

Structures for the detection of acoustic stimuli in the Atlantic codfish, *Gadus morhua*

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Codfish, *Gadus morhua*, were classically conditioned to respond to tonal stimuli with a change in heart rate. Thresholds were obtained at frequencies from 10 to 600 Hz. Sensitivity of receptors was determined by ablation operations. The sacculus had the lowest threshold at 150 Hz (-35 dB re 1 μ bar) and the lagena and utriculus might have successively higher thresholds. One fish was about 9 dB less sensitive at 150 Hz after swim-bladder ablation. A piezoelectric transduction mechanism was hypothesized for the sacculus. The lateral line might detect the acoustic stimulus and be most sensitive at 75 Hz to particle velocity (-14 dB re 1 μ var).

Subject Classification: 80.50.

INTRODUCTION

Von Frisch and Stetter¹⁻³ made the first detailed study of sound detection by ostariophysine fish. The pars inferior (sacculus and lagena), rather than the pars superior (utriculus and semicircular canals), were found to be the main organs of hearing.^{2,4} Von Frisch³ showed that the sacculus functioned in conjunction with the swim bladder to which it was connected by the Weberian apparatus and the transverse canal. The lagena, he believed, received its stimulus through a thin region of the skull, the lagena window. When the lagena and the swim bladder were both removed, the fish no longer responded to high-frequency sounds. After removal of the sacculus, making the fish dependent on the lagena, ablation of the swim bladder had little or no effect on sound detection.

It has been theorized that fish without gas chambers, such as sharks and flounders, could not detect sound-pressure waves.⁵ It was postulated that transduction only occurs through a shearing movement at the surface of the auditory hair cells and that without a gas bladder, pressure waves (a scalar quantity) could not cause a shearing movement. Several observations have cast doubt on this hypothesis. Sharks have been attracted by sound from great distances⁶ and the displacement stimuli have been calculated to be very low.⁷ Other fish without swim bladders are also sensitive to sound (Dijkgraaf, personal communication).^{8,9} In some of these studies, the possibility exists that the vector components of the sound stimulus may have been the adequate stimuli.

All studies of fish hearing are complicated by the presence of the lateral-line organs. The hair cells in these structures are embryologically and morphologically similar to the ear. Harris and van Bergeijk¹⁰ showed physiologically that the lateral line was probably sensitive to a vector component of sound. Dijkgraaf^{11,12} concluded that, despite the physiological studies, there was no behavioral evidence that the lateral line was responsive to sound. Cahn, Wodinsky, and Siler¹³ showed that fish responded differently to particle velocity (a vector component of sound) and to pressure. It was believed that these two types of responses were due to signals

received through the lateral line and ear, respectively.

Sound detection by Atlantic codfish (*Gadus morhua* Linnaeus) was first demonstrated by Froloff.¹⁴ He used classical conditioning with shock and obtained an increase in movement upon the presentation of sound. Buerkle¹⁵ published an audiogram for the Atlantic cod but later showed that most of his measurements had been masked by ambient noise.¹⁶

Brawn¹⁷ found that Atlantic codfish used their swim bladders to produce low-frequency sounds during reproduction and aggression. The codfish swim bladder was first described by Delaroche.¹⁸ The anterior projections of the swim bladder, about one-third as long as the body of the bladder, extend to a cavity behind the cranium. Parker¹⁹ hypothesized an auditory function for similar projections in the red cod (*Lotella bacchus*). Hagman²⁰ made detailed descriptions and illustrations of gadoid swim bladders. He suggested that the bladder extensions might function in conjunction with the labyrinth for the detection of pressure changes. Retzius²¹ described and illustrated the codfish labyrinth. He noted the large size of the sagitta, the absence of the macula neglecta, and the large lumen of the utriculus, which has no duct connecting it with the sacculus. Illustrations of the codfish labyrinth and swim bladder are given in Figs. 1 and 2. The present study considers the relative contribution made by these various structures for the detection of acoustic stimuli by codfish.

