	0.1	0.2	0.1	0.9	42	1	⧺
14	12 Dec 96	12:10–12:20	No					1	16	−
15	12 Dec 96	12:24–12:34	No					4	20	−
16	12 Dec 96	12:36–12:46	60Hz sine	0.1	1			1	21	+
17	12 Dec 96	14:00–14:10	60Hz sine	0.6	1.5			2	23	+
18	12 Dec 96	14:13–14:23	No					0	24	−
19	12 Dec 96	14:25–14:35	DC pulse	0.1	0.2	0.1	1.9	103	12	⧺
20	12 Dec 96	14:55–15:05	DC pulse	0.1	0.2	0.1	0.9	42	4	⧺
21	12 Dec 96	15:21–15:31	No					0	22	−
22	12 Dec 96	15:34–15:44	DC pulse	0.1	0.2	0.1	0.9	71	3	⧺
23	12 Dec 96	15:52–16:02	DC pulse	1	10	0.1	0.9	59	2	⧺
S. fasciatum										
24	13 Dec 96	10:41–10:51	No					0	28	−
25	13 Dec 96	10:54–11:04	60Hz sine	0.68	5			0	30	−
26	13 Dec 96	11:15–11:25	DC pulse	10	7	0.1	0.9	0	30	−
T. obesus										
27	13 Dec 96	14:15–14:25	No					1	14	−
28	13 Dec 96	14:28–14:38	DC pulse	1	0.2	0.1	0.9	44	22	⧺
29	13 Dec 96	14:49–14:59	No					2	11	−
30	13 Dec 96	15:02–15:12	DC pulse	1	1	0.1	0.9	71	9	⧺
31	13 Dec 96	15:29–15:39	DC pulse	1	7	0.1	0.9	52	5	⧺
32	13 Dec 96	16:04–16:14	No					3	22	−
33	13 Dec 96	16:18–16:28	60Hz sine	1	5			45	4	+

recorded the whole tank and the other followed the swimming positions of the shark. We measured the swimming patterns of the sharks for 10 minutes, when the electric source unit was on, and then with no electric stimulation for at least 30 minutes until the next experiment. The number of turns and the number of passes between the electrodes were counted from the video tape recordings after the experiments.

We used field mapping methods (0.675 A, 60 Hz, 34 per mil sea waters) to measure the intensity of the electric field. The field mapping measurement points were 1 cm interval within the limits (17 cm×12 cm). The intensity of the electric field around the electrodes was high but the intensity between the electrodes was low (Fig. 2A).

Partial Electric Field Experiment (PEF)

The methods used in the PEF are outlined in Fig. 3. The electric source unit

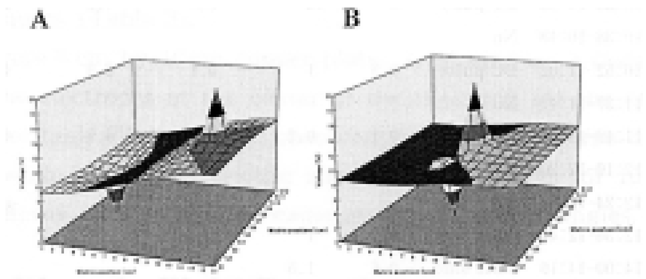

Fig. 2. The model of intensity slope of the electric field around the electrodes measured by field mapping methods. A: Electric Field Experiment (0.675 A, 60 Hz, 34 per mil); B: Partial Electric Field Experiment (1.03 A, 60 Hz, 34 per mil).

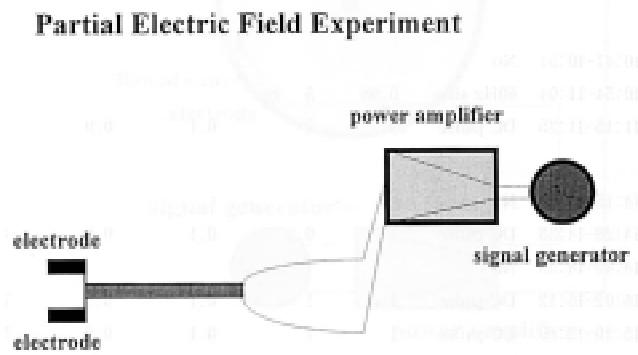

Fig. 3. Outline of the methods for the Partial Electric Field Experiment (PEF).

was the same as used in the EFE. Electrodes were separated by a distance of 30 cm or 2 cm. The 50 Hz or 60 Hz sine waves were 10 V (r.m.s.) and 2.0 A and 2.5 A, the DC pulse was 1 V to 10 V and 0.05 A to 5 A, and the pulse period was 0.1 seconds of stimulation and 0.9 seconds without stimulation (duty ratio is 10%).

