intervals between 2.5 and 10 seconds the relationship appeared to be approximately linear (Fig. 3), that is, the spikes reappeared after a constant number of stimuli regardless of the frequency of stimulation. With longer intervals, however, for example 15 or 20 seconds, the spikes did not reappear even after 30 to 40 minutes of stimulation. These results suggest that during each of the series of normal responses to stimulation some change occurred which outlasted the stimulus interval (provided this interval was 10 seconds or less), and which built up during successive responses until a critical level was reached, triggering the convulsive activity pattern. This change presumably dissipated itself during periods without stimulation.

The manner in which the manifestation of the pharmacological action of the convulsant hydrazides depends on on-going neuronal activity is reminiscent of the action of low doses of the hemicholinium HC-3 in blocking neuromuscular transmission (*4*). In this latter case, block of the neuromuscular junction results from the arrest of acetylcholine formation (*5*), and becomes apparent only after a finite number of impulses have traversed the junction and depleted the pre-existing store of the transmitter. This may be contrasted with the block produced by substances like curare and decamethonium, whose mechanism of action does not depend on whether or not the junction is active (*6*). The difference between the modes of action of the convulsant hydrazides and strychnine may be analagous, although there is no evidence that both these types of drugs necessarily act on the same neuronal system. Strychnine may act in the cortex, as it does in the spinal cord (*7*), by suppressing the action of inhibitory neurones, and it is possible that the convulsant hydrazides also act on an inhibitory system, blocking the synthesis of an inhibitory substance which is normally released during neuronal activity. Their convulsant action would not be evident until the pre-existing store of this material had been depleted by normal activity, and if the block of synthesis was only a partial one, the material would re-accumulate during a period in which no activity occurred. On the other hand, it would also be possible to explain the action of the hydrazides in terms of the accumulation of some substance that had an excitatory effect on the cortical neurones. The hypothesis that they act by blocking an inhibitory system recalls the proposal by Killam and Bain (*8*) that the action of the hydrazides is to block activity of enzymes catalyzed by vitamin B_6, and thus interfere with the production of gamma-aminobutyric acid, which has an inhibitory action on cortical neurones. This study suggests that if this were the case, it should be possible to demonstrate a net destruction or release of gamma-aminobutyric acid during normal neuronal activity in the cortex (*9*).

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References and Notes

1. P. Vanasupa, S. Goldring, J. L. O'Leary, *Electroencephalog. Clin. Neurophysiol.* **11**, 93 (1959); C. W. Dunlop, W. R. Adey, K. F. Killam, M. A. B. Brazier, *Am. J. Physiol.* **198**, 399 (1960).
2. B. D. Burns, *J. Physiol.* **112**, 156 (1951).
3. This latent period has been shown to be characteristic of the action of either topically or systemically applied thiosemicarbazide on spontaneously active cortex whether it be isolated or intact [J. B. Preston, *J. Pharmacol. Exptl. Therap.* **115**, 28 (1955)], and may be related to the period of time required for formation of the active hydrazone compound [see H. L. Williams and J. A. Bain, *Intern. Rev. Neurobiol.* **3**, 319 (1961)].
4. F. W. Schueler, *Intern. Rev. Neurobiol.* **2**, 77 (1960).
5. F. C. MacIntosh, R. I. Birks, P. B. Sastry, *Nature* **178**, 1181 (1956).
6. W. D. M. Paton and E. Zaimis, *Pharmacol. Rev.* **4**, 219 (1952).
7. K. Bradley, D. M. Easton, J. C. Eccles, *J. Physiol.* **122**, 462 (1953).
8. K. F. Killam and J. A. Bain, *J. Pharmacol. Exptl. Therap.* **119**, 255 (1957); K. F. Killam, *ibid.* **119**, 263 (1957).
9. This work was supported by grants from the United Cerebral Palsy Research, the Educational Foundation, Inc., and the Medical Research Council of Canada.
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12 August 1963

Sharks: Attraction by Low-Frequency Sounds

Abstract. *Large sharks (Carcharhinidae, Sphyrnidae), in their natural environment, were attracted to low-frequency (predominantly 20 to 60 cy/sec) pulsed sounds, but apparently not to higher frequency (400 to 600 cy/sec) pulsed sounds, or to low-frequency continuous sounds. The sharks apparently detected and oriented to the sounds in the acoustic far field.*

In a recent study conducted on the reefs off Miami, Florida, sharks were attracted to low-frequency pulsed sounds resembling those of struggling fish. The appearance of sharks in the vicinity of wounded or struggling fish is a phenomenon that has long been noted by fishermen and skin divers. Hobson (*1*) and Tester (*2*) have shown that olfaction plays a major role in the attraction of sharks. In some instances, however, the rapid appearance of sharks precludes the possibility that olfactory substances, which are carried at a relatively slow rate by currents, formed the initial attractive stimulus. Because vision is limited by poor visibility underwater, and because the struggling fish is sometimes hidden from view, it appears reasonable that some form of mechanoreception is involved.