I. METHODS

Codfish (37–54-cm standard length) were obtained by hook and line and otter trawl in the Narragansett Bay region at least six days before testing. They were kept in circulating sea water; and at low ambient temperatures, the water flow was decreased to maintain higher temperatures in the inside holding tanks.

When testing, animals were held in a 3-mm mesh-nylon net suspended in a plastic tank (53 cm long \times 30.5 cm diameter) and supplied with circulating salt water. The test tank, on a wooden support, rested on sound-insulating material (sandwiches of masonite and rubberized horse hair) inside a 1.13-m³ sealed reverberation

chamber. This chamber was constructed from a refrigerator with sheets of masonite set at angles on the inside. The chamber rested on sound insulation material as above. The test tank was provided with an overflow outside the chamber. Thus, a constant water level was maintained as was the low ambient noise level. Figure 3 shows the test apparatus. This and all test equipment were housed inside an isolated, underground room made of reinforced concrete.

The sound stimuli were produced with a Hewlett-Packard 650A oscillator and controlled by a switching device that activated a Raysistor (082013, Raytheon Co.), thus giving the stimulus a slow rise-decay time. The signal was amplified with a Dyna Mark IV amplifier and projected through a 41-cm (16-in.) speaker set in the wall of the reverberation chamber. For low stimulus levels, the output of the amplifier was attenuated. The sound field of the test tank was calibrated using LF310 and H11

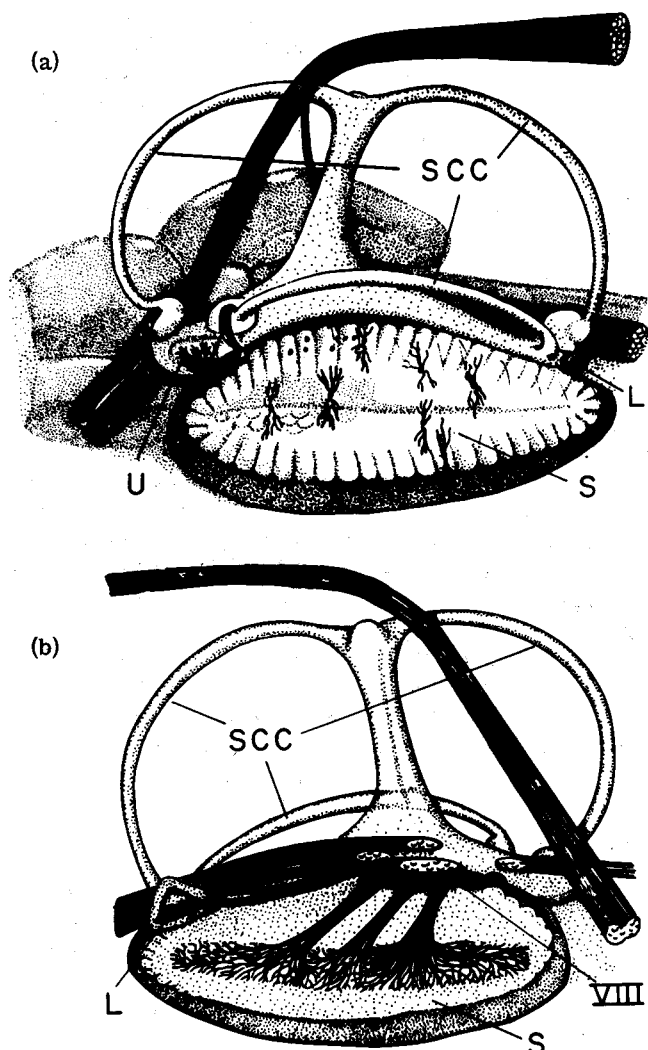


FIG. 1. The left labyrinth of a codfish showing: S, sacculus containing the sagitta; L, lagena containing the asteriscus; U, utricle; SCC, semicircular canals; and VIII, the eighth cranial nerve where it enters the medulla. Other nerves in the region of the labyrinth are indicated. (a) Lateral view including outline of brain. (b) Medial view.