The intensity of the electric field in the small area around the electrodes was high but the intensity between electrodes was low, measured by field mapping methods (1.03 A, 60 Hz, 34 per mil sea water) (Fig. 2B). The filed mapping measurement points were 1 cm interval within the limits (17 cm×14 cm).

The sharks tested in the PEF are listed in Table 2. In the experiments, four species, the silky shark, *C. falciformis*, the whitetip reef shark, *T. obesus*, the zebra shark, *S. fasciatum*, and the tiger shark, *Galeocerdo cuvier*, were tested with electrodes (5 cm×10 cm) separated by a distance of 30 cm. These sharks were tested from 10 to 15 December, 1996 in a circular tank (7 m in diameter and 1.2 m in depth) at the Okinawa Expo Aquarium (Fig. 4A). The other four species, the blacktip reef shark, *Carcharhinus melanopterus*, the banded houndshark, *Triakis scyllium*, the swell shark, *Cephaloscyllium isabellum*, and the cloudy catshark, *Scyliorhinus torazame*, were tested with electrodes (1 cm in diameter) separated by a distance of 2 cm. These sharks were tested from 26 to 28 February, 1996 in a transportation tank (180 cm×120 cm, 70 cm deep) at the Hekinan Seaside Aquarium (Fig. 4B).

The electrodes for PEF were not at fixed location in the tank because a pole with the electrodes could be moved around in the tank. The near the snout region of the sharks was approached with the dipole electrodes (Fig. 4). We tested each PEF experiment 5 or 6 times and then with no electric stimulation for at least 20 minutes until the next experiment. We recorded the swimming behavior of the shark with a video camera when the electric source unit was on and off.

RESULTS

Electric Field Experiment (EFE)

Carcharhinus falciformis

The tracks of the swimming patterns of the silky shark, *C. falciformis*, with no electric stimulation, with a 60 Hz sine wave stimulation, and a DC pulse stimulation are shown in Fig. 5. The shark swam close to the side of the tank and passed between the electrodes when the electric source unit was off (Fig. 5A). When the 60 Hz sine wave electric fields were being produced, the shark passed almost in the center between the electrodes (Fig. 5B). When the DC pulse electric fields were being produced, the shark immediately turned around (Fig. 6) and rarely passed

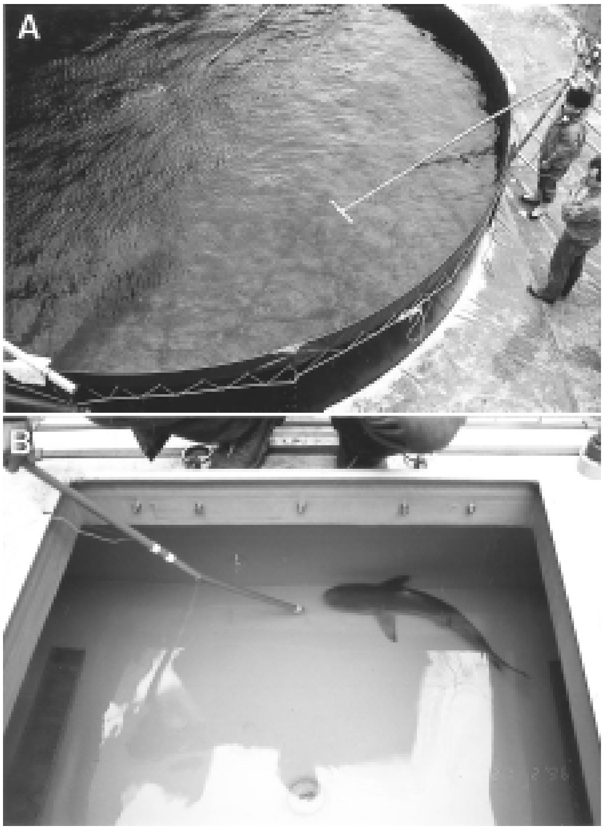

Fig. 4. The snout region of the tiger shark, *Galeocerdo cuvier* (A) and the blacktip reef shark, *Carcharhinus melanopterus* (B) were approached with the dipole electrodes.