The existence of the sense of hearing in sharks has been well established since the days of Parker (*3*), who obtained responses from the smooth dogfish, *Mustelus canis*, by striking the side of the tank with a hammer. More recently, Vilstrup (*4*) obtained from the spiny dogfish, *Acanthias vulgaris* (= *Squalus acanthias*), conditioned responses to sound; and Moulton (*5*) conditioned *Mustelus canis* to an oscillator tone. Clark (*6*) succeeded in establishing instrumental conditioning in large lemon sharks, *Negaprion brevirostris*, and observed that they responded to a submerged bell. Dijkgraaf (*7*) trained dogfish, *Scyliorhinus canicula*, with sound and electric shock. His preliminary results indicate that perception of a 180 cy/sec tone occurs mainly in the labyrinth. Olla (*8*) obtained responses from trained small hammerhead sharks at frequencies between 100 and 600 cy/sec. Kritzler and Wood (*9*) obtained an audiogram for a captive bull shark, *Carcharhinus leucas*. The shark responded to frequencies between 100 and 1500 cy/sec and was most sensitive to the band between 400 and 600 cy/sec. With identical sound sources at three positions, they observed that the shark was able to localize the source from a distance of at least 6.5 m (*10*).

Hobson (*1*) attempted to evoke responses from sharks to sounds in the field at Eniwetok Atoll. He played back recordings of various sounds through an underwater speaker when sharks were in the area and visible to observers. There was no indication that the sharks detected or responded to the sounds.

The initial phase of our study consisted of making recordings in the field to determine the frequency composition and pulse characteristics of the sounds of struggling fish. We used a Sony SRA-2, 262 D tape recorder and

Table 1. Sharks sighted during acoustic playback studies. Observation period, 15 minutes.

Type of sound	No. of observation periods	No. sighted	Sightings per period
Quiet (no sound)	28	1	0.04
Low frequency, pulsed	22	18	.82
High frequency, pulsed	15	2	.13*
Low frequency, continuous	12	0	.00

* An uncertain value, see text.

a USN AN/PQM-1A noise measuring set equipped with a hydrophone and about 100 m of cable. A diver placed the hydrophone near a cave containing a suitable fish and signaled the operator in the boat above to start recording, while a second diver speared the fish in such a way as to incite the most struggling.

We obtained the best recordings from a 12-kg black grouper, *Mycteroperca bonaci*. A spectral analysis of this sound was made on a Missilyzer (*11*) (Fig. 1*A*). The sound is composed primarily of low frequencies, although some moderately high frequencies are present, partly due to the spear hitting the rocks. The peak sound pressure occurs below 100 cy/sec and appears to have an amplitude of about +38 db relative to 1 microbar at 1 m. The distance from the source of the sound to the point where the amplitude diminishes to that of ambient noise, or the theoretical propagation distance for this sound, is at least 300 m in a calm sea.

In the next phase of the study we played back various sounds on the reef and noted their effectiveness in attracting sharks. Three types of sounds were used: (i) low-frequency pulsed sound, consisting of white noise passed through a 60-cy/sec, low-pass filter and pulsed with a transient-less switch; (ii) low-frequency continuous sound, similar to above but not pulsed; and (iii) high-frequency pulsed sound, for which a filter band of 400 to 600 cy/sec was used. A white noise generator of the photomultiplier type, and a SKL model 320 variable electronic filter were used. The sounds were put on tape and played back with the Sony recorder, an Eico ST40 amplifier, and a USN J9 underwater transducer.

We were interested in determining whether high or low frequencies played the major role in attracting sharks. The low-frequency pulsed sound (Fig. 1*B*) possessed the low-frequency characteristics and the pulse rate within bursts of the field recordings of struggling fish. The high-frequency pulsed sound resembled the high-frequency portion of the sound of struggling fish. The field recordings were not played back because of a poor signal to noise ratio and because they contained both low and high frequencies.

Playback was conducted at various spots on the reefs, in water approximately 15 m deep. The transducer was suspended from the boat at a depth of about 12 m. An observer was in the water at the surface above the transducer. Visibility varied between 15 and 25 m and the bottom was usually composed of low coral and rock with patches of sand.

The sounds were played for periods of 15 minutes with the intensity being varied every 10 or 15 seconds (except for the low-frequency continuous sound). Quiet periods of similar length with the transducer and observer in the water, preceeded the playback periods.

