THE EFFECT OF THE SWIMBLADDER ON HEARING IN FISH

AN EXPERIMENTAL STUDY ON THE EFFECT OF THE SWIMBLADDER ON HEARING SENSITIVITY IN AMEIURUS NEBULOSUS NEBULOSUS (LE SUEUR)

by

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SCOPE AND CONTENTS: This thesis is concerned with the study on the effect of the swimbladder on hearing sensitivity in Ameiurus nebulosus. The investigation has been performed by means of auditory threshold curves in normal catfish and in catfish in which the resonance of the swimbladder was eliminated. The results were compared. The thesis consists of an introduction to the investigation, followed by a review of the literature in relation to the problem, a description of the material and technique and of the experimental work, the results obtained with a discussion and a summary.

PREFACE

The research involved in this thesis will deal with one particular phase of the study on hearing in fish, namely the investigation of the effect of the swimbladder on the sensitivity of the auditory system.

This problem was raised as a sequel of the findings on hearing sensitivity previously performed in the laboratory of the Department of Biology at McMaster University.

I take this opportunity to express my appreciation for the kindness of Dr. H. Kleerekoper, whose help enabled me to undertake this investigation.

I am also indebted to Mr. W. Brouwer for his technical assistance in the course of the experimental work and to the Department of Biology of McMaster University for the grant received in 1955.

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INTRODUCTION

In observations on the threshold curve of hearing as a part of their experimental studies on the cyprinid, *Semotilus atromaculatus atromaculatus*, Kleerekoper and Chagnon (1954) found that between 800 and 2400 c.p.s. an increased hearing sensitivity occurred in the acoustic perception of the fish. Although they put these findings down to inaccuracies of their observations, similar experiments on hearing perception later on revealed a corresponding dip in the threshold curves of the cyprinids: *Rhinichthys*, *Notropis* and *Chrosomus*.

It was believed that this phenomenon was brought about by the cavity resonance of the air in the swimbladder.

In order to further investigate this phenomenon, it was considered that this could be done by a comparison of the auditory threshold curves in normal fish and in fish in which the swimbladder resonance was abolished.

On the basis of this consideration a research on the effect of the swimbladder on hearing sensitivity in fish has been carried out as is described in the following chapters of this thesis.

REVIEW OF LITERATURE

Although numerous investigators observed hearing in fish or studied the organs involved in the perception of vibrations of these animals, only a few of them made direct observations on the acoustical function of the swimbladder in the last seven decennia. Some of them (see below) attributed acoustical functions to the bladder based on anatomical studies of the Weberian ossicles and on the relationship between the swimbladder to the inner ear of fish.

Little work has been done on hearing sensitivity in fish prior to 1929.

A review of literature of these experimenters on problems very closely related to the one at hand, will be given here.

As early as 1820 Weber was the first to demonstrate that in the Siluridae and Cyprinidae, there exists a chain of ossicles, connecting the air-bladder with the auditory organ. He suggested that their function was related to hearing by transmitting sound vibrations from the air-bladder to the inner ear. The same observations were made by Cuvier and Valenciennes (1829). They described in general terms the relationship between the swimbladder and the posterior portion of the skull in the Atlantic form Myripristis jacobus. Both investigators suspected also a possible auditory function for this arrangement.

At the end of the nineteenth century, such workers as Hasse (1873), Wright (1884), Sagemehl (1885) and Bridge and Haddon (1889) adopted the view that the Weberian mechanism is chiefly concerned with the perception of hydrostatic pressure of the swimbladder. According to them the swimbladder could not have an auditory function. The strongest objection to the auditory function of the bladder and Weberian mechanism came from Bridge and Haddon (1892). Their conclusions were based on three facts, namely, that in many Siluroidae the walls of the swimbladder are too thick to allow them to vibrate synchronously with the rapidly recurring sound waves; secondly, that there was no evidence of exceptional ability of hearing in the Siluroidae and other Ostariophysi and thirdly that transmission of sound waves through the air bladder must be accompanied by a considerable loss of energy.

The views of these writers were refuted at some length by Sörensen (1895) who at an earlier date (1884) had already supported the theory of Weber. He found that the wall of the bladder was certainly capable of vibrating synchronously with rapidly recurring sound waves. When the wall of the swimbladder was vibrating, the tripus was thrown into vibrations, the movements of which were transmitted by way of the rest of the Weberian ossicles to the inner ear. The sound waves could be transmitted from the water to the airbladder without losing much strength.

Before 1930 the principal question at issue was, whether or not fish could hear at all. A series of papers in part favourable to the opinion that fish could hear and in part opposed to this view are reviewed by Parker (1918), Warner (1932) and von Frisch (1936). Of those in opposition were the articles by de Cyon (1878), Kreidl (1895 and 1896), Lee (1898), Körner (1905 and 1916), Brüning (1906), Marage (1906), Maier (1909), Bernouilli (1910) and Haempel (1911). These workers support in general that most fishes do not hear. This supposition is contradicted by an equally large number of investigators: Bigelow (1904), Piper (1906), Parker (1909 and 1910), Meyer (1910), Parker and van Heusen (1917), Westerfield (1921), McDonald (1921), von Frisch (1923), Manning (1924), Froloff (1925), Bull (1928) and Stetter (1929).

Many of the negative results, recorded in the earlier experiments on fish hearing are due, not to the absence of the sense of hearing on part of the fish species, but to the methods employed by all these investigators.

Weber's concept that the function of the Weberian ossicles in connection with the swimbladder as a resonator, could be understood as a transmission mechanism for sound vibrations had fallen into the background by these investigations and especially by the critiques of Hasse (1873), Bridge and Haddon (1889 and 1892) and Thilo (1908).

Certain important anatomical facts, first recognized by de Burlet (1929) put again forward Weber's theory. In a description of the pars inferior (sacculus and lagena) of the labyrinth of Ameiurus nebulosus (Siloroidae), supplemented by observations on several other siluroid fishes, de Burlet has pointed out morphologically, a system which exhibits analogies with the sound transmitting and perceiving mechanisms of tetrapods. The otolith of the sacculus close to the mouth of the canalis transversis, a transverse connection between the two sacculi, is provided with a specialized cuticular structure and is resting upon the sensory hairs of the macula. Obviously this structure has the purpose to transmit the vibrations from the canalis transversis to the sensory hairs of the macula. The vibrations are finally absorbed through the fluids of a perilymphatic conduit, a space below the sensory hairs of the macula and separated from the labyrinth by a thin membrane. On the score of these discoveries, de Burlet supposed the following course of sound waves to effect the auditory organ: through the bodywall, swimbladder, Weberian ossicles, sinus impar, canalis transversis to sacculus, eventually to cause movement of the cuticular structure with ensuing stimulus to the sensory hairs.

Evans (1930) studied the anatomy and morphology of the swimbladder and Weberian ossicles and the connection of the ossicles with the internal ear. He found that in Cyprinidae the bi-lobed swimbladder seemed to possess two functions: the posterior sac is a hydrostatic receptor (Evans and Damant, 1928), the size of which is directly related with this function, and the anterior sac is a receptor for vibrations. Both sacs are connected by a ductus communicans; the posterior sac is connected with the oesophagus by the ductus pneumaticus in Physostomi. Ductus communicans acts as an Eustachian tube and controls the air pressure within the anterior sac, thus allowing it to vibrate. The walls of the posterior sac consist of a thin layer of involuntary muscle fibres. Exterior to this muscular coat is a vascular layer. The walls of the anterior sac are differently constituted; superficial to a muscular coat there is a very strong external coat of fibrous tissue. Vibrations carried through the body wall to the air in the anterior sac, acting as a drum are communicated to tripus and thence by a chain of movable connected Weberian ossicles (scaphoid and claustrum) to sinus impar, a median prolongation of the perilymph containing spaces, surrounding the two auditory organs. The sinus impar records vibrations, which can only reach the sacculi. The series of ossicles are kept tense by a special muscle, the tensor tripodis.

In the face of these cumulative evidences for an auditory function of the Weberian ossicles and the swimbladder, Evans felt that Weber had a sounder physiological vision than some of his successors.