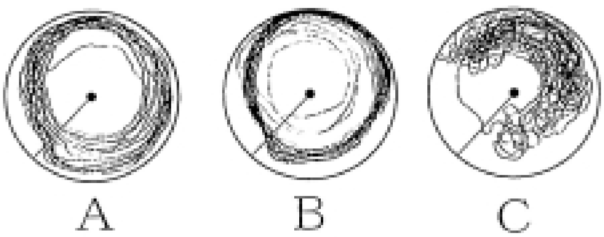

Fig. 5. The tracks of the swimming patterns of the silky shark, *Carcharhinus falciformis*. A: no stimulation (normal); B: 60 Hz sine wave electric field; C: DC pulse electric field.

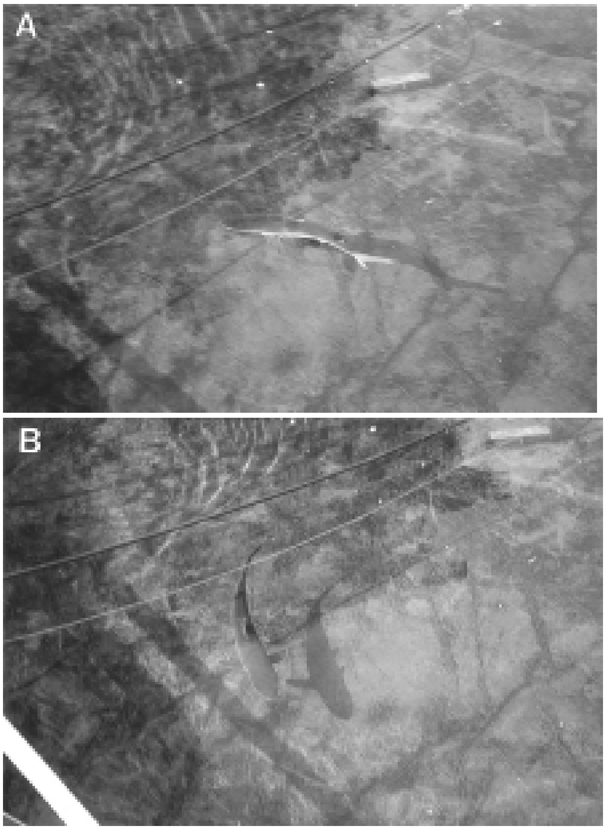

Fig. 6. The silky shark, *Carcharhinus falciformis*, immediately turned around in front of the electrodes (E) when the DC pulse electric fields were being produced by the EFE. A : no stimulation (normal) ; B : DC pulse electric stimulation, the shark immediately turned around.

between the electrodes (Fig. 5C, Table 2). The shark shook its head very strongly right and left when the DC pulse electric fields were being produced at all the time and all the position in the tank. Twenty-three experiments with this species resulted in similar swimming patterns with the normal, the 60 Hz sine wave and the DC pulse stimulation. When the electric source unit was off, the shark returned quickly to a normal swimming pattern.

The number of turns made by the silky shark during 10 minutes is shown in Tables 2 and 3. An average of 50.8 turns were observed during the DC pulse electric stimulation. The number of turns during the DC pulse electric stimulation was clearly higher than that of the normal swimming condition. The 60 Hz sine wave electric stimulation and normal conditions produced few turns by the shark.

Table 3. The number of turns made by three species, *Carcharhinus falciformis, Triaenodon obesus*, and *Stegostoma fasciatum*, exposed to the EFE.

Species name	No electric stimulation				DC pulse stimulation				60 Hz sine wave stimulation			
	average	range	SD	n	average	range	SD	n	average	range	SD	n
Carcharhinus falciformis	1.2	0–4	1.22	10	50.78	13–103	25.05	9	5.25	1–11	4.65	4
Triaenodon obesus	2	1–3	1	3	55.67	44–71	13.87	3	45	—	—	1
Stegostoma fasciatum	0	—	—	1	0	—	—	1	0	—	—	1

Table 4. The number of passes between the electrodes by three species, *Carcharhinus falciformis, Triaenodon obesus*, and *Stegostoma fasciatum*, exposed to the EFE.

Species name	No electric stimulation				DC pulse stimulation				60 Hz sine wave stimulation			
	average	range	SD	n	average	range	SD	n	average	range	SD	n
Carcharhinus falciformis	19.7	15–24	3.02	10	9.0	1–25	8.37	9	19.3	13–23	4.35	4
Triaenodon obesus	15.7	11–22	5.69	3	12.0	5–22	8.89	3	4	—	—	1
Stegostoma fasciatum	28	—	—	1	30	—	—	1	30	—	—	1

There are 5.3 on average for the 60 Hz sine wave electric stimulation and 1.2 for normal conditions (Table 3). The number of turns was not significantly different between the 60 Hz sine wave electric stimulation and the normal condition (Mann–Whitney U-test, $U_{(4,10)}=7.0$, 2 tie, $P=0.058$).

