AD-A120 443 ELECTRORECEPTION OF CONSTANT AND ALTERNATING FIELDS BY THE CATFISH ICTALURUS NEBULOSUS(U) NAVAL OCEAN SYSTEMS CENTER SAN DIEGO CA C S JOHNSON 21 JUN 82 NOSC/TR-805 1/1

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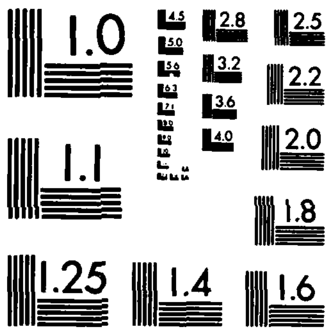
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Technical Report 805

ELECTROREPTION OF CONSTANT AND ALTERNATING FIELDS BY THE CATFISH *Ictalurus nebulosus*

CS Johnson

21 June 1982

Period of work: October 1980—October 1981

Prepared for
Naval Sea Systems Command

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NAVAL OCEAN SYSTEMS CENTER
San Diego, California 92152

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Commander

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Technical Director

ADMINISTRATIVE INFORMATION

The work reported herein was conducted during FY81 at the NOSC Marine Life Sciences Laboratory as part of Project ZR0000101, a NOSC Independent Research sponsored project.

The author thanks AJ Kalmijn for showing his experimental procedure at his laboratory at the Woods Hole Oceanographic Institution and for critically reading this manuscript and making many valuable and constructive comments and suggestions.

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Under authority of
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CONVERSION TO METRICS

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Detection thresholds of a catfish *Ictalurus nebulosus* to composites of single-frequency square-wave electric fields added to constant electric fields were measured. Thresholds were determined for electrical signals at six different dc to square-wave amplitude ratios ranging from 1:8 to 4:1. Its peak sensitivity was found to be near 5 Hz. The catfish responded primarily to the dc part of the signal when the dc amplitude was much larger than the amplitude of 1 or 5 Hz square waves. Conversely, it responded to the 1 or 5 Hz square-wave part of the signal when the square-wave amplitude was much larger than the dc. But it responded only to the dc part of a dc + 32 Hz composite signal regardless of the relative amplitudes.

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OBJECTIVE

Investigate the relative importance of ac and dc electric fields when presented at the same time to the catfish *Ictalurus nebulosus.* Through observation of the behavior of the fish, determine its detection thresholds to square-wave electric fields having both ac and dc components.

RESULTS

1. For signals of equal square-wave and dc amplitudes at frequencies between 0.5 and 64 Hz, the catfish was found to have peak threshold sensitivity near 5 Hz.
2. Thresholds were determined for electrical signals at six different dc to square-wave amplitude ratios ranging from 1:8 to 4:1.
3. With 1 or 5 Hz square waves, the catfish responded primarily to the dc part of the signal when the dc component amplitude was much larger than the amplitude of the square-wave component.
4. Conversely, it responded to the 1 or 5 Hz square-wave part of the signal when the square-wave component amplitude was much larger than the dc component.
5. With 32 Hz square waves, it responded only to the dc component of the composite signal regardless of the relative component amplitudes.

RECOMMENDATIONS

1. Repeat this experiment on several fish of the same species to verify the results.
2. Choose more carefully the salts used to vary the conductivity of the water in the experimental tank.

INTRODUCTION

Parker and van Heusen (ref 1) were the first to observe the responses of the catfish *Ictalurus nebulosus* to electric fields. They concluded, erroneously, that the fields were sensed via the taste buds distributed over the skin. Dijkgraaf (ref 2) showed experimentally that the electric fields were actually detected by ampullar organs. Roth (ref 3 and 4) showed behaviorally that *Ictalurus nebulosus* could discern the polarity of nonuniform dc electric fields. Kalmijn and Bernal, in Kalmijn (ref 5), showed that *Ictalurus nebulosus* can detect and orient in electric fields as small as 5 μV/cm. More recently Kalmijn et al (ref 6) obtained detection thresholds for *Ictalurus* of 1 μV/cm and showed that these catfish can orient in fields of 10 μV/cm to within 30° or better of the direction of the field (ref 7).

In the first part of the present experiment, thresholds were obtained for a constant dc field. Then, to investigate the relative importance of ac and dc fields presented to the catfish at the same time, thresholds were obtained for fields containing various amplitudes of both dc and square-wave signals.