The results of the anatomical studies of de Burlet and Evans are supported by the experiments on Phoxinus laevis by von Frisch (1931) and von Frisch and Stetter (1932). They are convinced that in general there is a true sense of hearing in fish and that this sense is very well developed in all fishes possessing Weberian ossicles (Ostariophysi). Phoxinus laevis with the pars superior of the labyrinth (utriculus and semicircular canals) removed may be trained to reach to sounds as easily as normal fish. They are only organs for equilibrium. After removal of pars inferior (sacculus and lagena) they cannot perceive tones of medium and high frequencies, but still react to deeper tones (below 100 - 150 c.p.s.). Medium high and high tones (upper limit about 5,000 - 6,000 c.p.s.) are therefore perceived solely through the pars inferior. Perception of deeper tones (25 - 150 c.p.s.) are probably through tactile organs of the skin. After removal of the swimbladder (which in this species is connected with the labyrinth through Weberian ossicles) the auditory sensitivity still persists, but the keenness of hearing seems to be lessened. It seemed from this experiment, that the connection between swimbladder and sacculus might increase the acuteness of hearing.

A similar anatomical occurrence of the labyrinth, especially of the modified saccular otolith for the reception of sound waves towards it and of the thin membrane below macula sacculi as is described in Siluroidae was shown in Phoxinus laevis by Wohlfahrt (1932) and in Characinidae and Gymnotidae by von Boutteville (1935). Therefore these evidences confirmed the theory of sound transmissions of de Burlet for all families of Ostariophysi, the families of which include: Cyprinidae, Siluroidae, Characinidae and Gymnotidae. In addition to her anatomical evidences, von Boutteville made observations on the threshold of perception in Phoxinus laevis, Hyphessobrycon flammeus, Hemigrammus caudovittatus and Pyrrhulina rachoviana (Ostariophysi) and in Gymnotus electricus (Gymnotidae, non-Ostariophysi). She was the first to determine the absolute auditory thresholds. The intensity of the sound generated by a loud-speaker close to the aquarium was measured in the air by means of a calibrated microphone. The upper limit of perception for Characinids lies between a^5 (7040 c.p.s.) and c^6 (8192 c.p.s.) and for Gymnotus between a^2 (880 c.p.s.) and c^3 (1024 c.p.s.). The average lowest intensity of the tone c^2 (512 c.p.s.), responded to by Characinids, was 13 phon and by Gymnotus about 35-40 phon.[I] It reveals a remarkable sensitivity when one takes in consideration the high impedance in the transmission of sound from air to water. The difference in acuity of hearing between Ostariophysi and non-Ostariophysi was striking.

In his study on the auditory organ and its swimbladder connection in fish Evans (1935) described three types of auditory relations of the anterior end of the swimbladder and their embryological origin in the families: Clupeidae, Mormyridae and Cyprinidae. In all three families a tympanic cavity could be recognized, which is adopted to receive sound vibrations and transmits them to the auditory organ. Evans found that in Cyprinidae the central area at the base of the cerebellum and connected

[I] The German phon scale is used as equivalent of the decibel scale.

on either side with the acoustic tubercles varies according to the habits of the fish. The facts concerning the auditory connections of the swimbladder and associated neurological conditions of the acoustic tubercles and central area are convincing arguments in favour of the view that fish have a good sense of hearing.

The labyrinth and their relation to the swimbladder and lateral line are thoroughly described for the sardine (Clupea plucharдis Walb.) by Wohlfahrt (1936). The relation indicates an acoustic function of the labyrinth swimbladder connection.

Special attention was paid by Farkas (1936) to hearing in Ostariophysi and non-Ostariophysi. Farkas tested the following fish: Ameiurus nebulosus, Misgurnis fossilis, Siluris glanis (Ostariophysi), Upomotis aureus, Rhodeus amarus (non-Ostariophysi) and especially Lebistes reticulatus (non-Ostariophysi). In all of these fishes except in Siluris glanis, Farkas was able to ascertain the ability of hearing. An excellent perception of sound was found in Lebistes with upper limits between 1,200 and 2,068 c.p.s. and lower limit as low as 44 c.p.s. Ameiurus and Rhodeus on the contrary, react to higher tones (between 2,093 and 4,186 c.p.s.). Rhodeus respond to tones with lower intensity than Lebistes. Hence the difference in sensitivity and the ability to perceive higher and lower tones by Ostariophysi may be attributed to Weber's ossicles. Farkas admits that the degree of sound perception differs among individual fish even in the same species.

The conclusion, that fish without Weberian ossicles have also a good hearing potentiality is again arrived at by Farkas (1938) in his paper on sound transmission mechanisms in teleosts (Lebistes). As he stated in experiments, neither the skin nor the swimbladder is concerned in hearing. In fact, the skin and the swimbladderwall hinder the sound transmission from the water to the bladder. The swimbladder should not be regarded as a resonator, because the sound stimulus will be weakened by the long tone conducting pathways through swimbladder and Weberian ossicles and because the sound waves will not be transmitted with the same intensity and quality. Farkas gives a detailed morphological description of the labyrinth.

Von Frisch (1938) studied the role of the sacculus and lagena in fish as the seat of the sense of hearing. He confirmed again that _Phoxinus laevis_ are deaf after complete elimination of pars inferior but not after removal at both sides of the lagena only. This means, that the sacculus functions as a hearing organ for the whole range (24.5 to 3,520 c.p.s.). Von Frisch thought that probably the lagena also responds to this range. The same was found in _Idus melanotus_.

Von Frisch emphasized the special perception mechanism of the Ostariophysi. In _Phoxinus laevis_ the saccular otolith is specially modified for the reception of sound waves directed towards it by the above mechanism, whereas the lagena seems to receive sound stimuli directly through the lagena "window" in the lateral wall of the skull. He mentioned that if this assumption is correct, the hearing ability of _Phoxinus laevis_, after elimination of the swimbladder, is really a function of the lagena. Actually by extirpation of the lagena in _Phoxinus laevis_ in which the swimbladder has been removed, the hearing ability was very much restricted or in most cases completely destroyed.

In a lecture delivered at University College, London, von Frisch

(1936) directed attention to the Mormyridae, the skull of which has a gasbladder on each side. These are connected directly with the sacculus. Originally developed as a double cavity of the swimbladder growing into the head, the connection with the swimbladder is lost later on by degeneration and the two small airbladders lie completely separated in the skull. Von Frisch thought that the function of these bladders might be the same as that of the swimbladder in Ostariophysi.

This opinion was corroborated by the experiments of Diesselhorst (1938) on the hearing ability of *Anguilla vulgaris*, *Lebistes reticulatis*, *Periophthalmus koelrenteri*, *Umbra krämeri* and Leponus species (non-Ostariophysi) including *Marcusenius isodori* (Mormyridae) and *Anabas scandens* (Labyrinthici). *Marcusenius* and *Anabas* showed an especially good hearing ability in comparison with the other non-Ostariophysi. The upper limit in *Marcusenius* was between 2,069 and 3,100 c.p.s., in *Anabas* over 650 c.p.s. The same results were obtained by Stipetic (1939) from *Gnathonaemus macrolepidotus* (Mormyridae) with an upper limit between 2,794 and 3,136 c.p.s. And from *Macropodus opercularis*, *M. cupanus*, *M. operculus concolor*, *Trichogaster trichopterus*, *T. leeri*, *Betta splendens* and *Colisa lalia* (Mormyridae) by Schneider (1941). The upper limits of hearing for these fishes was between 2,607 and 4,645 c.p.s., when $a^I = 435$ c.p.s. If the resonator (air chamber) was shunted out, the hearing limit fell to 518 - 652 c.p.s. This range was near the upper range of the fishes with no sound-transmitting apparatus. The keenness of hearing was also decreased.