The number of passes between the electrodes by the silky shark in 10 minutes is shown in Tables 2 and 4. The numbers of passes between the electrodes averaged 9.0 for the DC pulse electric stimulation, 19.3 for the 60 Hz sine wave electric stimulation, and 19.7 for the normal condition (Table 4). The number of passes between the electrodes was significantly different between the DC pulse electric stimulation and the normal condition (Mann–Whitney U-test, $U_{(9,10)}=12$, 2 tie, $P=0.007$). The number of turns for the DC pulse electric stimulation was lower than those of the 60 Hz sine wave electric stimulation and the normal swimming condition of the shark. The number of passes between the electrodes was not significantly different between the 60 Hz sine wave electric stimulation and the normal condition (Mann–Whitney U-test, $U_{(4,10)}=19.0$, 2 tie, $P=0.867$).

The number of turns in each experiment of the DC pulse stimulation with the silky shark is shown in Fig. 7A. When the electric current was low, many turns were observed.

The number of passes between the electrodes during each experiment of the DC pulse stimulation with the silky shark is shown in Fig. 7B. When the electric current was high, many passes were made between the electrodes. A higher electric field does not always result in a greater behavioral response by the shark.

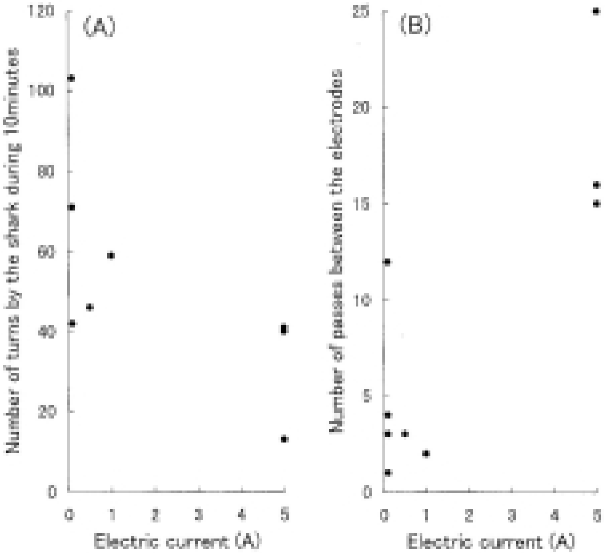

Fig. 7. The number of turns in each experiment (A) and the number of passes between the electrodes during each experiment (B) with the silky shark, *Carcharhinus falciformis*.

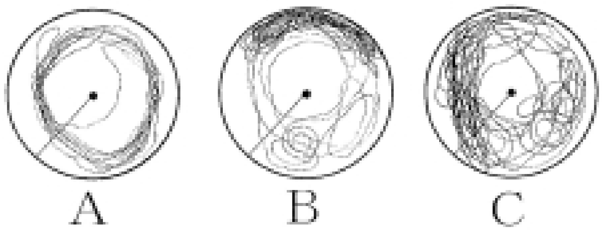

Fig. 8. The tracks of the swimming patterns of the whitetip reef shark, *Triaenodon obesus*. A: no stimulation (normal); B: 60 Hz sine wave electric field; C: DC pulse electric field.

Triaenodon obesus.

The tracks of the swimming patterns of the whitetip reef shark, *T. obesus*, with no electric stimulation, with a 60 Hz sine wave stimulation, and a DC pulse stimulation are shown in Fig. 8. The shark swam close to the side of the tank and passed between the electrodes when the electric source unit was off (Fig. 8A). When the 60 Hz sine wave electric fields were being produced, the shark immediately turned around, passed a few times between the electrodes and swam far a way from the electrodes (Fig. 8B). When the DC pulse electric fields were being produced, the shark immediately turned around, but the shark passed between the electrodes (Fig. 8C). The shark strongly shook its head right and left when exposed to both the 60 Hz sine wave electric stimulation and the DC pulse electric stimulation were being produced at all the time and all the position in the tank. However the head shaking of the silky shark was stronger than that of the whitetip reef shark. When the electric source unit was off, the shark quickly returned to a normal swimming pattern.

