Contributions from the Biological Laboratory of the U. S. Fish Commission, Woods Hole, Massachusetts.

HEARING AND ALLIED SENSES IN FISHES.

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It is a well-known fact that many fishes are extremely sensitive to disturbances in the water such as are caused by splashing with an oar, stamping in a boat, or striking the side of an aquarium. When, for instance, the opaque wall of a fish tank containing young king-fish, sea-robins, or killi-fish is struck a vigorous blow with the fist, the fishes usually respond by giving a short, quick leap, and, if such blows are frequently repeated, surface fishes are often driven to the bottom and kept there. Notwithstanding the sensitiveness indicated by such reactions, most of these fishes appear to be unaffected by loud talking or other like noises originating in the air. Fishermen are familiar with these peculiarities and often take them into account in the practice of their art.

Such facts as these are also usually accepted as evidence that fishes can hear (as an example, compare the statements made by W. C. Harris in Dean Sage's "Salmon and Trout," 1902, p. 311), but a simple experiment will show, I believe, that this assumption is not necessarily correct. If one end of a wooden rod is vigorously tapped while the other is beneath the level of the water a disturbance is produced that will call forth an obvious response from most fishes of moderate sensitiveness. Such a disturbance will likewise affect a human being, for if one holds the head beneath the water the vibrations from the rod can be easily heard, and if the hand be placed in the water near the rod they can be distinctly felt.

Since, as Müller (1848, p. 1229) long ago pointed out, we can feel as well as hear these vibrations, it follows that such evidence as that already given can not be accepted as conclusive proof that fishes hear, for it is conceivable that their responses may be entirely through their sense of touch, i. e., dependent on their skins. Moreover, fishes possess a special system of tegmentary sense organs, the lateral-line organs, which are completely absent from us, and it may be that these are in some way the recipient organs for the disturbances already described. When, therefore, a fish responds to water vibrations of the kind mentioned, we are not justified in concluding that it hears, for it may respond through the skin or the lateral-line organs and not through the ears.

It may be reasonably asked at this point, What constitutes hearing? Everyone will agree, I believe, that the sensation we get through the skin from a vibrating rod in water should not be called hearing, and what is true for us should hold for the lower vertebrates. Hearing in these animals may therefore be defined as that sensory activity resulting from a stimulation of the ear by material vibrations. This is in essential accord with the definition given by Kreidl (1895, p. 461) to the effect that hearing is that sensation which is mediated by the nerve that is homologous with the auditory nerve of man. When, therefore, a fish responds to sound vibrations the question at once arises whether the stimulus is received by the skin, the lateral-line organs, or the ear. And until this question can be answered, at least so far as the ear is concerned, the query whether fishes hear or not must remain open. In dealing with this general subject I shall take up, first of all, the question whether fishes respond to sound vibrations through the ears.

THE EARS.

Introductory.—The internal ears of fishes were described as early as 1610 by Casserius, and were studied in some detail in the following century by Geoffroy, Scarpa, Comparetti, and Hunter. The attitude taken by many of these early workers on the question of the ability of fishes to hear or not is well illustrated by a quotation from Hunter (1782, p. 383), who at the conclusion of his paper on the organs of hearing in fishes made the following statement:

> As it is evident that fish possess the organ of hearing, it becomes unnecessary to make or relate any experiment made with live fish which only tends to prove this fact; but I will mention one experiment to shew that sound affects them much and is one of their guards, as it is in other animals. In the year 1762, when I was in Portugal, I observed in a nobleman's garden, near Lisbon, a small fish-pond full of different kinds of fish. Its bottom was level with the ground and was made by forming a bank all round. There was a shrubbery close to it. Whilst I was lying on the bank, observing the fish swimming about, I desired a gentleman, who was with me, to take a loaded gun and go behind the shrubs and fire it. The reason for going behind the shrubs was that there might not be the least reflection of light. The instant the report was made the fish appeared to be all of one mind, for they vanished instantaneously into the mud at the bottom, raising, as it were, a cloud of mud. In about five minutes after they began to appear, till the whole came forth again.