No work was done on this theme during the following years until Poggendorf (1952) broached the subject in an article dealing with the investigation of the absolute threshold in *Ameiurus nebulosus* and the observations on the Weberian apparatus in Ostariophysi. He determined the absolute auditory threshold curve of catfish in the frequency range of 60 to 10,000 c.p.s. It was found that the threshold (expressed in dynes /cm^2) was almost constant at frequencies from 60 to 1600 c.p.s., while the threshold rapidly increased with increasing the frequency above 1600 c.p.s. Bilateral extirpation of the malleus caused a reduction of the sensitivity of 1/30 to 1/100 of the normal, but the shape of the threshold frequency curve remained unchanged. The form of this curve was explained as a result of the acoustic properties of the Weberian apparatus that independently of the frequency a certain minimal amplitude of the endolymph was necessary for the excitation of the sensory cells. Poggendorf was not able to eliminate the acoustical function of the swimbladder in *Ameiurus nebulosus*, neither by extirpation of the bladder nor by filling it with Ringer's solution or with paraffin oil, both of which were either evacuated or absorbed. The operation injured the animals seriously and although it was possible to continue the training, the responses obtained were uncertain. Therefore the anterior part of the swimbladder of *Phoxinus laevis* was isolated and submitted to frequencies of 200 to 3,000 c.p.s. when submerged in water. The vibrations of the wall of the bladder revealed a maximum amplitude at frequencies above 1,100 c.p.s. The resonant frequency of the swimbladder was calculated.

In summarizing the literature of the most important statements, it may be said that an acoustic function of the swimbladder is generally supposed. Some authors investigated the effect of the swimbladder resonance on hearing, however nobody measured accurately the frequency range in which hearing sensitivity is increased as a result of this resonance.

MATERIALS AND TECHNIQUE

Ameiurus nebulosus nebulosus (Le Sueur) was selected as a species which is easily trained to associate sound with food and is strongly resistant to surgical intervention.

The catfishes supplied by the Department of Lands and Forests, Hamilton, Ontario, were kept together in a tank or when used for experiments in aquaria. Small pieces of cooked liver served as food.

The size of the fish used in the experiments varied from 11 to 13 cm. in length.

For these experiments a low frequency oscillator (model Ediswan type 666) with a continuously variable frequency range of 5 to 6,000 c.p.s. served as a source of sound, transmitted by electromagnetic speakers. The output of the oscillator could be regulated. (figure I)

The speakers submerged in the aquarium, were kept waterproof by wrapping in plastic sheets and held in position by means of bars and clamps. In each aquarium there was one speaker. The speakers could be connected independently to the oscillator by means of tumbler switches. For each test the speaker could be turned on very gently through a volume control, so that the fish was not warned by the "click" of the switch. (figure 2)

Sound intensities in the water were measured with a crystal hydrophone and a standing wave meter (model Polytechnic, type 275). (figure 1) It was possible to measure the sound intensities at different levels above the bottom and at accurately known positions in the aquaria. The several outputs of the oscillator were plotted against the corresponding values of sound intensities expressed in millivolts as measured by the standing wave amplifier at the frequencies of 210, 254, 330, 410, 550, 750, 1,000, 1,300, 1,500 and 1,840 c.p.s. Graphs were plotted for each of the speakers with the accessory aquarium.[I] Later on the millivolt scale was converted to the decibel scale, the zero point of which represents the lowest intensity at which a normal catfish just can hear a sound with a frequency of 750 c.p.s.

The experiments were carried out in aquaria 75 cm. long, 30 cm. wide and 35 cm. deep. A screen divided each aquarium breadthwise into two equal sections; the fish was kept in one section and in the other the speaker was suspended. This prevented the fish from coming close to the speaker. To prevent the fish from sucking air to raise the hydrostatic pressure in the swimbladder, a screen consisting of cords stretched over a rectangle of iron bars, was suspended in each aquarium about 5 cm. under the surface of the water. (figure 3)

The depth of the water in the aquaria was maintained at 23 cm.

At the front side of the aquaria a wooden shield was placed to prevent the fish from seeing the experimenter. Small wide angle lenses placed in the shield, one for each aquaria, allowed the experimenter to observe the whole section in which the fish was kept.

Evidently catfish in the dark were in a more active and responsive state than in the light, so that the aquaria were shaded at the

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[I] This work has been carried out by Mr. W. Brouwer during the summer of 1955.

backside by means of a cardboard 120 cm. in height, to give the fish a dusky environment.

When the fishes were subjected to experiments, food was given by means of an iron wire at the end of which a small piece of cooked liver was pinned.

The fish remained in the aquarium for the duration of the experiments.

Surgical Operations

For the purpose of eliminating the influence of the swimbladder on hearing, the bladder was opened in the following way.

One per cent solution of urethane (ethyl carbamate) was used to anaesthetize the catfish. Before the operation the fish was kept in a small tank, containing the anaesthetic, until the animal became calm and showed loss of equilibrium. An "operating table", consisting of a board with upright flexible bands was used to support the fish. The table with the animal was placed on the slant in a developing tray filled with urethane solution. Only the snout remained in the anaesthetic; the rest of the fish was kept above the surface. The fish continued to respire throughout the operation.

Through a horizontal incision of about 1/3 of an inch long in the lateral body wall below the lateral line and about 1/4 of an inch posterior to the pectoral fin, the anterior part of the swimbladder was exposed, the lateral walls of which are in close contact with the inner surfaces of the skin.

Because the anterior dorsal wall is attached to the vertebral column, the author was not able to eliminate the whole bladder without serious injury to the animal. Therefore the tough bladderwall was opened and a piece cut out of such a size (about 1 cm. in diameter) that healing was impossible. Hemorrhage did not occur.

The effect of the anaesthetic was lost after about ten minutes.

Disinfection was not necessary. The edges of the wound recovered after about three days. The operative orifice remained open for a long time.

Although the swimbladder did not collapse, the pressure inside was abolished and the volume very much decreased, visible at the outside by the compressed body walls behind the pectoral fins. (figure 4)

To put the lateral line out of action a piece of the nerve was removed near the gill clefts. The nerve is very superficial and is easily reached at this point.

EXPERIMENTAL WORK

This section deals with the measurements of the sensitivity of the auditory system to pure tones of different frequencies in normal as well as in operated catfishes.

By using the Pavlovian type of conditioning, which is applicable only to responses that are mediated by the autonomic nervous system, Ameiurus nebulosus could be trained to feed in connection with a sound. This conditioning was performed in the following way. Several times a day the fish was exposed to vibrations of a desired frequency. Fifteen seconds after the sound was turned on a piece of liver was presented by means of the feeding needle below the horizontal hanging screen. After 60 to 90 trials the animal gave a positive response, i.e.,swam to the screen within five seconds after the sound was turned on to obtain the food. The fish learned to snap at the food on the needle after 5 to 10 trials from the beginning of the training.

Intermittendly the catfishes were tested for reactions to stimuli other than the sound in question. The same actions were made by the observer as during the experiment mentioned above, but without being followed by a sound stimulus and feeding. Spontaneous movements to the screen occured when the sound stimuli were presented with intervals of less than 5 minutes.

Each fish was trained first on a tone with a frequency of 750 c.p.s., a sound to which normal catfish seem to be most sensitive (according to Poggendorf, 1952). After conditioning, in order to establish respectively the lower and upper limit of hearing in the fish the frequencies were gradually decreased or increased.

The threshold of hearing was determined by measuring the threshold for responding to sound. Starting with a tone that was well above the threshold, its intensity was gradually reduced at regular intervals until no response could be recorded indicating that the fish no longer heard the sound. The intensity was further decreased below this value and then increased until the fish responded again. The method in which the threshold was gradually approached from sub-threshold value was repeated several times with intervals of 15 to 30 minutes.

This procedure was repeated for all the frequencies tested in the following order: 750, 1,000, 1,300, 1,500, 1,840, 550, 410, 330, 254, and 210 c.p.s. Measurements on any one frequency were completed before proceeding to another frequency. After being trained on 750 c.p.s. conditioning on theother frequencies succeeded after 10 to 20 trials.

The intensity that was just adequate to evoke a response within 10 second for the lower frequencies (750, 550, 410, 330, 254 and 210 c.p.s.) or within 15 seconds for the higher frequencies (1,000, 1,300, 1,500 and 1,840 c.p.s.) was recorded as positive, indicating a positive response of the fish at the intensity in question.