The whitetip reef shark averaged 55.7 turns during the DC pulse electric stimulation, 45 for the 60 Hz sine wave electric stimulation, and 2.0 during the normal condition (Tables 2 and 3). The number of turns was significantly different between the DC pulse electric stimulation and the normal condition (Mann–Whitney U–test, $U_{(3,3)}=0$, $P=0.05$). The number of turns of the 60 Hz sine wave was also clearly different from that of the normal condition. Many turns by the shark were observed during the DC pulse electric stimulation and the 60 Hz sine wave electric stimulation. Normal swimming of the shark included very few turns.

In the whitetip reef shark, the number of passes between the electrodes averaged 12 for the DC pulse electric stimulation, 4 for the 60 Hz sine wave electric stimulation and 15.7 for the normal swimming condition (Table 4). The number of passes between the electrodes during the DC pulse and the 60 Hz sine wave electric stimulation was lower than during normal swimming. However, the number of passes between the electrodes was not significantly different between the DC pulse electric stimulation and the normal condition (Mann–Whitney U–test, $U_{(3,3)}=2.5$, 1 tie, $P=0.37$). The number of passes through the 60 Hz sine wave was clearly fewer than that of the normal condition (Table 4).

Stegostoma fasciatum.

The tracks of the swimming patterns of the zebra shark, *S. fasciatum*, with no electric stimulation, with a 60 Hz sine wave stimulation, and a DC pulse stimulation are shown in Fig. 9. In contrast to the other two, this species did not change its

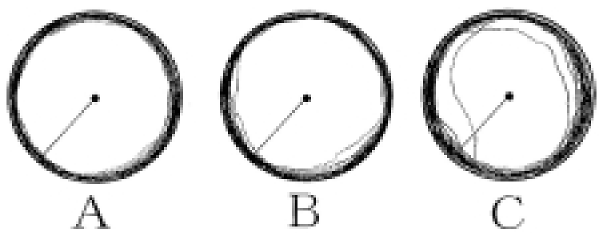

Fig. 9. The tracks of the swimming patterns of the zebra shark, *Stegostoma faciatum*. A: no stimulation (normal); B: 60 Hz sine wave electric field; C: DC pulse electric field.

swimming patterns when the electric source unit was on (Fig. 9B, C). The zebra shark did not turn around during the DC pulse stimulation, the 60 Hz sine wave stimulation, or the normal condition (Tables 2 and 3). The number of passes of the zebra shark did not differ between the normal condition and the electric stimulation by the DC pulse and the 60 Hz sine wave (Tables 2 and 4).

Partial Electric Field Experiment (PEF)

The behavioral responses of the sharks during the PEF are shown in Table 5. Four species, the silky shark, *C. falciformis*, the whitetip reef shark, *T. obesus*, the blacktip reef shark, *C. melanopterus*, and the banded houndshark, *T. scyllium*, showed a strong response to the electric field, swimming very fast and sometimes bumping the wall of the tank. The sharks attempted to escape from the electrodes when the electric source unit was on (Table 5). The swell shark, *C. isabellum*, and the cloudy catshark, *S. torazame*, did not show a response to a 5 mA electric stimulation. However they showed a weak response (their head moved only slightly) to a 400 mA electric stimulation (Table 5). The sharks did not attempt to escape from the electrodes when the electric source unit was on. Two other species, the zebra shark, *S. fasciatum*, and the tiger shark, *G. cuvier*, did not show a response to the electric field (Table 5). Their swimming speeds and direction of the swimming course did not change when they were exposed to the electric field. The behavioral response patterns were thus different among the species.

DISCUSSION

Elasmobranchs are known to respond to weak electrical stimulation (Kalmijin, 1971, 1974, 1978 ; Ryan, 1981). In behavioral tests, sharks and skates appeared most responsive to frequencies in the range from 0 (direct current) to about 8 Hz (Kalmijin, 1971, 1974). Sisneros et al. (1998) reported that best frequency of clearnose skate (*Raja eglanteria*) was at 1–2 Hz for embryos, showed an upwards shift to 5 Hz in juveniles, an a downward shift to 2–3 Hz in adults. The receptors detecting these weak, low-frequency electric fields are the ampullae of Lorenzini, delicate sensory structures in the elasmobranch's protruding snouts (Murray, 1962 ; Dijkgraaf and Kalmijin, 1963). The ampullae of Lorenzini of elasmobranchs are sensitive to weak electrical fields produced by the nerves and muscles of other animals (Kalmijin, 1971, 1978). On the other hand, electric stimulation in the present study repelled several sharks.

In the EFE and the PEF, the silky shark, the whitetip reef shark, the blacktip reef shark, and the banded houndshark attempted to escape from the electric fields.