The results (Table 1) are based on 77 observation periods which took place on 9 days in the spring of 1963. The low-frequency pulsed sound proved effective in attracting sharks to the area of the transducer where no sharks were previously seen. The low-frequency continuous sound did not attract sharks. Although two sharks were attracted to the high-frequency pulsed sound, we are not certain they responded to the high frequencies because we later found some low-frequency noise on the tape. The quiet periods indicate the number of sharks likely to enter the observation area for reasons other than attraction to the sounds.

Included among the 18 sharks sighted during the low-frequency pulsed sound periods were 9 bull sharks, *Carcharhinus leucas*; 2 hammerhead sharks *Sphyrna* sp.; 2 lemon sharks, *Negaprion brevirostris*; 1 tiger shark, *Galeocerdo cuvieri*; and 4 unidentified carcharhinid sharks. They were from 1.5 to 3 m in length. The one shark seen during the quiet periods was a nurse shark, *Ginglymostoma cirratum*.

The sharks sighted during the playback periods displayed certain modes of behavior which one would not expect to see if they appeared by chance alone. Initially, in nearly all instances,

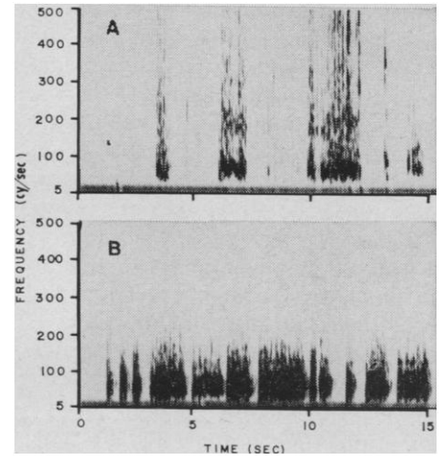

Fig. 1. (*A*) Spectral analysis of recorded struggling sounds of speared black grouper, *Mycteroperca bonaci*, and (*B*) of the low frequency pulsed sound (before transducer) used in playback. Darkness of trace indicates sound amplitude.

they swam directly toward the transducer along a straight line representing a radius of the circular field of visibility. After the initial direct approach the sharks veered away at distances of from 1 to 12 m from the transducer and departed, sometimes lingering or circling a few minutes near the limit of visibility. The shark seen during the quiet periods did not swim toward the transducer but along a line representing a chord of the field of visibility, passing about 14 m from the transducer.

The results bear several important implications. Sharks in their natural environment can be attracted by certain sounds. Since significant attraction was achieved only with the low-frequency pulsed sound it appears that not all sounds audible to sharks will attract them. The band of 400 to 600 cy/sec of the high-frequency pulsed sound coincides with Kritzler and Wood's band of maximum sensitivity in the bull shark. A pulsed quality, similar to struggling fish, and a predominance of low frequencies seem to be necessary to attract sharks.

Hobson's failure to observe auditory responses in his sharks is not necessarily inconsistent with our data. We rarely observed a sudden change in behavior when the sound was stopped for some time and then resumed while a shark was visible to the observer. It appears that, while auditory stimuli may attract sharks from relatively long distances, some other stimuli such as

visual or olfactory ones may be necessary to initiate feeding behavior.

Attraction to sounds involves some form of directional hearing. With the exception of Kritzler and Wood, most previous investigators of this phenomenon in fish have found it only at very close range or not at all (*12*). In our experiments, the possibility that the sharks simply followed a sound gradient seems remote because we frequently changed the intensity. True directionality is also suggested by the oriented attitude of the sharks upon entering the field of visibility.

An important factor is the maximum distance from which the sharks are attracted and whether it is acoustically near or far field (*13*). At present, however, we have no reliable method for measuring this distance. A comparison of the numbers of sharks seen during the periods of quiet and the periods of sound seems to indicate an attraction distance of well beyond the limit of visibility at 15 to 25 m. The near field of a dipole source such as our J9 transducer, extends to only about 15 m (*14*) at 20 cy/sec, the approximate low end of our transmitting system. Because the limit of visibility was usually beyond 15 m we can say that the sharks were hearing and orienting to the sounds in the far field.

The far field pressure wave of the low-frequency sound used in playback is theoretically detectable above ambient noise at about 2000 m in a calm sea. If sharks are capable of detecting pressure waves, then it is reasonable that they may respond at great distances from the source. Sharks, however, do not possess an obvious pressure detector such as a gas bladder, and it seems more likely that they would detect particle displacement. The maximum far field particle displacement of the sound used at 25 m is about 100 Å. The lowest measurement of sensitivity in the lateral-line of fish is 10 Å (*15*). The sound we used would have a displacement of 10 Å at about 250 m. Thus, although the sharks may be in the far field, the displacements are not small enough to rule out the possibility of utilization of the lateral-line, an organ regarded by some as a near field displacement detector (*13; 16*).