The latent period of response of sound stimuli was slightly increased, as the intensity of one frequency was lowered or as the frequency was raised to higher and less perceptible sounds.

The catfish was fed at each positive reaction.

The condition of the fish was not affected by the surgical intervention. They lay flat on the bottom of the aquarium most of the time.

Their locomotion was somewhat labored as a result of the loss of hydrostatic pressure. The low pressure in the bladder caused that the fish tried to suck air at the surface of the water. The air escaped through the operative orifice after a few seconds. This restlessness of the fish was prevented by the horizontal screen. Each fish, operated as well as normal, was usually found on the same place in the aquarium. These places were characterized by a high intensity of sound.

RESULTS AND DISCUSSION

Determinations on the perception of the frequency range in normal catfish resulted in an establishment of the lower limit of 30 c.p.s. and an upper limit of over 6,000 c.p.s. (the maximum frequency available was 6,000 c.p.s.), whereas in operated fish it is respectively about 50 c.p.s. and as high as 4500 c.p.s.

For the investigation presented in this thesis, four operated fishes were tested, one of which was examined also before the surgical intervention.

In order to establish their auditory threshold curves the procedure described in the previous chapter was followed.

For all the frequencies tested, the experimentally established values of the minimum intensities in millivolts, at which the responses occurred, were plotted against the frequency on the logarithmic scale. The threshold curve was obtained by connecting the symbols, each of which represents the arithmatical mean of the above mentioned values for a specific frequency.

The threshold curves of the four fishes are represented respectively in figures 5, 6, 7 and 8; that of the normal fish in figure 5 (lower curve). All the operated fishes examined have approximately the same shape of threshold curve, i.e., approximately the same hearing sensitivity for the frequency range of 210 to 1,500 c.p.s. with individual differences of 2 to 4 db. (figure 9)

The threshold curve of fish I compared with the curve of the same fish before the operation (respectively upper and lower curve in figure 5) demonstrates a loss of sensitivity in the whole frequency range from 210 to 1,500 c.p.s. The striking decrease in sensitivity (in operated fish) in the frequency range from 750 to 1,500 c.p.s. is a result of the decrease or absence of resonance in the opened swimbladder. (See also figures 6, 7 and 8)

The same phenomenon is demonstrated in figure 10, in which the average absolute threshold curve of the four operated catfishes is compared with the absolute auditory threshold curve for catfish (*Ameiurus nebulosus*), established by Poggendorf (1952). The absolute auditory threshold curve must be seen as a statistical concept rather than as some fixed figure, above which the individual hears and below it does not hear.

The strong increase of sensitivity in the range from 330 - 210 c.p.s. is probably a result of the ability of the lateral line to perceive vibrations of low frequency. This was investigated in one of the catfishes (figure 7) in which the lateral line nerve was at first left intact and later cut at both sides. Observations by Parker and von Heusen (1917) also proved that the lateral line organs of *Ameiurus nebulosus* are stimulated by low tones of an underwater source (43 to 344 c.p.s.) but not by higher tones (344 to 2,752 c.p.s.) Further investigations on this problem is necessary.

The value of the threshold is determined by the kind and locus of measurements of the stimulus, the response that is used, the technique employed, the frequency of repitition of sound stimuli and the condition of the fish themselves.

The intervals between the successive intensities are subordinated to the available outputs of the oscillator, which can be regulated only with intervals of 1 to 2 db., dependent on the desired frequency. This means, that each record of an intensity, just adequate to evoke a response has not an absolute, but an approximative value.

Another effect on response was the method, in which the threshold was approached. A clear difference in the records of the lowest intensities was observed most times, when either the threshold was approached from above or from below. The average threshold will be different for the two methods.

As a conclusion of the results obtained, it might be said that in *Ameiurus nebulosus* and probably in the fishes mentioned in the Introduction, the acuity of hearing is increased by the swimbladder at the resonant frequency of the latter.

SUMMARY

1. The hearing sensitivity was observed in *Ameiurus nebulosus nebulosus* (Le Seuer).

2. To abolish the effect of the swimbladder, the bladder was opened. Apparently the health of the fish was not affected by the surgical intervention.

3. After conditioning of the fish to associate food with sound the actual threshold curve was determined for the frequency range of 210 to 1840 c.p.s. The threshold was expressed in db.; the reference level 0 db. was the lowest intensity at which a normal catfish could hear a tone of 750 c.p.s.

4. The threshold curve for normal catfish was almost constant for the frequency range from 210 to 1,500 c.p.s.

5. The sensitivity in operated fish was decreased in the whole frequency range; for the frequencies from 330 - 750 c.p.s. about 12 db., for the frequencies of 1,000, 1,300 and 1,500 c.p.s. respectively 22, 27 and 30 c.p.s.

6. The strongly decreased sensitivity at the higher frequencies is a result of the loss or decrease of resonance of the opened swimbladder.

7. The increased sensitivity of the operated fish in the frequency range from 330 to 210 c.p.s. might be attributed to the ability of the lateral line to perceive vibrations of low frequency.

8. The lowest intensity at which a fish responded to a sound stimulus was affected by the method in which the threshold was approached.

9. The latent period of the response of the fish to sound stimuli revealed a slight increase when the intensity of one frequency was lowered or when the frequency was raised to higher and less audible sounds.

10. It is concluded that the resonance of the airbladder raises the hearing perception in fish for a frequency range corresponding to the resonant frequency of the bladder.

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Figure 1. Low frequency oscillator with volume control (left) and standing wave meter with crystal hydrophone (right).