MATERIAL AND METHODS

The experiments were carried out on a single 180-mm-long *Ictalurus nebulosus LeS* caught at Lake Wohlford near San Diego, California. An experimental arrangement and a procedure very similar to those of Kalmijn and Bernal were used. A rectangular plastic tank 0.75 by 1.5 m was used in the experiments. Water was maintained at a depth of 0.1 m and a temperature of 18 ± 2°C. A uniform horizontal electric field was produced in the tank by means of ten equally spaced salt bridge electrodes (water-filled plastic tubes) along each short side of the tank. The resistivity of the fresh water was adjusted to 2 kΩ-cm by adding Insta [illegible]ean salts, manufactured by Aquarium Systems, East Lake, Ohio, to doubly deionized water.

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1. Parker, GH, and AP van Heusen, The Responses of the *Amiurus nebulosus* to Metallic and Nonmetallic Rods, Amer J Physiol, vol 44, p 405–420, 1917.
2. Dijkgraaf, S, Electroreception in the Catfish, *Amiurus nebulosus*, Experientia (Basel), vol 24, p 187–188, 1968.
3. Roth, A, Electroreception in the Catfish, *Amiurus nebulosus*, Z vergl Physiol, vol 61, p196–202, 1968.
4. Roth, A, Elektrische Sinnesorgan beim Zwergwels *Ictalurus nebulosus (Amiurus nebulosus)*, Z vergl Physiol, vol 65, p 368–388, 1969.
5. Kalmijn, AJ, The Detection of Electric Fields from Inanimate and Animate Sources Other than Electric Organs, Handbook of Sensory Physiology, vol III/3, p 147–200, A Fessard (ed), Springer-Verlag, Berlin, Heidelberg, New York, 1974.
6. Kalmijn, AJ, CA Kolba, and V Kalmijn, Orientation of Catfish (*Ictalurus nebulosus*) in Strictly Uniform Electric Fields: I. Sensitivity of Response, Biol Bulletin, vol 151, no 2, p 415, 1976.
7. Kalmijn, V, CA Kolba, and AJ Kalmijn, Orientation of Catfish (*Ictalurus nebulosus*) in Strictly Uniform Electric Fields: II. Spatial Discrimination, Biol Bulletin, vol 151, no 2, p 415–416, 1976.

Following the procedure of Kalmijn (ref 8), three black plastic tubes 43 mm in inner diameter and 150 mm long were positioned in the tank as shown in figure 1. A large-mesh plastic screen was positioned between the tubes and electrodes to separate the experimental area from the electrodes. The arrangement for producing the electrical signals is also shown in the figure.

The fish was released from the center tube by removing that tube from the tank. It then swam to one of the two remaining tubes for shelter. If the fish went to the "wrong" tube, that tube was immediately removed from the tank, forcing it to swim across the tank to the remaining "correct" tube, where it was allowed to remain undisturbed for a short period. This procedure was repeated many times with a dc electric field present or absent, to train the fish to go to the tube at one side of the tank when a field was present and to the other side when a field was not present. Visual cues were allowed so that the fish could tell one side of the tank from the other. It should be noted that Kalmijn (ref 8) always had a field present, and they trained the fish to go to the right or left, perpendicular to the field direction.

Data were collected by a staircase method (see Cornsweet, ref 9) with a 6 dB (factor of two) step size; ie, the stimulus intensity was reduced by 6 dB when the response was "correct" and increased by 6 dB when it was "wrong." Each data point consisted of ten "signal on" and ten "signal off" trials in random sequence, immediately preceded by twenty (ten on and ten off) trials in random order but well above threshold intensity, to maintain the fish's behavior. The trials were separated by 1-minute intervals. It took the fish 2 to 3 seconds to make its response. Each data point was measured at least four times. Data points were spaced at least one hour apart to allow the fish to rest, and no more than four were taken in a day.

RESULTS

The basic signal used was a symmetrical square wave to which a dc bias was added. By changing the proportion of dc bias to the square-wave amplitude, the dc to ac content ratio of the signals was varied. If the dc bias added was equal to the square-wave amplitude,* the resulting wave form was that of a pulse train with voltage switched from zero to a positive voltage with equal on and off times. In this case as the frequency of the signals is reduced, approaching zero, the signal is sensed by the fish as simply a dc voltage that is either on or off. Since the fish took 2 to 3 seconds to make responses, frequencies below about 0.4 Hz are essentially voltage on or off for the fish. At 0.4 Hz the catfish simply swam back and forth across the middle of the tank as the voltage was switched on and off, since it did not have the time to get to one or the other of the tubes. For this reason the frequency range below 0.5 Hz could not be investigated.