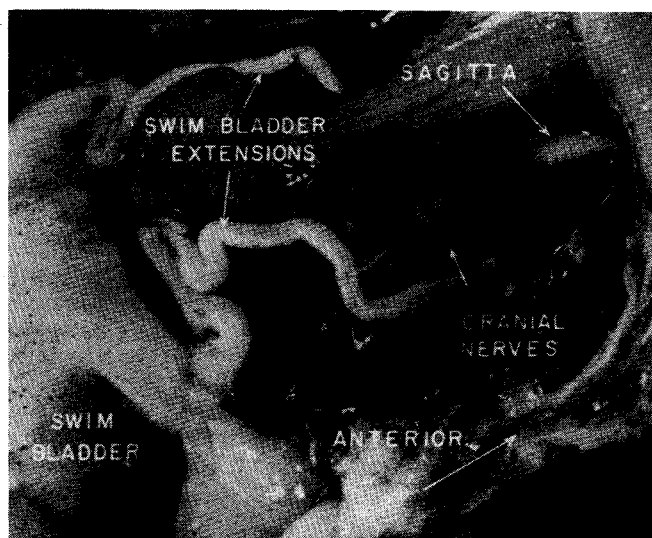


FIG. 2. Photograph of a freshly dissected codfish showing the anterior end of the swim bladder with its projections. The end of the right projection has been displaced for better viewing. Part of the cranium was removed revealing the left sagitta.

hydrophones (Chesapeake Instrument Corp.) and an HS-1 vertical particle-velocity transducer (Geo-Space Corp.). Both hydrophones had been calibrated and the manufacturer's specifications were used to determine the particle-velocity amplitude. The largest directional component of particle velocity was used to calibrate the sound field and this was in almost all cases in the vertical direction, which may have been a function of the transducer. Good sinusoidal waveforms were observed for all frequencies on an oscilloscope. With the following exceptions, the sound field was relatively uniform (3 dB or less variation). For pressure, there was a 6-dB variability at 18.7 Hz, 4 dB at 37.5 Hz, and 8 dB at 500 Hz. For particle velocity, 75 and 300 Hz had variations of 9 and 10 dB, respectively. Ambient noise could not be measured with the LF310 but was lower than -21 dB/octave (pressure spectrum level -42 dB), which was the

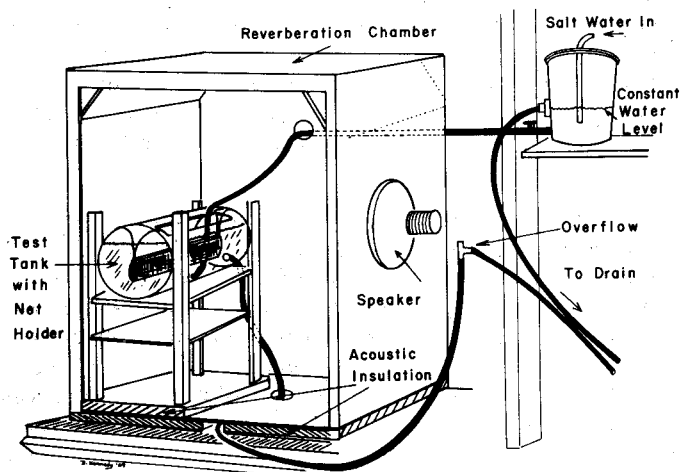


FIG. 3. A representation of the experimental system used in obtaining auditory thresholds.