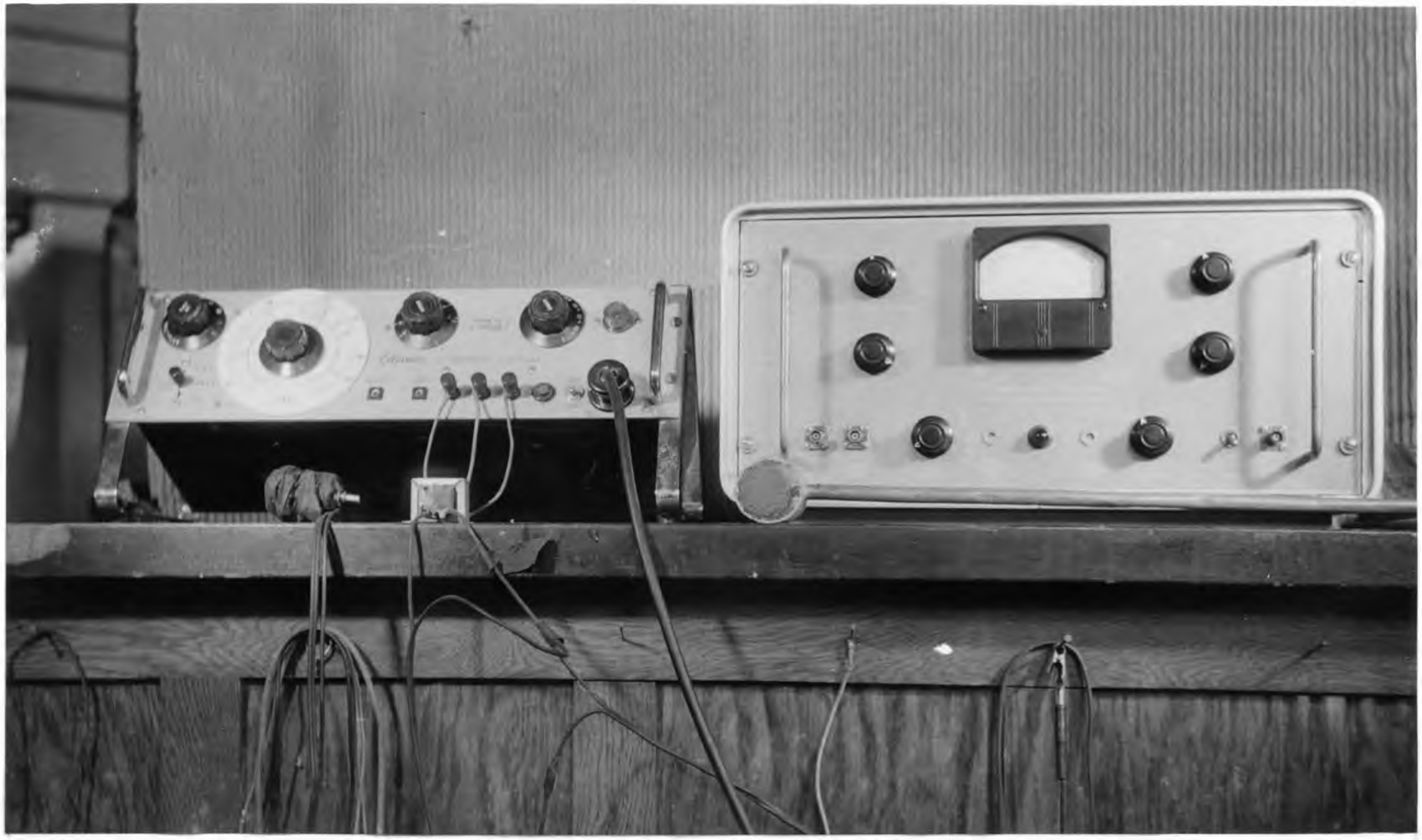


Figure 2. Circuit of low frequency oscillator with volume control and speakers.

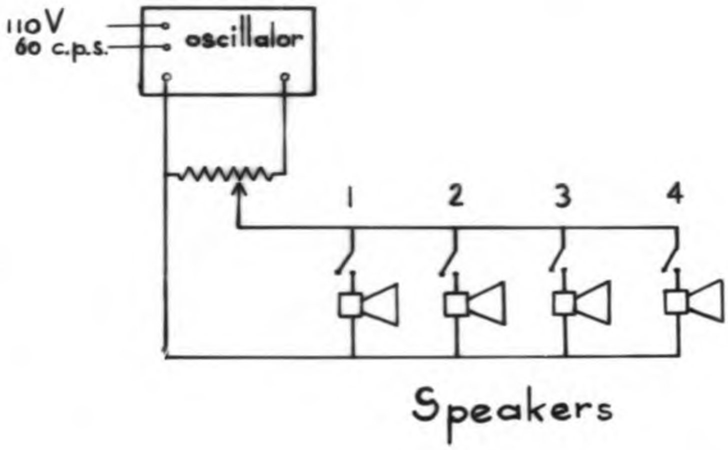

110V
60 c.p.s.
oscillator
1
2
3
4
Speakers

Figure 3. Aquarium with catfish and horizontal screen in right section and submerged speaker in left section. Both sections divided by a screen. Shield with wide angle lenses before the aquarium is removed.

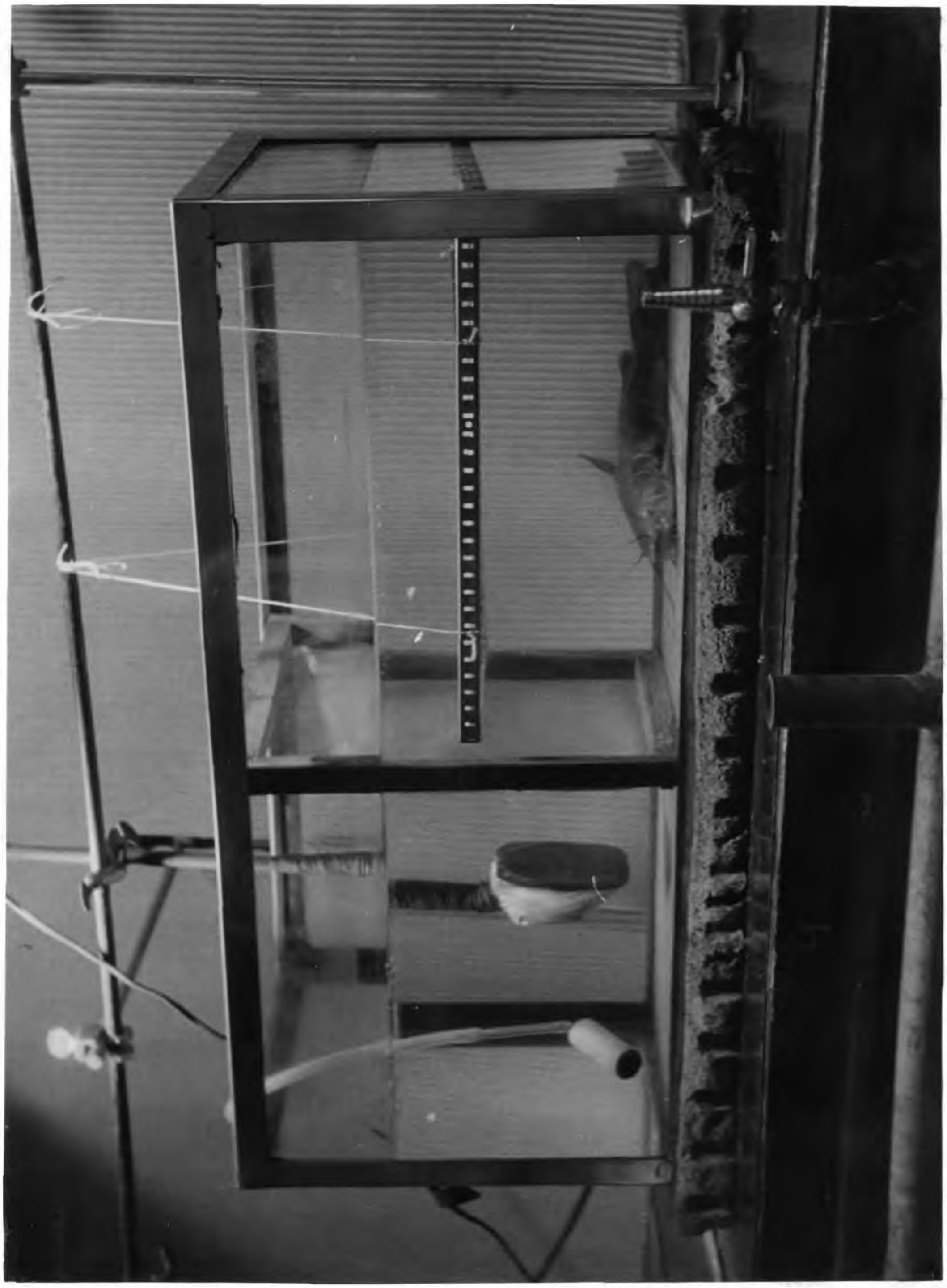


Figure 4. *Ameiurus nebulosus nebulosus* (Le Sueur). Normal fish (right) and operated fish (left) with compressed body walls behind pectoral fins.

Figure 5. Threshold curve of perception of vibrations by catfish I. Lower curve of normal fish; upper curve of the same fish after the swimbladder is opened. (Open circles indicate the lowest intensities to which the fish responded in each test range; solid circles indicate the arithmetical means of the values for the frequencies in question; broken line indicates the probable course of the curve.)