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8. Kalmijn, AJ, Electro-Orientation in Sharks and Rays: Theory and Experimental Evidence, Scripps Institution of Oceanography Reference Series, Contract 73-39, p 1–22, 1973.

9. Cornsweet, TN, The Staircase Method in Psychophysics, Amer J Psychol, vol 75, p 485–491, 1962.

*The amplitude of the square wave is defined as half the peak-to-peak value.

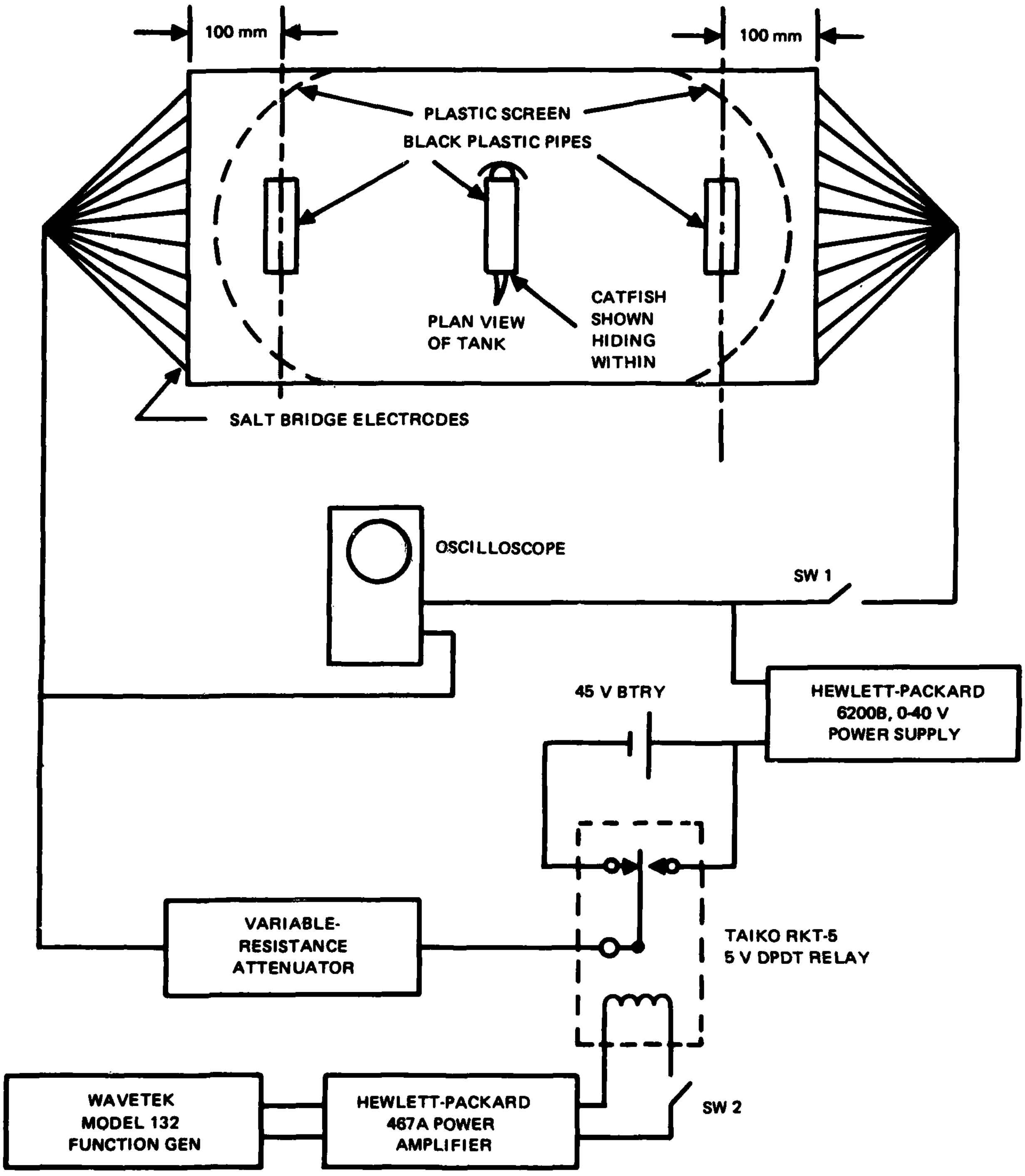

Figure 1. Schematic diagram of the experimental arrangement. The tank is shown at the top of the figure with the three plastic tubes used by the fish to hide in. The dashed curves represent the plastic screen used to separate the fish from the ends of the salt bridge electrodes. Square-wave signals from the Wavetek function generator were amplified and used to operate a relay. The relay switched a 45V battery in and out of the circuit, providing the square-wave signal. The series power supply produced the dc part of the signal. A variable-resistance attenuator was used to change the total signal in 6 dB steps, and an oscilloscope was used to monitor the fidelity of the square waves.

The detection threshold of a dc field, measured first, was found to be 14 ± 2 μV/cm or 23 ± 1 dB relative to 1 μV/cm. All uncertainties given herein are standard errors of the mean values.