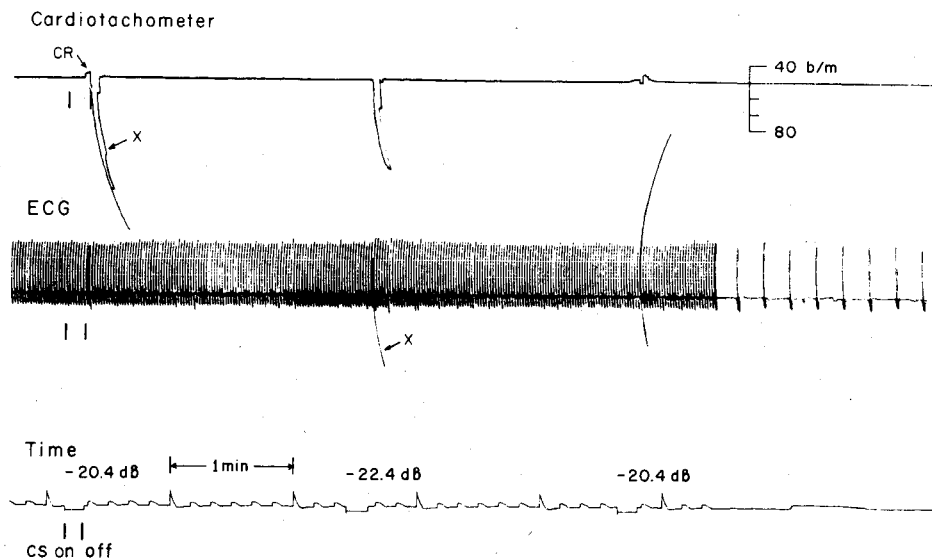


FIG. 4. Record from a codfish showing the cardiotachometer trace (giving the beat-by-beat rate), ECG, and time. Three trials are indicated by the depressed-time base line and the acoustic pressure is given for each trial. The vertical lines for the first trial show the onset and termination of the CS for all three records. There was a CR on the first and third trials. At the end of each trial the US caused artifacts (indicated by \times) in the ECG and the cardiotachometer records. The appearance of the artifact depended on the phase of the ECG when the US occurred. After the third trial the recording rate was increased to show the form of the ECG.

level of the instrumentation noise. In this paper, all stimulus measurements are given as pressure in dB *re* 1 μ bar (dyn/cm^2). Particle-velocity measurements are specified and given as dB *re* 1 μ var ($6.7 \times 10^{-6} \text{cm}/\text{sec}$). The μ var is a reference level proposed by Siler²² which is almost the particle-velocity amplitude that accompanies one μ bar of sound pressure in the farfield. During all testing, the voltages going to the speaker in the reverberation chamber were measured. These voltages, in conjunction with the calibrations, were used to determine the acoustic pressure and the particle velocity present at threshold.

Electrocardiograms (ECG) were obtained using an indifferent electrode in the water and a second electrode in the pericardial cavity. This electrode was made from a No. 32 multistrand silver-coated copper wire. At one end, a stop was made with an overhand knot and a sequin that had been immersed in insulation. About 0.5 cm from the stop, 1 cm of the Teflon insulation was removed. The exposed section lay just below the heart in the pericardial cavity after implantation with a curved needle.

Classical conditioning of heart rate was used to determine the threshold. Conditional stimuli (CS), pure tones, lasted a maximum of 11 sec. During the last 0.14 sec of the CS for all trials, the fish received an ac shock (3 to 40 V) through clips on the dorsal and ventral fins. The magnitude of this unconditional stimulus (US) depended on the stage of training and the temperature. The CS was shortened if a distinct conditional response (CR) was observed. The CR consisted of a bradycardia (slowing of the heart rate) with three intervals between heart beats, occurring during the presentation of the CS that were longer than any others during the previous 20 sec. On a few occasions it was not certain that this criterion had been met and so the trial was repeated. Details of the conditioning and testing procedures are the same as for the tautog and are given in another publication.²³ Figure 4 is reproduced from the

original recording and shows three trials close to a threshold. Presence of the CS is indicated by the depressed-time trace. On the first and third trials, a positive CR occurred, as can be seen from the upward deflection of the cardiotachometer record giving the heart rate in beats/min (b/m).

Thresholds were determined using an up-and-down procedure with 2-dB changes in the stimulus level and a minimum of ten stimulus reversals. The midpoints of all excursions were averaged to obtain the threshold level. All fish were first conditioned at 150 Hz and the stimulus was lowered in steps so as to maintain a distinct CR. Figure 5 shows the first-day training curves from two fish. Extra training was necessary at certain stimulus levels before the fish would respond to lower stimuli. The level at which this occurred is termed a plateau. Because of the distinct penultimate plateau shown by most fish near -30 dB (i. e., Fish A in Fig. 5), thresholds were not calculated at 150 Hz until the fish had exhibited CRs to stimuli below -32 dB. At other frequencies, threshold was calculated after ten reversals of the stimulus level at the lowest plateau reached. On a few fish, more than one threshold determination was made. Since the differences were usually less than 3 dB, only the lowest level is reported.