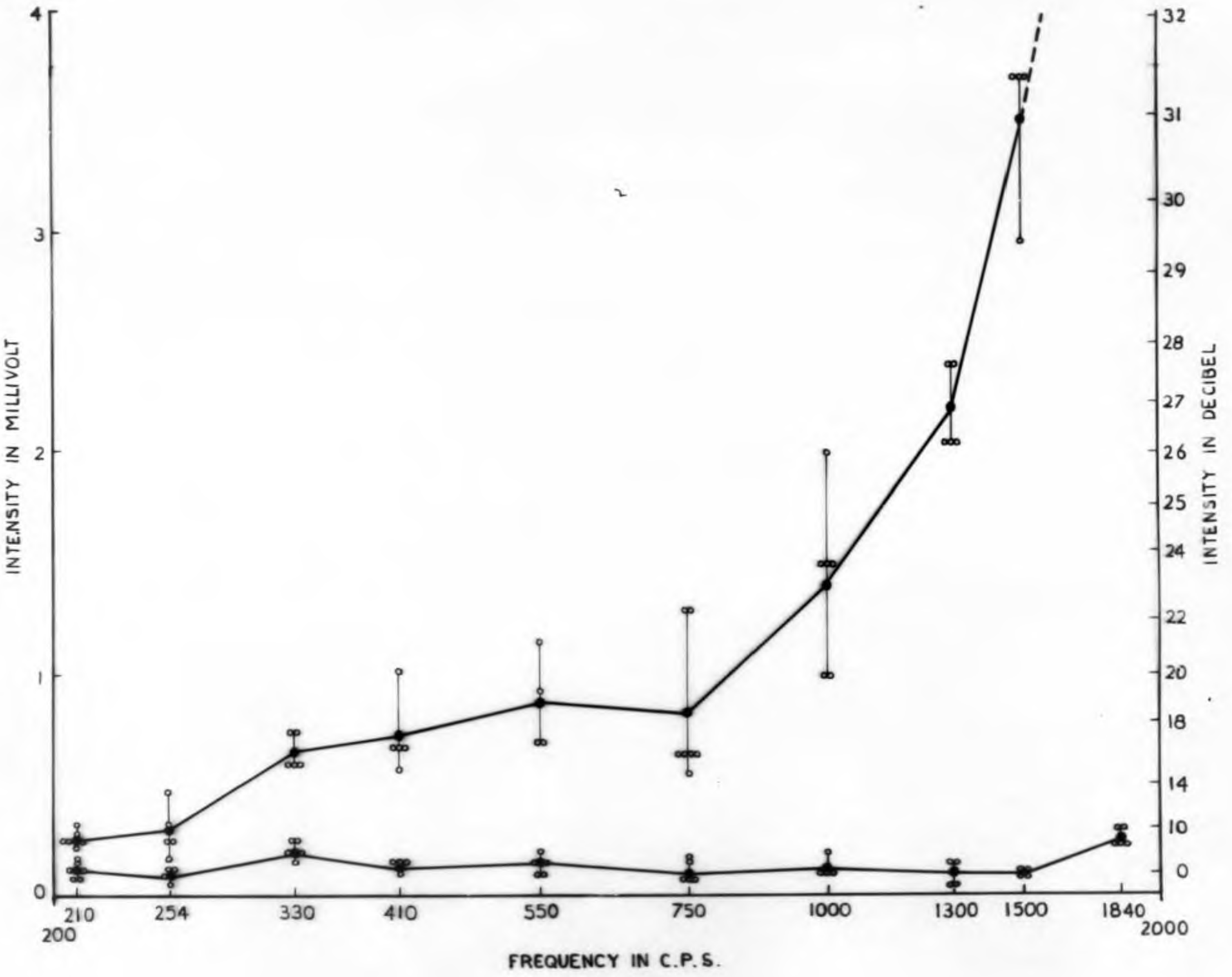

INTENSITY IN MILLIVOLT
0
1
2
3
4
INTENSITY IN DECIBEL
0
10
14
18
20
22
24
25
26
27
28
29
30
31
32
200
210
254
330
410
550
750
1000
1300
1500
1840
2000
FREQUENCY IN C.P.S.

Figure 6. Threshold curve of perception of vibrations of operated catfish II. (For description of symbols see figure 5).

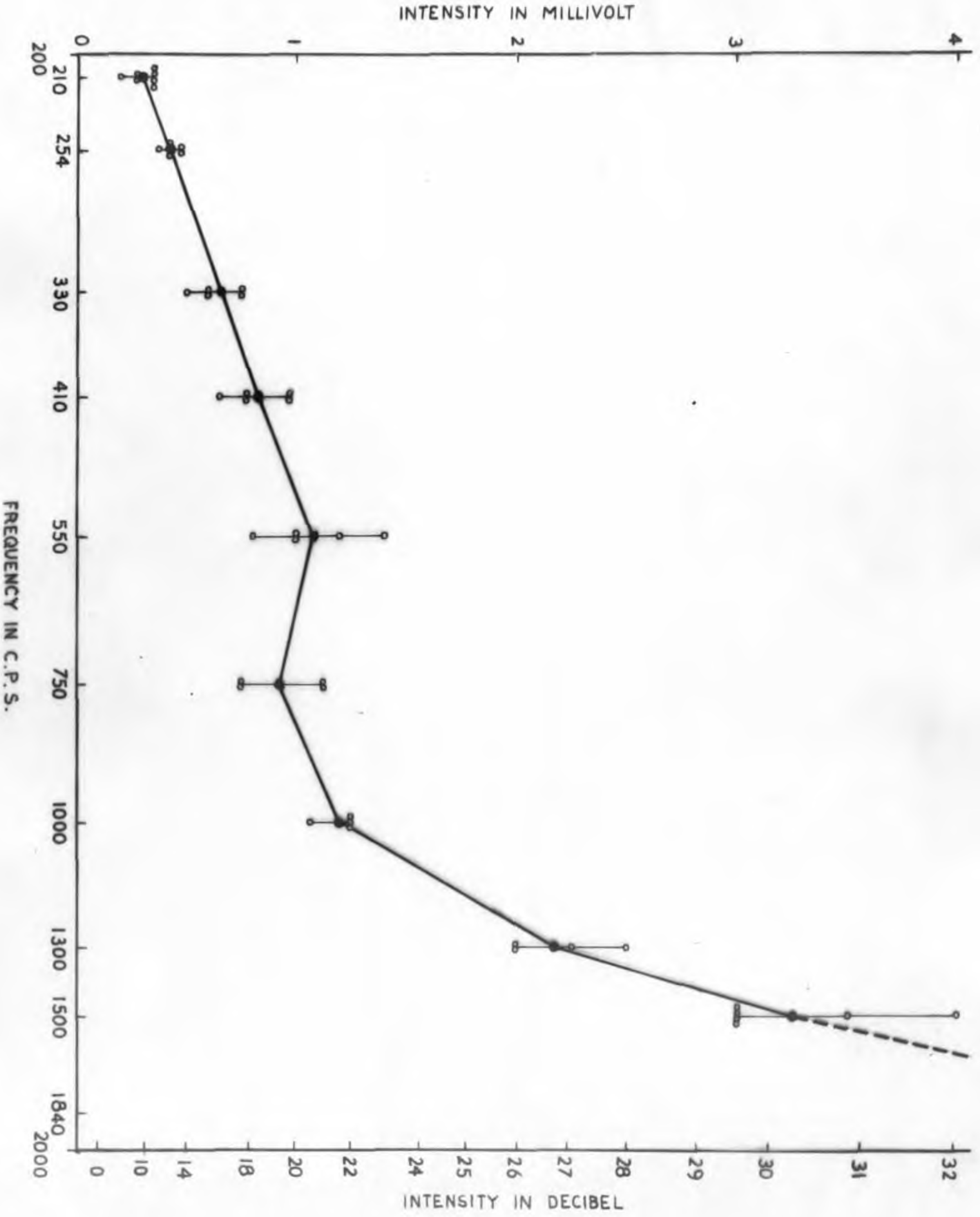
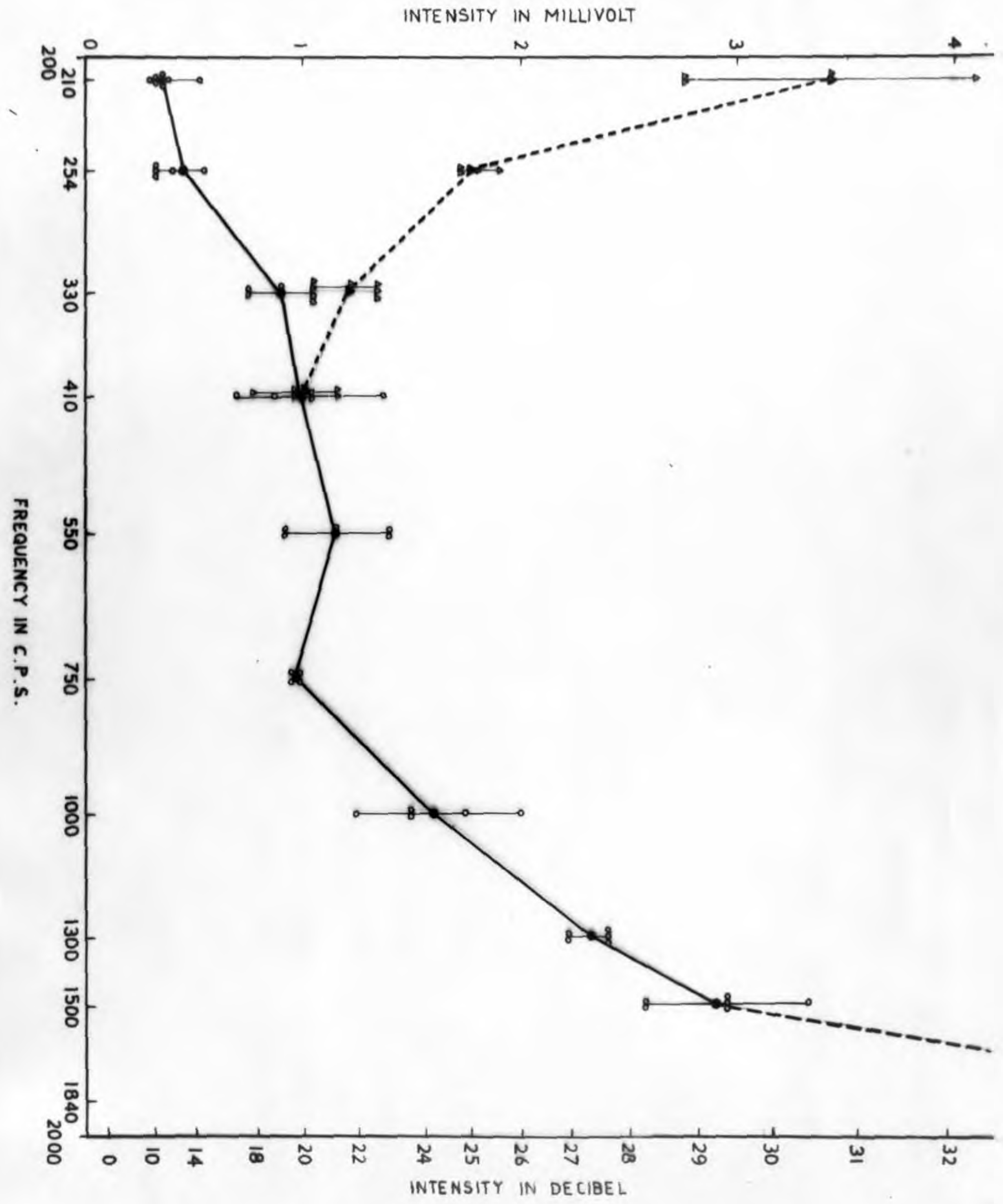