Next, data were taken by inserting a pulse train with equal on and off times, ie signals with amplitudes from zero to some positive value and back again. Since these signals are equivalent to a square wave with equal positive and negative amplitudes added to a dc bias of the same amplitude, they have equal dc and square-wave amplitudes by our definition. Data were taken at frequencies from 0.5 Hz to 64 Hz with these half-square-wave, half-dc signals. The threshold pulse amplitudes are plotted in figure 2 in dB relative to 1 μV/cm. Detection sensitivity peaked near 5 Hz at 23 ± 1 μV/cm, dropping above 10 Hz and below 3 Hz to about 29 dB re 1 μV/cm. For the signals used here, which contain equal ac and dc amplitudes, sensitivity to ac signals was found only in the frequency range from 3 to 10 Hz. Above and below this band the fish responded to the average dc value of the signal; ie, the thresholds are consistent with those for dc-only signals. The 29-dB out-of-band sensitivity is accounted for as follows. The threshold for dc was 23 dB and the ac portion of the signals had a duty cycle of 50%; thus the threshold for the composite was 23 dB plus 6 dB, or 29 dB.

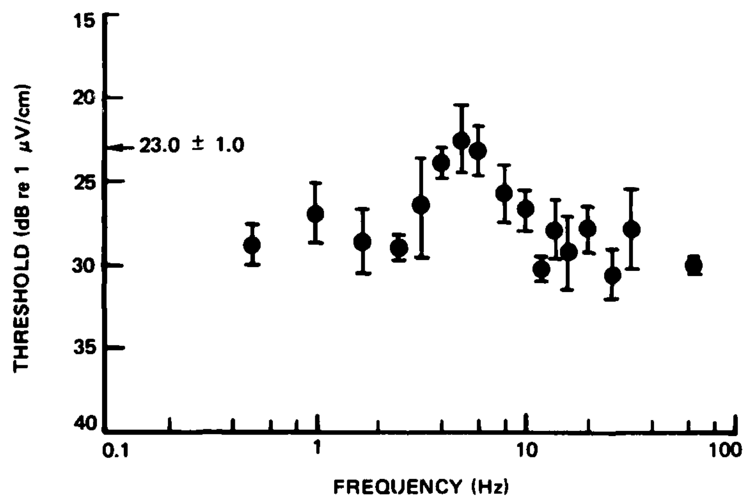

Figure 2. Plot of detection thresholds versus frequency for a square-wave pulse train with equal on and off times. The indicated errors are the standard errors of the mean values computed from the data. 23 ± 1 dB is the measured threshold for a dc signal. The thresholds plotted are the total (dc plus ac) amplitudes of the pulses in dB relative to 1 μV/cm.