The labyrinth, lateral line, and swim bladder were surgically modified to determine their relative contribution to sound perception. The fish were anesthetized using a solution of ethyl-m-aminobenzoate methanesulfonate. During the operation, the gills were usually suffused with sea water or with solutions of anesthetic as concentrated as 1 : 20 000.

For the removal of the sagitta (saccular otolith) and the utricle, a median cut was made in the epithelium between the pads bearing pharyngeal teeth. A hemostat was used to hold the pads back while the skull was opened with a dental drill burr. The sagitta was then pulled free with an angular probe. The utricle was removed by forceps together with most of the pars su-

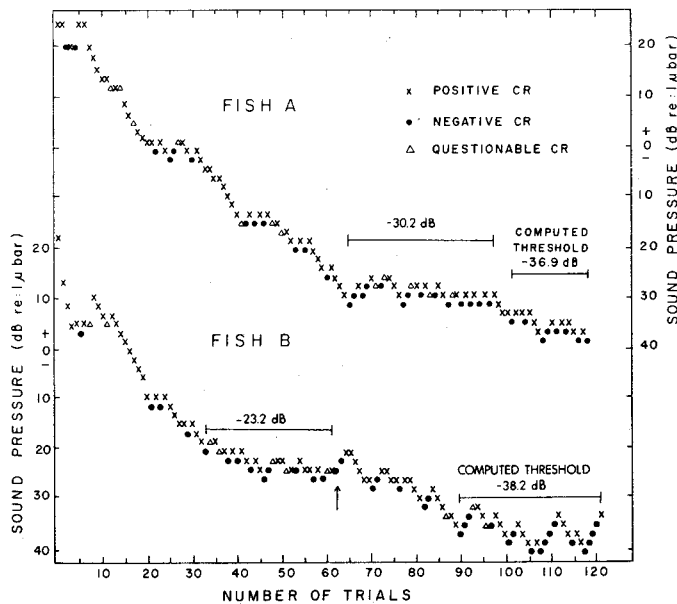


FIG. 5. Training curves on the first day from two codfish show the presence or absence of a CR on each trial. In questionable cases the stimulus level was repeated. The threshold and the range of tests over which it was computed are shown. The range of trials and the average pressure level are also given for the penultimate plateaus. An arrow indicates a period of twenty minutes when no tests were given.

perior. Controls for the effect of this operation had only one sagitta removed (two fish) and, with the skull opened, the saccular walls were injured but the sagittae were not disturbed (two fish).

Muscle was cut from a 2×4-cm area on the top of the head and a triangular opening was made in the skull in order to remove the lagenae. By using forceps and a syringe, the membranes and fluid were cleared down to the level of the medulla. The lagenae were then removed with forceps. The cranial opening was covered with Surgident periphery wax, two brass pins were inserted through the cranial septum, and the area was covered with cranial cement.

The nerves to the main lateral line were cut at a point above the posterior edge of the operculum after a small flap of integument had been cut away. All lateral-line organs on the head were located with a dissecting microscope and cauterized with a fine tipped soldering iron.

For swim-bladder modification, an incision was made between the pelvic fins. By pushing the internal organs to one side, the forward part of the swim bladder was exposed and then, as a control, a threshold determination was made. On another fish with the lateral line destroyed, the anterior projections of the swim bladder were pulled back into the body cavity with a thin hooked brass rod and a threshold was determined. To ablate the swim bladder of the same fish, the projections were cut off and an incision was made in the lateral wall of the bladder. Care was taken not to cut the rete mirabile. All gas was then gently pressed out of the bladder and abdominal cavity, with the fish submerged in the holding tank. As in all operations, the incision was closed with

surgical silk. The fish was allowed to recover slightly from the anesthetic by being placed in the net holder and carried in an inverted position to the test tank. An additional check was made for the presence of air bubbles before placing the fish in the testing position. About one hour later training was begun on both control and experimental fish.