INTENSITY IN MILLIVOLT
0
1
2
3
4
FREQUENCY IN C.P.S.
200
210
254
330
410
550
750
1000
1300
1500
1840
2000
INTENSITY IN DECIBEL
0
10
14
18
20
22
24
25
26
27
28
29
30
31
32

Figure 7. Threshold curve of perception of vibrations of operated catfish III. Dotted line indicates the threshold curve after cutting the lateral lines. (Open triangles indicate the lowest intensities to which the fish after cutting the lateral lines responded in each test range; solid triangles indicate the arithmetical means of the values for the frequencies in question. For description of the other symbols see figure 5).


INTENSITY IN MILLIVOLT
0
1
2
3
4
FREQUENCY IN C.P.S.
200
210
254
330
410
550
750
1000
1300
1500
1840
2000
INTENSITY IN DECIBEL
0
10
14
18
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22
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27
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29
30
31
32

Figure 8. Threshold curve of perception of vibrations of operated catfish IV (for description of symbols see figure 5).

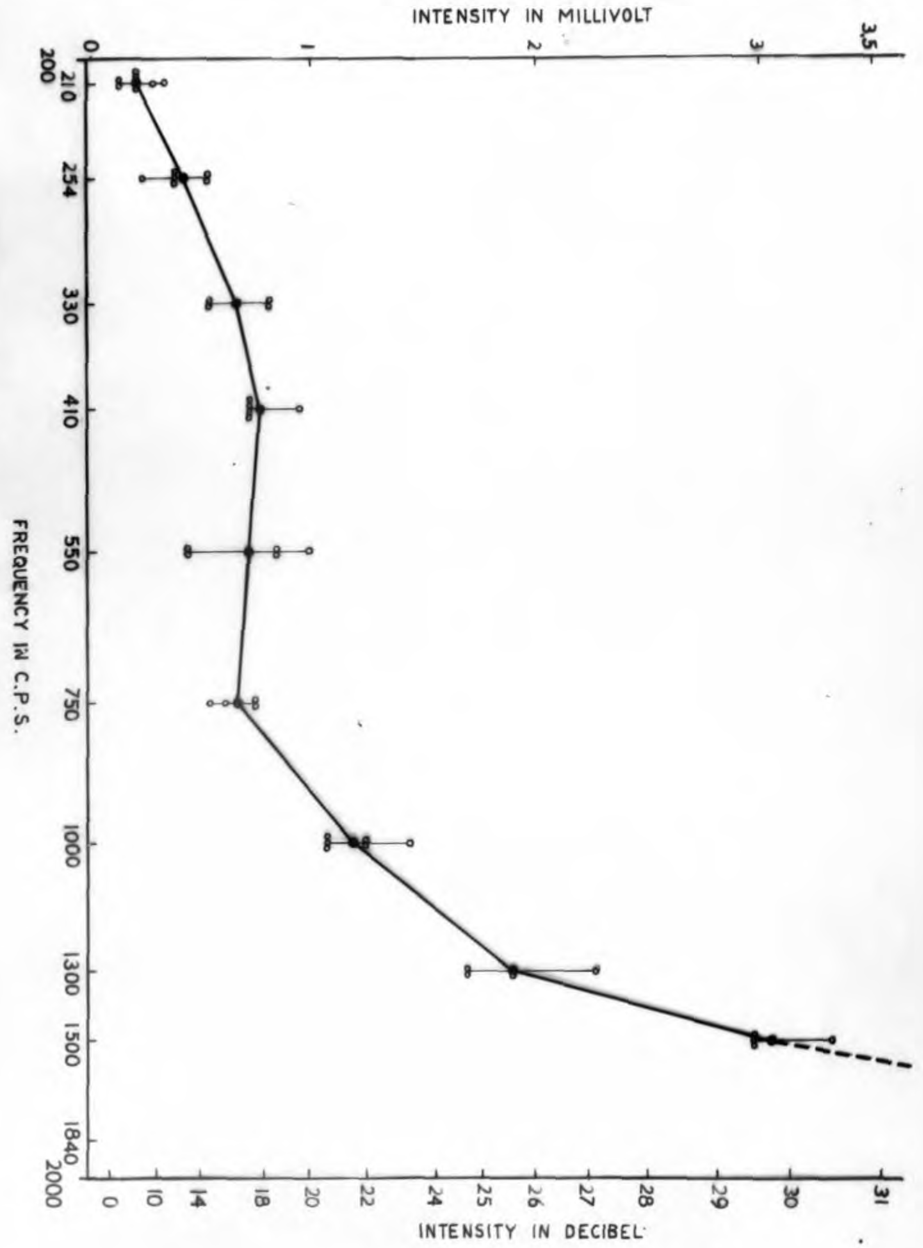

INTENSITY IN MILLIVOLT
0
1
2
3
3.5
FREQUENCY IN C.P.S.
200
210
254
330
410
550
750
1000
1300
1500
1840
2000
INTENSITY IN DECIBEL
0
10
14
18
20
22
24
25
26
27
28
29
30
31

Figure 9. Threshold curves of perception of vibrations of the catfishes I, II, III and IV.