Table 5. Behavioral response during the PEF of eight species of sharks. ⧺ : strong response ; + : weak response ; − : no response.

Species name	Electrode distance	Stimulation	Electric current	Potential difference	Response
Carcharhinus falciformis	30	No			−
	30	60 Hz sine	2.5 A	10 V	⧺
	30	DC pulse	1.25 A	7 V	⧺
	30	DC pulse	820 mA	5 V	⧺
	30	DC pulse	147 mA	1 V	⧺
Triaenodon obesus	30	No			−
	30	60 Hz sine	2.5 A	10 V	⧺
	30	DC pulse	1.25 A	7 V	⧺
	30	DC pulse	820 mA	5 V	⧺
	30	DC pulse	147 mA	1 V	⧺
Stegostoma fasciatum	30	No			−
	30	60 Hz sine	2.5 A	10 V	−
	30	DC pulse	1.25 A	7 V	−
	30	DC pulse	820 mA	5 V	−
	30	DC pulse	147 mA	1 V	−
Galeocerdo cuvier	30	No			−
	30	60 Hz sine	2.5 A	10 V	−
	30	DC pulse	5 A	10 V	−
	30	DC pulse	1.25 A	7 V	−
	30	DC pulse	820 mA	5 V	−
	30	DC pulse	147 mA	1 V	−
Carcharhinus melanopterus	2	No			−
	2	50 Hz sine	2.0 A	10 V	⧺
	2	DC pulse	700 mA	5 V	⧺
	2	DC pulse	400 mA	5 V	⧺
	2	DC pulse	5 mA	1 V	⧺
Triakis scyllium	2	No			−
	2	50 Hz sine	2.0 A	10 V	⧺
	2	DC pulse	700 mA	5 V	⧺
	2	DC pulse	400 mA	5 V	⧺
	2	DC pulse	5 mA	1 V	⧺
Cepahloscyllium isabellum	2	No			−
	2	50 Hz sine	2.0 A	10 V	−
	2	DC pulse	700 mA	5 V	+
	2	DC pulse	400 mA	5 V	+
	2	DC pulse	5 mA	1 V	−
Scyliorhinus torazame	2	No			−
	2	50 Hz sine	2.0 A	10 V	−
	2	DC pulse	700 mA	5 V	+
	2	DC pulse	400 mA	5 V	+
	2	DC pulse	5 mA	1 V	−

It is suggested that the sharks have an aversion to the electric fields used in our experiments. Elasmobranchs use weak bioelectric fields emanating from prey animals, but the stimulation of our experiments is probably stronger than any naturally encountered electric stimulus. We think that the sharks were not able to tolerate the stimulation. During the EFE, the silky shark and the whitetip reef shark passed almost in the center between the electrodes. Field mapping of the intensity of the electric field (Fig. 2) suggests that the center intensity between the electrodes has the lowest electric field. We think that the shark may sense the lower electric field in the center and pass through there.

Devices using electric fields have been developed for protection against shark attacks, for example, the electric dart (Baldridge, 1974), electric shark barrier (Smith, 1991), and the Shark POD (Taylor, 1998). Baldridge (1974) reported that by using a pulsed stimulus of only about 20–30 V, breadboard models of the electric antishark dart have been very successful. He reported that a tiger shark was paralyzed immediately, however, much work remains to be done in miniaturizing the power supply and circuitry and perfecting the delivery system before such weapons could be made generally available to divers. The Shark POD was measured to pulse an electric potential of ±30 V and 60 V in potential difference (in air) (Fukui et al., 1997). This electric potential (60 V) of the Shark POD is 6 to 300 times higher than in our experiments (0.2–10 V). Our findings suggest that a lower electric potentials are useful for shark repellents. However, the behavioral response patterns were different among the species.

In the EFE, dramatic responses to the electric filed were observed in the silky shark and the whitetip reef shark. No responses to the electric field were observed with the zebra shark. In the PEF, large responses to the electric field were observed in the silky shark, the whitetip reef shark, the blacktip reef shark, and the banded houndshark. But four other species, the zebra shark, the tiger shark, the swell shark, and the cloudy catshark did not change their swimming pattern or responded only weakly to the electric field. The behavioral response patterns also differed with the intensity and kind of electric field among the species in the present study. For example, the silky shark responded more strongly to the DC pulse electric stimulation than the 60 Hz sine wave electric stimulation, but the whitetip reef shark showed a stronger response to the 60 Hz sine wave electric stimulation than the DC pulse electric stimulation. Thus, we think that the behavioral response patterns of each species are related to the wave form, frequency, and voltage of the electric fields. Baldridge (1974) reported that a tiger shark was paralyzed immediately by a 20–30 V pulse stimulus. However, in our experiments the tiger shark did not respond to the electric field. Our electric stimulation was lower than Baldridge's stimulation. We think that the tiger shark responds to a higher electric field than the electric field used in our experiments.