II. RESULTS

Figure 6 gives composite thresholds from 20 fish with unmodified labyrinth and lateral line. Thresholds were measured at approximately octave intervals from 10 to 600 Hz. The range of values, mean, and number of fish tested is shown for each frequency. At most frequencies, the standard deviation and two times the error of the mean are indicated. Standard deviations were 1.9 to 3.2 dB. Because the ambient noise level could not be measured, it is possible that absolute thresholds may be lower than reported here.

Thresholds obtained at 150 Hz after the various ablation and control operations are shown in Fig. 7. Unmodified fish had a mean threshold of -35 dB. After removing the sagittae (saccular otoliths) and, in two fish, the saccular maculae, the acoustic sensitivity decreased about 6 dB. No difference was observed if only the sagittae were extirpated; therefore, the saccular membranes were not thereafter removed. As a further test for possible maculae function without the otolith, a histological examination was performed on one fish five weeks after only the saccular otoliths had been removed. No hair cells were found in the area where the sacculus had been. All fish which served as controls for this operation and one fish with the lagenae removed had normal thresholds. Thus, the loss of endolymph resulting

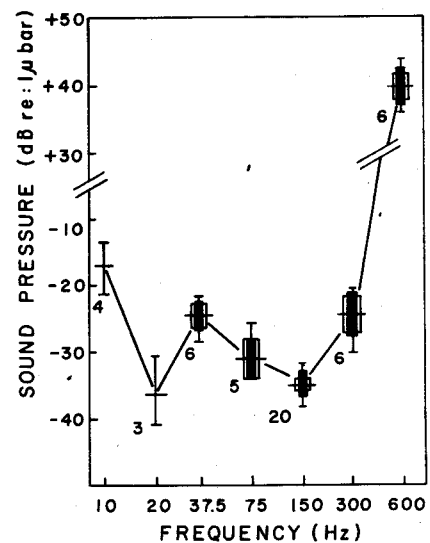


FIG. 6. The composite thresholds from codfish with unmodified labyrinth and lateral lines. For each frequency the total range of values (small cross bar), mean (longer cross bar), and number of fish tested are shown. At the higher frequencies the standard deviation (solid rectangle) and two times the error of the mean (hollow rectangle) are indicated on each side of the mean.

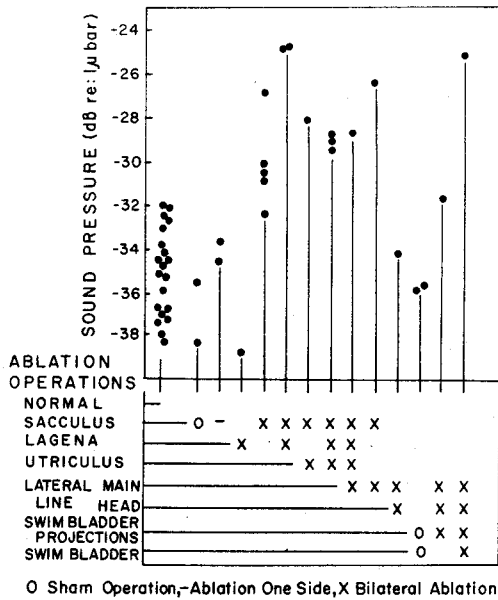


FIG. 7. Thresholds at 150 Hz from unmodified fish and from fish after various ablation and control operations. Each point represents the lowest threshold obtained from one fish after the indicated operations.

from ablation operations did not influence thresholds. Within a few hours after being operated upon, some experimental and control fish were tested. No consistent difference was found in these controls or between results from fish which were retested at a later time. Therefore, the threshold determinations were apparently not influenced by the effect of the surgery or anesthetic.

The next most sensitive receptors in this particular sound field were apparently the lagena and the lateral-line head organs. Destruction of the entire labyrinth resulted in thresholds in the same range as those of fish with only the sagittae removed and of one fish with the main lateral-line nerve cut in addition to removal of the labyrinth. Two fish with the sagittae and lagenae removed had thresholds about 11 dB higher than normal. After ablation of only the lateral line, one fish possessed a normal threshold.