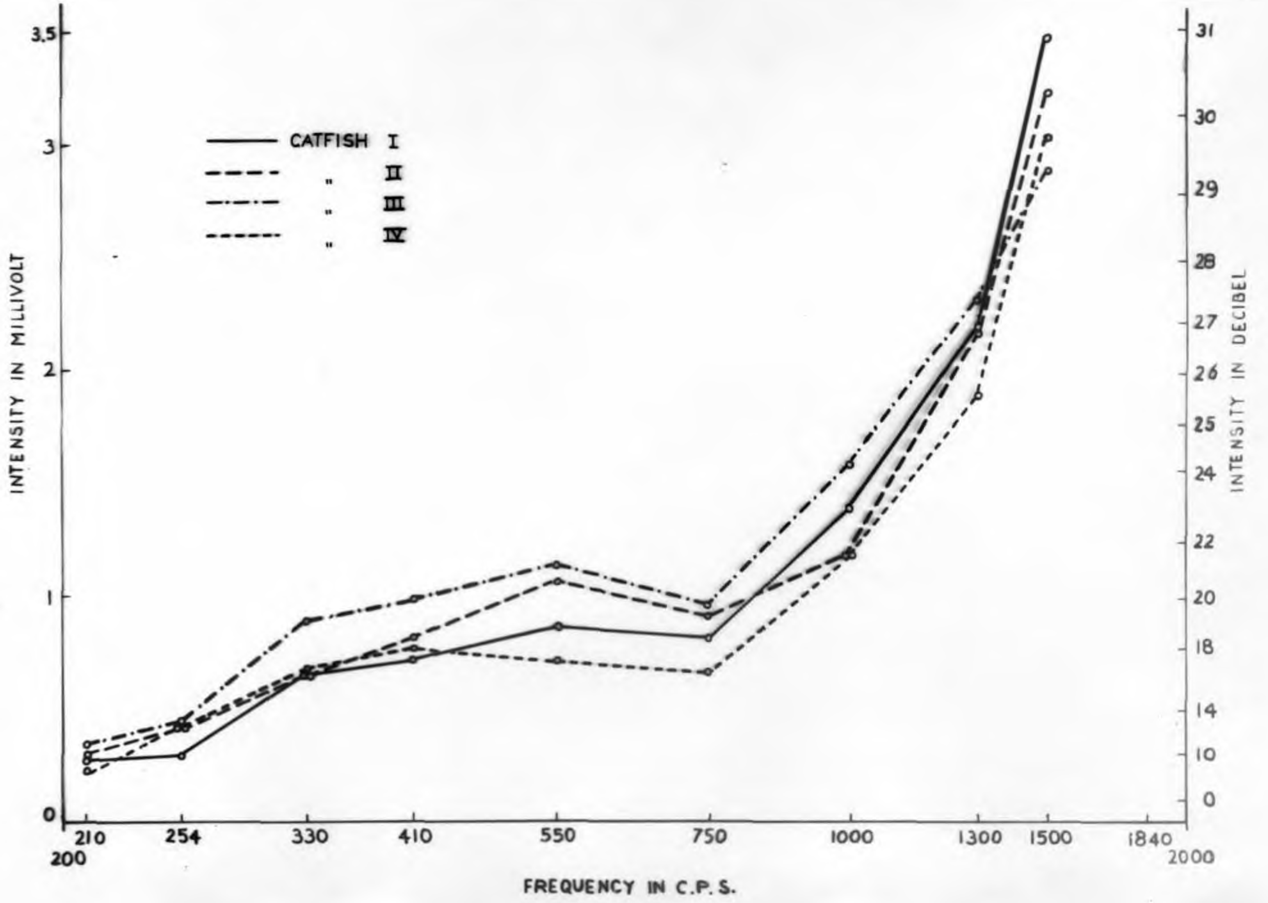
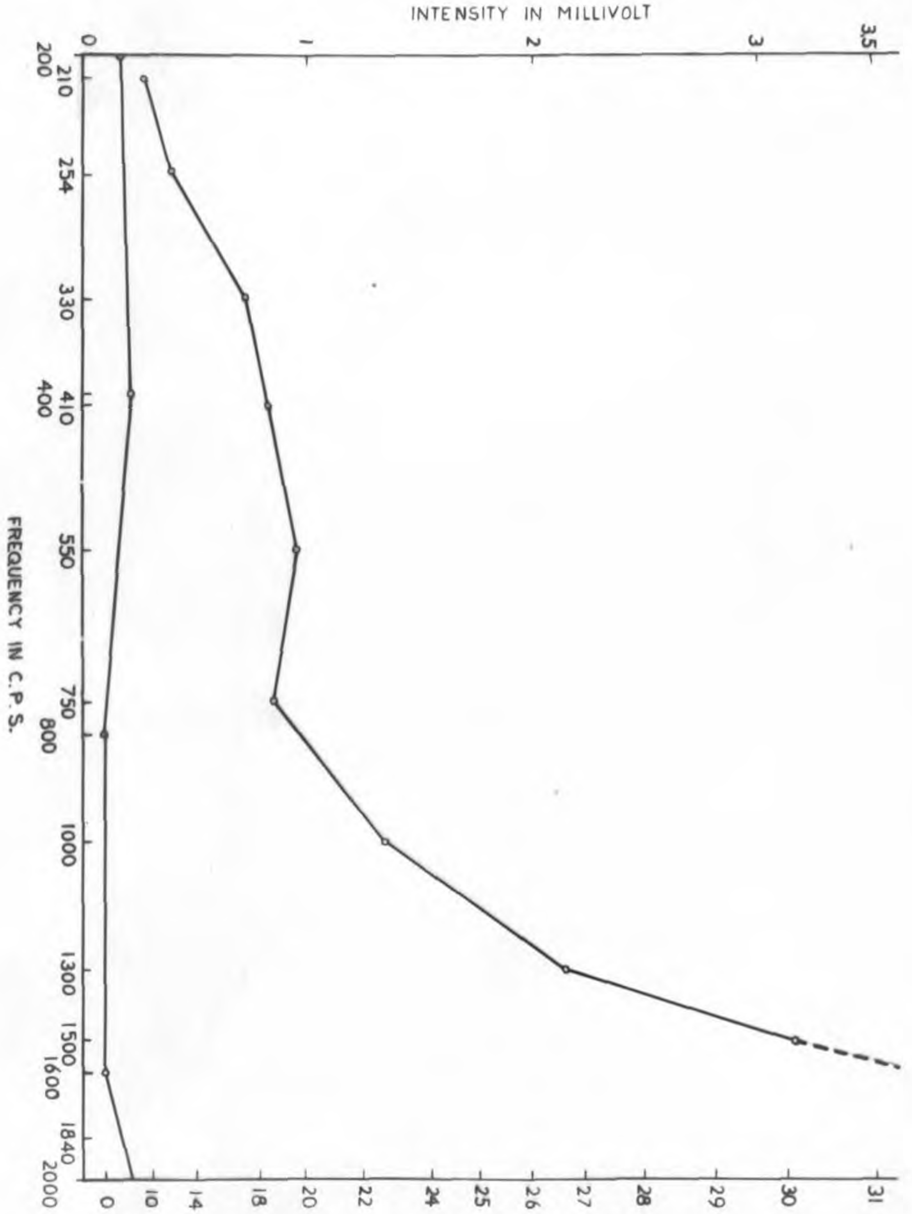

3.5
3
2
1
0
CATFISH I
" II
" III
" IV
INTENSITY IN MILLIVOLT
31
30
29
28
27
26
25
24
22
20
18
14
10
0
INTENSITY IN DECIBEL
210
200
254
330
410
550
750
1000
1300
1500
1840
2000
FREQUENCY IN C.P.S.

Figure 10. Average auditory threshold curve of four catfishes in which the swimbladder resonance is abolished (upper curve) and the absolute auditory threshold curve of normal catfish (established by Poggendorf, 1952) (lower curve).


INTENSITY IN MILLIVOLT
0
1
2
3
3.5
FREQUENCY IN C.P.S.
200
210
254
330
400
410
550
750
800
1000
1300
1500
1600
1840
2000
INTENSITY IN DECIBEL
0
10
14
18
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