This passage shows very clearly that in the opinion of Hunter the internal ears of fishes, like those of the higher vertebrates, are organs of hearing. Without further experimental evidence this view was accepted by Müller (1848, p. 1238) in his well-known chapters on the physiology of the senses, and by many other eminent authorities, such as Owen (1866, pp. 342 and 346), Günther (1880, p. 116), and Romanes (1892, p. 250). To these investigators the presence of the internal ears seemed, as it did to Hunter, sufficient ground for concluding that these animals could hear.

Within recent years, however, this opinion has been called in question, or even denied. Some of the grounds for this change of view may be stated as follows: Bateson (1890, p. 251), in some investigations on the sense organs and perception of fishes, observed that the report from the blasting of rocks caused congers to draw back a few inches, flat-fishes (like the sole, plaice, and turbot) to bury themselves, and pouting to scatter momentarily in all directions; other fishes seemed to take no notice of the report. When the side of a tank containing pollock or soles was struck with a heavy stick, the fishes behaved as they did toward the report of the blasting. Pollock did not respond, however, to the sound made by rubbing a wet finger on the glass window of an aquarium or to the noise made by striking a piece of glass under water with a stone, provided the means of producing the noise was not seen by the fishes. Bateson concluded that, while it may be regarded as clear that fishes perceive the sound of sudden shocks and concussions when these are severe, they do not seem to hear the sounds of bodies moving in the water but not seen by them.

Without knowledge of Bateson's observations, Kreidl (1895) carried out a series of experiments with the view of testing the powers of hearing in the gold-fish, *Carassius auratus*. This species was chosen because of the ease with which it could be kept in the laboratory and, further, because it is one of those fishes that have long been reputed to come at the sound of a bell. After an extended series of experiments, Kreidl (1895, p. 458) concluded that normal gold-fish never respond to sounds produced either in the air or in the water, though they do react to the shock of a sudden blow given to the cover of the aquarium. Individuals rendered abnormally sensitive by strychnine gave no response to the sound of a tuning-fork or a vibrating-rod even when these were in contact with the water, though the fishes responded at once to such slight shocks as tapping the aquarium, etc., or even clapping the hands vigorously in the air.

To test whether these responses were dependent upon the auditory nerves, Kreidl removed these nerves and the attached ear-sacs from a number of individuals, and, after poisoning them with strychnine, subjected them to stimulation by sound. In all cases they were found to respond precisely as the poisoned animals with ears did. Kreidl, therefore, concluded that gold-fishes do not hear by the so-called ear, but that they react to sound-waves by means of an especially developed cutaneous sense, or, to put it in other words, the gold-fish *feels* sound but does not *hear* it (Kreidl, 1896, p. 581).

After having reached this conclusion, Kreidl was led to take up a specific case of the response of fishes to the sound of a bell, and an opportunity for doing this was found at the Benedictine monastery in Krems, Austria. Here the trout of a particular basin were said to come for food on the ringing of a bell. Kreidl (1896, p. 583), however, found that they would assemble at sight of a person and without the ringing of the bell. If they were not then fed, they soon dispersed and no amount of bell-ringing would induce them to return. If, however, a pebble or a small piece of bread was thrown into the water they immediately swam vigorously toward the spot where the disturbance had occurred. Moreover, if a person approached the basin without being seen and rang the bell vigorously no response was observed. From these facts Kreidl (1896, p. 584) concluded that the assembling of the fishes was brought about through sight and the cutaneous sense, and not through hearing, and that the conclusion reached with the gold-fish might be extended to other kinds of fishes.

Kreidl's conclusions were supported by the observations of Lee (1898), who studied the reactions of several species of fishes to such sounds as the human voice, the clapping of hands, and the striking of stones together in air and under water. In all of his experiments Lee (1898, p. 137) obtained no evidence whatever of the existence of a sense of hearing, as the term is usually employed, although he found that the fishes were exceedingly sensitive to gross shocks, such as the jarring of their tank or concussions upon its walls. Lee, moreover, called attention to the fact that the papilla acustica basilaris, which is the special organ of hearing in the internal ears of the higher vertebrates, did not occur in the fishes. From the observations and experiments of Bateson and of Kreidl, and from his own work, Lee (1898, p. 138) believed that the conclusion was justified beyond doubt that fishes do not possess the power of hearing, in the sense in which the term is ordinarily used, and that the sole function of the ear in fishes is equilibration.