Data from the first day of training are given for two fish in Fig. 5 with the calculated threshold and the average level of the penultimate plateau. Fish A had no modifications made on the labyrinth or lateral line. Previous to training, fish B had both lagenae ablated and sham operations performed on both sacculi. After removing the saccular otoliths, this fish had a threshold of -24.7 dB.

Two control fish responded normally after the sham operation on the swim bladder (Fig. 7). After the swim bladder projections had been withdrawn, the threshold was about 3 dB higher in the one fish with an unmodified labyrinth but no lateral line. Ablation of the swim bladder caused an additional sensitivity loss of about 6 dB. After testing and while still in the test tank, this fish was sacrificed and no gas was found in the bladder, abdominal cavity, or gut.

Data for one fish using its lateral line (i. e., labyrinth destroyed) that was tested at other frequencies are presented in Fig. 8. It had thresholds within the range obtained from normal fish at frequencies from 20 to 75 Hz [Fig. 8(a)]. When all threshold values for this fish are plotted against particle velocity, a unimodal curve results with 75 Hz as the most sensitive frequency at -14 dB re $1 \mu\text{var}$ [Fig. 8(b)].

Sensitivity at most frequencies did not change over the temperature range of 4° to 14°C . However, fish could not be trained at 300 Hz to the lowest levels with temperatures below 9°C . All data for 300 Hz given in Fig. 6 were obtained at temperatures above 9°C . Just before the end of testing, between 5 January and 3 February 1970, 13 fish were tested and only one reached threshold criteria. Similar difficulties had been encountered one year earlier and were correlated with the codfish breeding season. The difficulty was not due to temperature, because thresholds had previously been obtained from fish maintained at 4° to 6°C .

III. DISCUSSION

This study shows that at 150 Hz, the most sensitive receptor possessed by the codfish was the sacculus. It is almost certain that the lateral line was sensitive to the same acoustic field to which the labyrinth responded (e. g., response of fish with labyrinth removed). With the stimulus used, it is impossible to determine which sound component any one structure was detecting. The data plotted in Fig. 8 allow for the suggestion that the lateral line was responding to the vector components of the sound field. Physiological studies support this view.⁵ It may be that the lateral lines of other fish will be shown to have similarly shaped threshold curves. Tau-tog, under certain conditions and when tested in the same sound field, showed a unimodal response curve to particle velocity with maximum sensitivity near 75 Hz.²³ Weiss²⁴ obtained a response curve from goldfish with maximum sensitivity near 50 Hz. He used a specific

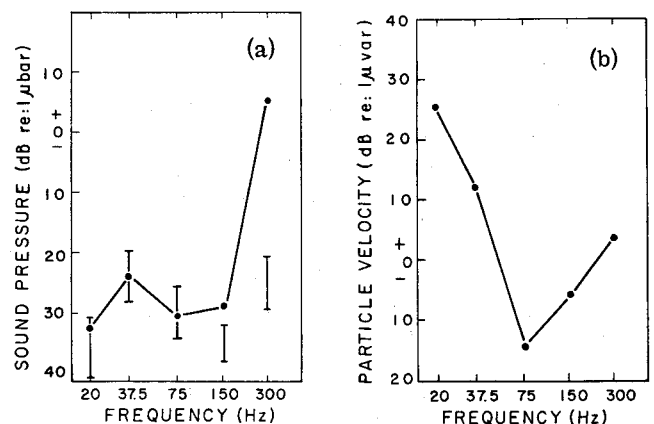


FIG. 8. Thresholds from one codfish with the labyrinth ablated and probably responding with the lateral line. (a) Data plotted against sound pressure with the range of threshold values from unmodified fish (see Fig. 5) indicated; (b) The same data plotted against sound particle velocity.

training technique, with limited reinforcement, and attributed the results to a response by the lateral line.