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References and Notes

1. E. S. Hobson, *Pacific Sci.* **17**, 171 (1963).
2. A. Tester, *ibid.*, p. 145.
3. G. H. Parker, *Science* **29**, 428 (1909).
4. T. Vilstrup, *Structure and Function of the Membranous Sacs of the Labyrinth in Acanthias vulgaris* (Munksgaard, Copenhagen, 1952).
5. J. M. Moulton, personal communication.
6. E. Clark, *Science* **130**, 217 (1959).
7. S. Dijkgraaf, *Nature* **197**, 93 (1963).
8. B. Olla, thesis, Univ. of Hawaii (1962).
9. H. Kritzler and L. Wood, *Science* **133**, 1480 (1961).
10. L. Wood, personal communication.
11. Kay Electric Co.
12. W. A. van Bergeijk, in *Marine Bio-acoustics*, W. N. Tavolga, Ed. (Pergamon, New York, in press).
13. G. G. Harris and W. A. van Bergeijk, *J. Acoust. Soc. Am.* **34**, 1831 (1962).
14. G. G. Harris, in *Marine Bio-acoustics*, W. N. Tavolga, Ed. (Pergamon, New York, in press).
15. J. W. Kuiper, thesis, Groningen, Netherlands (1956), cited by S. Dijkgraaf, *Biol. Rev.* **38**, 51 (1963).
16. Contribution No. 500 from the Marine Laboratory, Institute of Marine Science, University of Miami. This study, directed by Dr. Warren J. Wisby, was supported by funds from project Nonr 840-19, Office of Naval Research. The assistance of J. D. Richard, R. L. Aaron, R. Dann, J. Clark, J. C. Steinberg, M. Kronengold, and W. Cummings is gratefully acknowledged.

3 September 1963

Directional Movement and Horizontal Edge Detectors in the Pigeon Retina

Abstract. *There are ganglion cells in the pigeon retina that respond selectively, some to any edge moving in a particular direction only, others to any vertically moving horizontal edge. This selective response to a specific stimulus arises from the selective sensitivity of each neuron to a particular spatiotemporal configuration in its afferent influences, and is independent of specific pathways.*

In a recent paper Barlow and Hill (*1*) have shown that many ganglion cells of the rabbit retina respond selectively to movement in one direction and not in the reverse. Similar observations have been made in the frog retina (*2*) and in cortical cells of the cat (*3*). In general the works of Maturana *et al.* (*2*), Hubel and Wiesel (*3*), Mountcastle (*4*), and Barlow and Hill (*1*) show that in the central nervous system of vertebrates there are classes of highly specific cells that respond maximally or exclusively to a particular stimulus. Now we wish to present some of our observations on directional cells in the pigeon retina and to discuss some aspects of what seems to us is the fundamental insight that these findings give into the functional organization of the central nervous system.

We recorded the activity of single retinal cells from cut and intact optic nerves in curarized pigeons by means of metal-filled micropipettes. Thus we studied six classes of ganglion cells which differ in the visual configuration to which they respond. Of these we shall now mention only two. We shall not be concerned with the quantitative aspects of the responses which may vary markedly from cell to cell, but only with the mode of response. Nonetheless, we should mention that in general the size of the response (number of spikes and frequency) depends on the direction of contrast, the intensity of contrast, and the speed of movement.

Directional movement detectors form about 30 percent of the accessible cell population. They have five fundamental characteristics:

1) Small receptive fields (defined as the area from which a response can be elicited), which vary between ½° and 1° in diameter (55 to 110 μ on the retina).

2) An optimal or exclusive response to the movement of an edge in one direction but not in the reverse (Fig. 1). The sharpness of the required edge depends on the size of the receptive field: the smaller the field, the sharper the edge needed.

3) An absence of response to phasic changes of the ambient light.

4) Directional mode of response independent of:

a) the intensity of the ambient light (we tried intensities up to four logarithmic units apart);

b) the direction of contrast across the moving edge: the mode of response is the same for moving objects lighter or darker than the background (Fig. 1, *B, C*);

c) color, at least to the extent that this can be judged by using different combinations of colored objects and backgrounds made with colored papers and lights (we used narrow band color filters);

d) the part of the receptive field in which the object moves (Fig. 1*D*).

5) A uniformly *on-off* receptive field. If there are exclusive *on* or *off* spots, these show no special relation to the direction of optimal response. The mode of response is not modified by a spot of light shone *on-off* on any part of the receptive field, nor by a ring surrounding the field or a crescent or any variegated background shone *on-off* in any part of the surroundings while the ob-