AUDITORY SENSITIVITY IN THE BULLHEAD CATFISH
(ICTALURUS NEBULOSIS)*

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Abstract.—The auditory sensitivity of 4 specimens of the bullhead catfish (Ictalurus nebulosis) was determined by shock-avoidance training in an aquatic shuttle box. The range of hearing extended from 100 to 4000 cycles per second, with the maximum sensitivity around 600 to 700 cycles per second.

Previous work by Stetter¹ indicated that bullhead catfish, then called Ameiurus nebulosus, had a hearing range extending to 13,139 cycles per second (Hz). Poggendorf² also tested the auditory range of a single specimen of bullhead catfish but did not find sensitivity beyond the 5000 Hz limit commonly reported in the general literature for fishes. Because the structure of the fish ear, which involves macular organs weighted with large otoliths, does not appear to be suitable for high frequency response,³ the auditory range of the bullhead catfish needs careful reassessment.

Procedure.—Five bullhead catfish (Ictalurus nebulosis)⁴ were individually trained by a shock-avoidance technique to cross a barrier in an aquatic shuttle box in response to a tonal stimulus.

Tonal stimuli were generated by a Hewlett-Packard oscillator model 204B and monitored for frequency with an Atec model 6A75 electronic counter. Amplitude was monitored with a Hewlett-Packard model 427A voltmeter. An onset switch designed by J. F. Crump and built by J. Palin of Princeton University set the rise and fall time of the tonal stimuli at 0.2 second. The signal intensity was controlled by a Hewlett-Packard model 350D attenuator, amplified by a McIntosh 40 watt audio amplifier model MC-40, and presented by two U.S. Navy J-9 underwater projectors.

The unconditioned shock stimulus was provided by the 110 v a-c line stepped down through an isolation transformer and a variable autotransformer and switch-operated to give 0–24 v a-c pulses between wire-grid electrodes on the sides of the tank. The shock level was found to be most effective at 5 v a-c.

The intertrial interval, the trial duration, and conditioned-unconditioned stimulus interval were monitored by two Standard Electric Time Company model S-1 clocks. A Digital Electronics Company Digiac 3010 computer controlled the intertrial interval, the conditioned-unconditioned stimulus interval, and the presentation or termination of both the tonal and shock stimuli. The computer was programmed to vary the intertrial interval between 47-, 60-, and 73-second periods to prevent time conditioning. Six Clairex type CL707 HI, photocells, placed in a vertical array three on each side of the barrier opposite 12 v bulbs, detected the movement of the subject across the barrier and provided the d-c pulse required to trigger the computer. The lamps and photocells were powered by three Electro Products model EC-2 power supplies.
The experimental tank was an aquatic shuttle box. The tank dimensions were small (4 × 4 × 8 in.) to confine the water mass to a minimum. A diaphragm of rho-c rubber, which has a density approximating that of water, was used to insure sonic transparency and to divide the tank into two equal cubes. A small passage hole (1 in.²) was cut in the center of the diaphragm to give the subjects free access to either compartment of the tank. Each half of the tank had wire-grid electrodes on the side walls wired to provide a shock system that could be switched to either the right or the left compartment as required. The subject had to cross through the hole in the barrier to the opposite half of the tank to escape or avoid the shock. The ends of the tank were composed of the speaker faces of the J-9 projectors. The two projectors were driven 180 degrees out of phase to maintain a push-pull system, thereby giving a relatively uniform sound field. The ambient noise level and both the magnitude and harmonic content of the tonal stimuli were determined with an Atlantic Research Corporation model LC-10 hydrophone operating into an Atlantic Research Corporation model LG-1004 preamplifier and finally into a General Radio Company model 1900 wave analyzer. Calibration standards for the hydrophone and preamplifier were provided by the U.S. Navy Underwater Sound Reference Laboratory, Orlando, Florida.

Each subject was placed in the experimental tank and acclimated for several minutes. The stimulus to be conditioned (500 Hz at 25 db above 1 dyne/cm²) was then turned on and 10 seconds later the unconditioned shock stimulus of a 0.5 second pulse per second was presented until the fish crossed the barrier, or until one minute of shocking elapsed after which the subject was pushed through the barrier with a fish net. As soon as the subject’s body, excluding the tailfin, had passed through the barrier, all stimuli were terminated. After the programmed intertrial interval another training trial was started, and continued until 25 trials had been completed. The subject was then removed from the tank, thus ending the session. Training at the rate of one session per day generally lasted for 25 days. Avoidance conditioning to a combination of light and sound was found to be more rapid than conditioning to sound alone. After acquisition, the light was dimmed by a rheostat to one fourth of the level of the previous day and finally turned off so that only sound conditioning remained. The catfish seemed especially sensitive to visual cues and, therefore, care was taken that their view of the experimenter was blocked by a screen.