The generalization to be drawn from the work just summarized, viz, that fishes do not hear, though they may respond to sound-waves by the skin, has seemed to me not wholly in accord with certain well-known facts in the natural history of these animals. Among these facts may be mentioned the undoubted ability on the part of some fishes to make sounds. If a fish has this power it might naturally be supposed to hear the sounds it makes. Lee (1898, p. 137) has called attention to the small number of sound-producing fishes as evidence against the view that fishes in general hear. But the fact that there are such fishes has always appealed to me in quite the reverse way and should, in my opinion, serve to indicate the species most worthy of attention in any investigation of the sense of hearing. It must be admitted, however, that fishes may possibly produce sounds that they themselves can not hear, but that other animals may hear and take warning from. Thus when small swell-fish, *Chilomycterus schœpfi*, are thrown into a tank containing hungry scup, *Stenotomus chrysops*, they are immediately set upon by the latter. In defense the swell-fishes inflate themselves with sea water till their tegmentary spines stand out rigidly, and at the same time they make a peculiar sound by gritting the two front teeth of the lower jaw against the inner surface of those of the upper jaw. It is not known that this sound is heard by the swell-fish, though it may be. All that one can say with certainty is that the sound seems to be directed against the foe, for it is made, so far as I know, only when the swell-fish is molested. Granting, however, that the swell-fish does not hear its own sound, one would still be rash to conclude that this was an argument against the hearing of fishes, for the vast majority of animals toward which the sound is directed are fishes themselves, and these presumably hear the sounds.

Another good instance of the production of sound by a fish is found in the squeteague or weak-fish, *Cynoscion regalis*. The grunting noise made by this fish is, however, produced only by the males, and this specialization is very difficult to understand unless one assumes an ability on the part of one or other sex to hear. Since the sounds made by both the swell-fish and the squeteague are in no sense shocks or concussions but resemble more closely, in rate of vibration and in intensity, such sounds as might be obtained from the ordinary action of an instrument like a tuning-fork of low pitch, it seems to me that they afford evidence in favor of the sense of hearing rather than the reverse.

A second reason for questioning the generalization advocated by Kreidl, and by Lee, is the character of the observations upon which it is based. Both authors state that no positive evidence in favor of hearing could be obtained. But it must be borne in mind that in many animals known to possess a sense of hearing the auditory reflexes are perhaps the least conspicuous of any connected with the more important sense organs, and that consequently the most careful scrutiny of the movements of fishes must be made before one can with certainty declare that hearing is absent. A perusal of the papers already summarized led me to the conclusion

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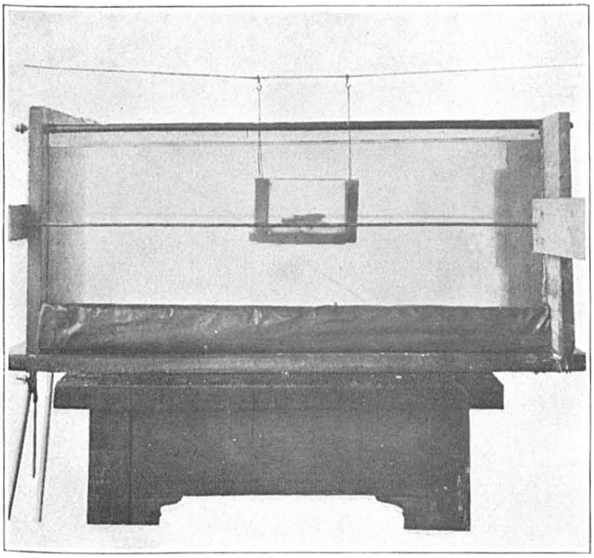

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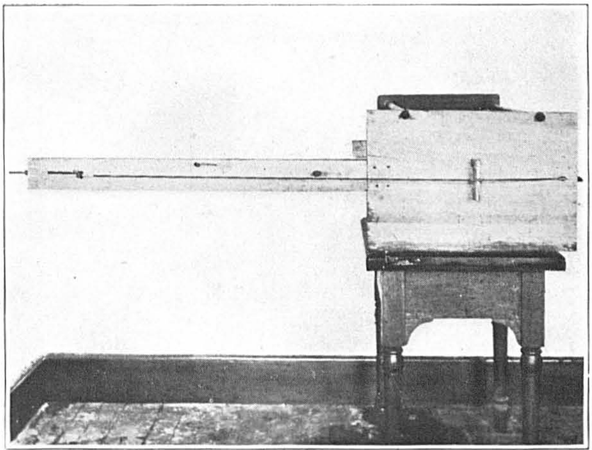