Thresholds from fish with the labyrinth removed were lower than those from fish with only the sacculae and lagenae (Fig. 7). This apparent contradiction may be resolved by proposing that the fish were attending to the utriculi in preference to the lateral line with its lower threshold. Fish apparently continued to utilize the remaining labyrinth receptors after the sagittae were removed and lagenae ablated.

Most fish with unmodified labyrinths showed penultimate training plateaus at similar levels as fish A in Fig. 5. The level of the penultimate plateau from this fish was -30.2 dB, which is quite close to the average threshold obtained from the five fish with only the two sagittae ablated (i. e., -30.1 dB). Fish B (Fig. 5) had sham operations performed on both sacculae and double lagenal ablations before being tested. Training data showed a higher penultimate plateau (-23.2 dB) than did unmodified fish. The threshold (-38.2 dB) was, however, within the range of unmodified fish. Similar results were obtained from another fish trained to threshold with only the lagenae ablated. When both sagittae were also ablated, fish B had a threshold of -24.7 dB, which is close to the level of the penultimate plateau during the earlier training session. Based upon these data, it has been proposed that the presence of the penultimate plateau in the codfish at 150 Hz may have been due to the fish attending to a less sensitive receptor. With additional training, the fish learned to respond with its most sensitive receptor (i. e., the sacculus). Tavolga and Wodinsky²⁵ found similar training plateaus but tentatively attributed them to learning phenomenon. The present study shows for the first time that individual labyrinthine receptors do have different thresholds that may be the basis of such plateaus.

Figure 2 is a photograph of a freshly dissected codfish showing the anterior end of the swim bladder, the swim-bladder projections, and their relationship to the ear. The projections usually abut the cranium near the foramen for the ninth and tenth nerves. Next to these nerves inside the cranium is the labyrinth (Fig. 1). The foramen can thus act as a window in the skull for acoustic stimuli transmitted by the swim-bladder projections to the labyrinth. The position of the projections was not uniform among fish. Although most fish were similar to the one shown in Fig. 2, some had projections that were tangled in a clump just forward of the swim bladder.

Results from the one fish with the lateral line and swim bladder ablated showed a decreased sensitivity of 9 dB. The accepted hypothesis of fish hearing would have predicted that the stimulus would not have been detected at all; because the labyrinth should not be directly sensitive to acoustic pressure and the swim bladder was not present to transduce the sound pressure into a displacement stimulus adequate for the labyrinth.⁵ It is, of course, possible that the vector components of the sound could have been stimulating the labyrinth directly, but this does not seem likely. It would not be expected

that the labyrinth was only about 3 dB less sensitive to particle velocity than the lateral line which is on the surface of the fish and has apparently evolved to detect this type of stimulus. Assuming both sets of receptors had the same threshold, it is probable that the vector components of the sound would be attenuated more than 3 dB before reaching the labyrinth because of the lower compliance of the animal's tissue. It therefore appears that the labyrinth was responding directly to acoustic pressure and the possible transduction mechanism involved must be considered.

It is possible that a density discontinuity in the labyrinth was functioning in a manner analogous to that of the swim bladder. However, if the density difference between the otoliths and the endolymph was sufficient for this purpose, then the lagena may be more sensitive to the shearing movement than the sacculus with its more massive otolith.

A piezoelectric mechanism seems to be a likely means of transduction. Morris and Kittleman²⁶ showed that the otoliths from fish are composed of aragonite that possesses a piezoelectric property comparable to that of Rochelle salt, which has a high piezoelectric effect. Degens, Deuser, and Haedrich²⁷ have further elaborated the chemical and crystalline composition of otoliths from a number of different species. Both groups of investigators conclude that otoliths may directly function in the detection of sound or pressure changes due to vertical movement. This hypothesis is developed further elsewhere.²⁸

The detection of acoustic stimuli by the codfish is not a simple process mediated by one receptor. In the labyrinth, the sacculus has the lowest threshold, and the lagena and utriculus might have successively higher thresholds. The swim bladder increases the sensitivity of the sacculus by about 9 dB and may also influence other labyrinth structures. The lateral line apparently responds to the vector component of the stimulus.

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