Strong responses to an electric field are documented for the dusky shark, *Carcharhinus obscurus*, the bull shark, *C. leucas*, and the white shark, *Carcharodon carcharias* (Smith, 1991 ; Taylor, 1998). Hence, we think that an electric field is a useful method for protection from some species during shark attacks. However, the electric field seems to have little effect once the sharks start to feed. Taylor (1998) reported that during the Shark POD test, tiger shark, *G. cuvier*, lemon shark, *Negaprion acutidens*, great hammerhead, *Sphyrna mokarran*, whaler, *Carcharhinus amblyrhyncos*, and tawny shark, *Nebrius ferrugineus* came to the bait. She stated that these experiments reinforced her feeling that once a shark starts eating, the desire to feed overrides the instinct of self preservation. Further studies are needed to determine conclusively whether these reactions are different by species and wave form, frequency and voltage of the electric field.

In line fisheries, longlines, drop lines, and rod and reel, depredation of catch fishes by sharks has been documented (Sivasubramanium, 1965 ; Hirayama, 1976 ; Kobayashi and Yamaguchi, 1978 ; Yano, 1996b). Hirayama (1976) reported that the depredation rate of tuna longlines by sharks was calculated to range between 1.64–14.45% of the tuna catch. Kobayashi and Yamaguchi(1978) reported that the depredation rate of tuna longlines by sharks was estimated to be up to 7.5% of the total catch. In the Ryukyu Islands, high depredation of the catch by sharks is known in bottom drop lines and rod and reel fisheries (Yano, 1998, 1999). In particular areas around the islands depredation rates by sharks were estimated of 10 to 30% of the total catch (Yano, unpublished). In those areas, several species of *Carcharhinus* and *G. cuvier* are mainly observed to depredate catch fishes (Yano, 1998). Several species of *Carcharhinus* were observed to respond to electric fields by previous researchers and the present study. Taylor (1998) reported that the big Queensland grouper, *Epinephelus lanceolatus*, was unaffected by electric stimulation. If teleost fishes are unaffected by electric stimulation, the development electric field generating equipment for use on fishing gear may decrease the depredation rate of the catch fishes by sharks. For example, electrodes attached to the line gear could pulse electric fields around the hooks.

ACKNOWLEDGMENTS

We thank H. Mizuno, E. Fukui, K. Terada, S. Iwata, and K. Nakano and the Aichi Prefecture Government, for their support of the research fund and help with the experiments ; to the staff members of the Okinawa Expo Aquarium, the

Hekinan Seaside Aquarium, and the Aichi Fisheries Research Institute, and the students of the Institute of Medical Electronics, University of Tokyo, for their assistance with the experiments; to S. Kajiura and A. Bush, at the Hawaii Institute of Marine Biology, for their valuable advice and review of the manuscript.

REFERENCES

Baldridge, H. D. 1974: Shark attack. 263 pp., Berkley Medallion Books, New York.

Dijkgraaf, S. and A. J. Kalmijin. 1962: Verhaltensversuche zur Funktion der Lorenzinischen Ampullen. Naturwissenschaften, 49, 400.

Dijkgraaf, S. and A. J. Kalmijin. 1963: Untersuchungen über die Funktion der Lorenzinischen Ampullen an Haifischen. Z. Vgl. Physiol. 47, 438–456.

Fukui, E., M. Suzuki and K. Nagamatsu. 1997: Measurements of intensity of electric field of Shark POD. In "Report of anti-shark attack, physiology and behavior of sharks Ⅱ" (ed. by K. Yano), 36–37, Shark research project team of Aichi Prefecture Government. Hekinan. (In Japanese)

Hirayama, N. 1976. Study on predation damages to hooked tuna by shark in longline fishery. J. Tokyo Univ. Fish., 62(2), 125–136.

Hueter, R. E. and P. W. Gilbert. 1990: The sensory world of sharks. In "Discovering sharks" (ed. by S. H. Gruber), 48–55, American Littoral Society, Highlands, New Jersey.

Kalmijin, A. J. 1971: The electric sense of sharks and rays. J. Exp. Biol., 55, 371–383.