Peters and Buwalda (ref 10) measured the frequency response of freely swimming *Ictalurus nebulosus* to sinusoidal and triangular signals from 0.03 to 25 Hz by electrophysiologically recording the spikes from the ramus lateralis ventralis nervi vagi. They found the greatest sensitivity in the frequency range from 3 to 7 Hz. Although they did not use square waves, their results can be compared with the present ones. Square waves contain frequencies of all integral multiples of the primary frequency (see for example Panter, ref 11), and triangular waves also contain higher frequency components. Since the sensitivity of the fish drops off rapidly above 10 Hz, however, only the lowest primary (fundamental) frequencies influence fish behavior. Thus square, triangular, and sinusoidal waves are in effect equivalent for this experiment. With a 5 Hz square-wave input, for example, about all the fish sensed was the 5 Hz fundamental. Peters and Buwalda (ref 10) showed that the sensitivity of fish decreases much more slowly below 3 Hz than it does above 7 Hz. Since they used signals entirely ac in content, they observed no flattening of the fish's response above 10 Hz. In the frequency range below 3 Hz, they showed continuously declining sensitivity to the lowest frequency tested, 0.03 Hz. The present data show that the fish responds to the dc part of the signal at frequencies below about 2 Hz.

Figure 2 shows the considerable scatter or uncertainty in most of the data. In fact, the twelve measurements for 5 Hz are clumped in two groups with average values of 28 ± 1 dB (seven measurements) and 15 ± 1 dB (five measurements) compared to the plotted average value of 23 ± 1 dB. These results suggest that the fish may have responded part of the time to the square-wave part of the signal and part of the time to the dc part. The other data in figure 2 did not show such a distinct separation, but only four measurements were made at each of the other frequencies. The fish was trained first on dc signals and may have been biased by that.

The threshold for the dc signal (14 ± 2 μV/cm) is considerably above the 1 μV/cm measured by Kalmijn et al (ref 6). There are two plausible reasons for this wide variance: (1) The experimental procedure reported here was different from that of reference 6 and may not be as appropriate for measuring thresholds. (2) The ionic content of the salts used to adjust the resistivity of the water in the experimental tank may affect the sensitivity of the fish. Such effects have been found by others (Roth, ref 12, and Kalmijn, private communication 1981).

In the next measurements the frequency of the square wave was fixed at 1, 5, or 32 Hz, the ratio of dc to square-wave amplitude in the signal was held constant at 1:8 (−18 dB), 1:4, 1:2, 1:1, 2:1, or 4:1 (+12 dB), and detection thresholds were determined by varying the total signal amplitude in 6 dB steps. The six ratios of dc amplitude to square-wave amplitude were used at each of the three frequencies.

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10. Peters, RC, and RJA Buwalda, Frequency Response of the Electroreceptors ("Small Pit Organs") of the Catfish, *Ictalurus nebulosus LeS,* J Comp Physiol, vol 79, p 29–38, 1972.
11. Panter, PF, Modulation, Noise and Spectral Analysis, p 22, McGraw-Hill, New York, San Francisco, Toronto, London, Sidney, 1965.
12. Roth, A, Zur Funktionsweise der Elektrorezeptoren in der Haut von Welsen (*Ictalurus*): Der Einfluss der Ionen im Suesswasser, Z vergl Physiol, vol 75, p 303–322, 1971.

The results of these measurements are plotted as figure 3. A single cycle of the electrical stimulus is shown below the dc to square-wave ratio plot, which is expressed in dB, to show the relative dc to square-wave amplitudes on a linear scale. Data from each of the three frequencies used are connected by straight lines, and the three plots are given 10 dB vertical separation for clarity. The detection thresholds are plotted in dB relative to the amplitude of the dc component of the signal. By plotting the data in this way, only variations in threshold values due to sensitivity to the square-wave part of the signal appear as variations on the vertical scale. If the fish were responding only to the dc part of the signal, thresholds would appear constant and independent of the dc amplitude to square-wave amplitude ratio in the signal. If the fish were responding only to the square-wave part of the signal, on the other hand, the thresholds would be expected to decrease 6 dB (a factor of 2) for each 6 dB increase in square-wave amplitude relative to the dc amplitude.

The data in figure 3 show that for 32 Hz, the thresholds are essentially constant and independent of the dc to square-wave ratio. For 32 Hz, the fish appeared to respond only to the dc part of the signal.

For the 5 Hz signal, the thresholds in general decreased as the square-wave portion of the signal was increased, remaining constant when the dc portion was equal to or greater than the square-wave portion. These data indicate that the fish responded to whichever signal component was larger, the square-wave or the dc.

The data for 1 Hz show a similar result but not as pronounced, presumably because of the lower sensitivity to square-wave signals at 1 Hz.

These results suggest that, in the range of frequencies to which they are sensitive, free-swimming *Ictalurus* can discriminate between square-wave and dc electrical signals when both are present simultaneously.