After the acquisition of an avoidance response to over 90 per cent of the trials, thresholds were obtained for the range of frequencies to which the subject would respond. At the start of a threshold determination session, 5 to 10 reinforced trials were run in the same manner as in acquisition training. Following these trials, 30 trials were run without shock. A positive response to the sound stimulus was recorded if the subject had crossed the barrier or was partway through and moving to complete the crossing within 10 seconds after the onset of the tonal stimulus. At that time the shock ordinarily would have been presented. Shock was not used in the threshold determination trials because of the danger of experimental neurosis near and below the threshold intensities. When a positive response was observed, the sound intensity was decreased by 5 db.
When no positive response was observed, the sound intensity was increased by 5 db. This "up-and-down" or "staircase" method of threshold determination was devised by the Statistical Research Group at Princeton University during World War II and was described by McCarthy. The staircase method was used because the technique allows rapid measurement of threshold values. The threshold could then be calculated as the average of the values lying midway between positive and nonpositive responses. Usually five or six up-and-down sweeps were required to bracket the threshold and the average of the midpoints of these sweeps was taken to be the threshold values. Cornsweet discussed this technique in 1962.

After determination of the threshold for the training frequency, another adjacent frequency threshold was evaluated. By testing frequencies further and further from the training tone, the entire range of the subject above and below the training tone was determined. Reinforced trials were used after each change of frequency to prevent any effect of generalization gradient. These reinforced trials were at an intensity well above the previous threshold determination at a neighboring frequency to insure being above the threshold intensity of the new frequency. All threshold values were determined at least twice on different days, which were sometimes weeks apart to reduce any error or change with time or experience. The separate threshold determinations were consistently within 5 to 10 db of the previous values at the same frequency. An average of the separate threshold determinations was used as the final threshold value.

Spontaneous crossing responses were controlled with an optimum barrier hole size and a suitable intertrial interval. The intertrial interval was critical, and after it was determined, the spontaneous crossings were reduced to the category of rare events. The repetitions involved in the staircase method of threshold determination and the replicated threshold values also controlled spontaneous crossing errors.

Results.—Figure 1 shows the mean of the intensity threshold values for the four subjects as a function of frequency. In Figure 1, 0 db is the 1 dyne/cm² intensity level. Both the range and the standard deviation of the thresholds are indicated. The frequency range of the audiogram for the bullhead catfish extended from 100 to 4000 Hz. Peak sensitivity occurred at 600 and 700 Hz at a level of 28 db below 1 dyne/cm² for the mean and at 700 Hz at 35 db below 1 dyne/cm² for the most sensitive portion of the range.

Discussion.—The mean sensitivity of the catfish in this study was about 6 db greater than that reported for goldfish. The frequency range extended to 4000 Hz. Thus, hearing in fishes can be explained by the frequency and volley mechanisms of hearing without invoking a place principle. Indeed, fish have no homolog to the cochlea. Only with the evolution of the cochlear homolog—the basilar papilla of the amphibia—does a place mechanism appear in the form of a tuned peak in the audiogram of frogs with neural units responding only to a specific frequency. Wever traced subsequent evolution of the cochlea in reptiles.

Attempts to postulate a place mechanism remain without evidence and studies purporting to indicate place mechanisms by demonstrating masking...
remain inconclusive.\textsuperscript{17} Evidence for frequency and volley mechanisms of hearing in fishes has been obtained by Dudok van Heel\textsuperscript{18} who noted that the high-frequency response to tones improves with a rise in body temperature, and by Enger\textsuperscript{19} and Furukawa and Ishii\textsuperscript{20} who observed frequency following in auditory neurons.

\textbf{Conclusions}.—The behavioral technique of shock-avoidance conditioning of catfish to tonal stimuli in an aquatic shuttle box yielded curves of intensity thresholds as a function of frequency for the auditory range of the bullhead catfish. The range extends from 100 to 4000 Hz with a peak sensitivity at 600 and 700 Hz at a level of 28 db below 1 dyne/cm\textsuperscript{2}. Catfish, as well as other fishes, hear by the frequency and volley mechanisms.

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\textsuperscript{4} Weiss, B. A., "Generating and calibrating a uniform aquatic sonic field for behavioral bioacoustics," in preparation.
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