Kalmijin, A. J. 1974: The detection of electric fields from inanimate and animate sources other than electric organs. In "Handbook of sensory physiology", vol. Ⅲ/3 (ed. by A. Fessard), 147–200, Springer-Verlag Berlin- Heidelberg, New York.

Kalmijin, A. J. 1978: Electric and magnetic sensory world of sharks, skates, and rays. In "Sensory biology of sharks, skates, and rays" (eds. by E. S. Hodgson and R. F. Mathewson), 507–528, Office of Naval Research Department of the Navy, Arlington.

Kobayashi, H. 1978: The hooked rate of longline-caught fish and shark damage. Bull. Mie Univ. (5), 117–128.

Murray, R. W. 1962: The response of the ampullae of Lorenzini of elasmobranchs to electrical stimulation. J. Exp. Biol., 39, 119–128.

Nelson, D. R. 1983: Shark attack and repellency research: an overview. In "Shark repellents from the sea" (ed. by B. J. Zahuranec), 11–74, Westview Press, Washington, DC.

Ryan, P. R. 1981: Electroreception in blue sharks. Oceanus, 24(4), 42–44.

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

Sivasubramanium, K. 1965. Predation of tuna longline catches in the Indian Ocean, by killer whales and sharks. Bull. Fish. Res. Stn., Ceylon, 17(2), 93–96.

Smith, E. D. 1991: Electric shark barrier: initial trial and prospects. Power Engineering Journal, July, 167–176.

Taylor, V. 1998: Testing the Shark POD. Shark News, 11, 10–11.

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

Yano, K. 1996 a : Shark attack off Atsumi Peninsula, Aichi, Japan on 9 April, 1995. In "Report of anti-shark attack, physiology and behavior of sharks" (ed. by K. Yano), 1–4, Shark research project team of Aichi Prefecture Government. Hekinan. (In Japanese)

Yano, K. 1996 b : The relation between sharks and human : shark attack and human attack. Kaiyo Monthly 28(7), 448–459 (In Japanese).

Yano, K. 1998 : Sharks : Biology of chondrichthyan fishes. 223 pp., Tokai Univ. Press, Tokyo. (In Japanese)

Yano, K. 1999. Chondrichthyans of the Ryukyu Islands, Japan. Proc. 5th Indo-Pac. Fish Conf., Noumea : 351–365.

電気刺激に対するサメ類の反応実験

矢野　和成・森　秀樹・南川　清・上野　照剛
内田　詮三・長井　健生・戸田　実・増田　元保

抄　録

電界印加実験および局部電界発生実験（電撃実験）を用いて，電気刺激に対するサメ類の反応について研究を行った．

電界印加実験（EFE）は，クロトガリザメ，ネムリブカ，トラフザメの３種類で行った．実験方法は，直径７メートルの円形水槽の中心部と縁辺部に銅板電極を設置し，電流を流して実験魚の遊泳行動の観察を行った．実験は方形波パルスと 60Hz 正弦波交流を電力増幅し，電極間に印加した．電界印加実験は１回の実験につき10分間行い，ビデオカメラによる撮影と目視による行動観察を行った．３種類の実験魚の通常の遊泳行動は，円形水槽の縁に沿って遊泳していた．クロトガリザメとネムリブカは，電界印加を与えたところ，頭部を左右に振り急激な方向変換をし，その回数は通常の遊泳行動よりも多かった．そして，電極付近には近づかず，電極間もほとんど通過することがなく，これら２種は電界を嫌う行動がみられた．一方，トラフザメは電界印可を行っても遊泳行動に変化が現れることがなかった．

局部電界発生実験（PEF）は，EFE の実験魚３種とイタチザメについては円形水槽で，ツマグロ，ドチザメ，ナヌカザメ，トラザメでは長方形水槽（180㎝×120㎝×70㎝）で実験を行った．クロトガリザメ，ツマグロ，ネムリブカ，ドチザメは，電撃刺激に対して非常に強い逃避行動の反応がみられた．ナヌカザメとトラザメでは，電撃刺激に対して頭部をほんの僅か振る程度の非常に弱い反応があり，逃避行動もみられなかった．イタチザメとトラフザメは電撃刺激に対してまったく反応しなかった．

以上のように電気刺激に対して非常に強い逃避行動がみられる種類もいるが，まったく反応しない種類もみられ，これら刺激に対する反応には種類別に違いがあることが判明した．そのため，電気刺激に対する反応が強い種類では，サメ類の人的被害防止あるいは漁業への食害防止のために電気刺激を利用できることが示唆された．