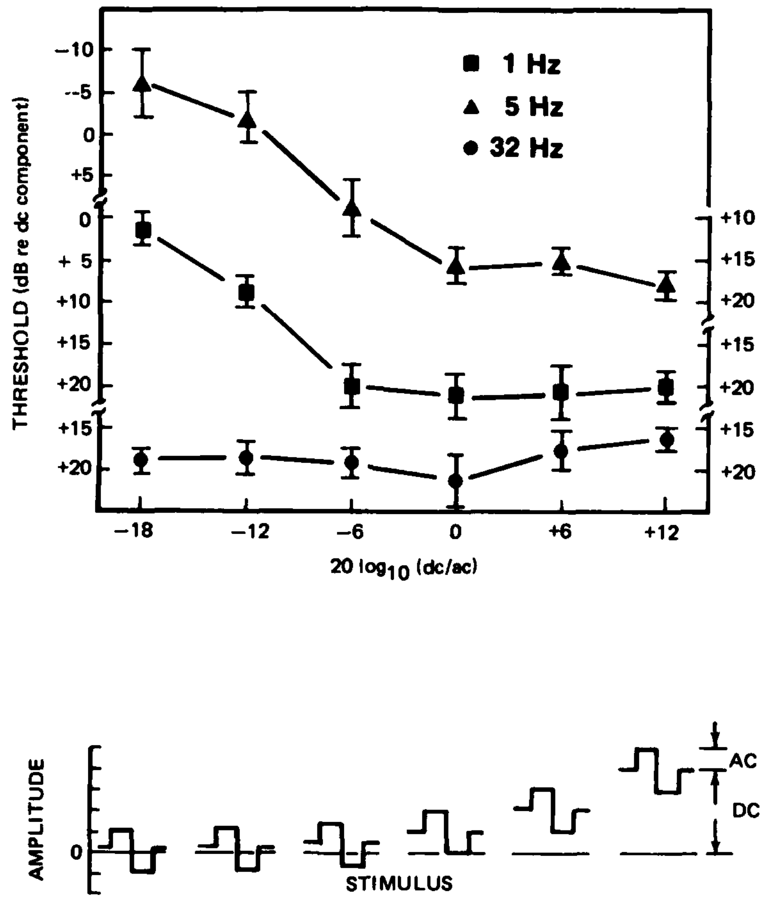

Figure 3. The upper plot shows detection thresholds versus the ratio of dc to square-wave amplitudes, expressed in dB, in the signals used for frequencies of 1, 5, and 32 Hz. The thresholds are computed relative to the impressed dc amplitude in the composite signal rather than to the 1 μV/cm reference amplitude as in figure 2. Six dc amplitude to square-wave amplitude ratios were used. Data from the three frequencies are connected by straight lines, and the three plots are separated by 10 dB on the vertical scale. Errors shown are the standard errors of the mean values. Plotted below on a linear scale is one cycle of each signal measured, showing the relative dc and square-wave amplitudes in the signals used.

CONCLUSIONS

The detection thresholds of the catfish *Ictalurus nebulosus* to square-wave electric fields comprising both alternating current (ac) and direct current (dc) components have been determined behaviorally. The catfish was tested with signals of equal square-wave and dc amplitudes at frequencies between 0.5 Hz and 64 Hz, and its peak sensitivity was found to be near 5 Hz (fig 2). Thresholds at 1, 5, and 32 Hz were determined for signals of six different ratios of dc amplitude to square-wave amplitude ranging from 1:8 to 4:1. When the dc amplitude was much larger than the square-wave amplitude at 1 and 5 Hz, the fish responded primarily to the dc part of the signal (fig 3). When the square-wave amplitude was much larger than the dc amplitude, on the other hand, the fish responded primarily to the square-wave part of the signal. At 32 Hz, the fish responded only to the dc part of the signal regardless of the square-wave amplitude.

RECOMMENDATIONS

This experiment should be repeated on several fish of the same species to verify the results. It is also important to choose more carefully the salts used to vary the conductivity of the water in the experimental tank.

REFERENCES

1. Parker, GH, and AP van Heusen, The Responses of the *Amiurus nebulosus* to Metallic and Nonmetallic Rods, Amer J Physiol, vol 44, p 405–420, 1917.
2. Dijkgraaf, S, Electroreception in the Catfish, *Amiurus nebulosus*, Experientia (Basel), vol 24, p 187–188, 1968.
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