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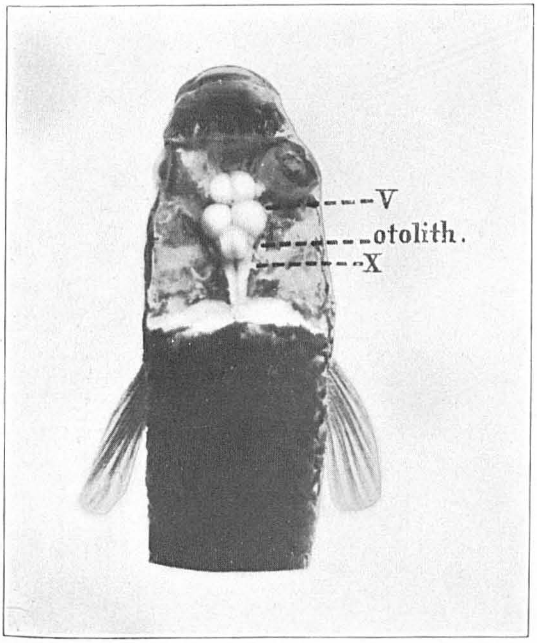

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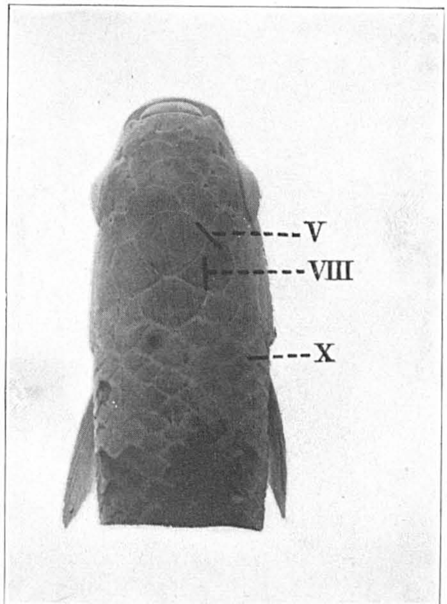

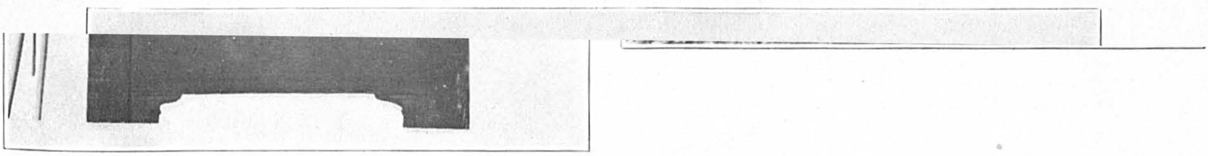

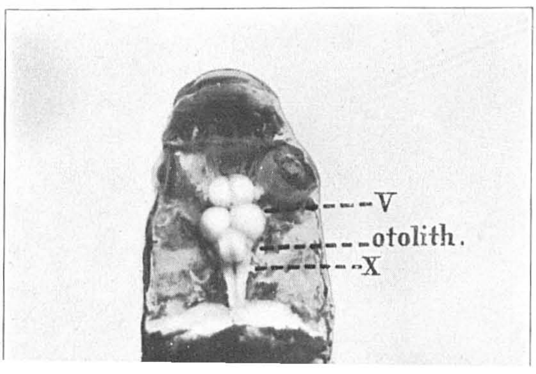

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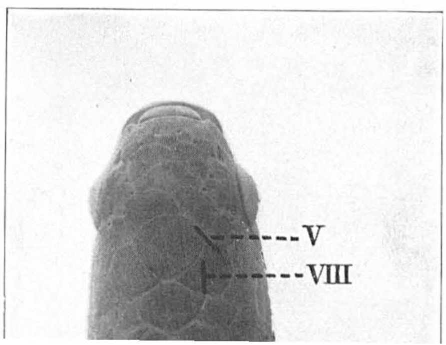

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that something more might be attained in this direction, and I therefore resolved to give particular attention to the reactions of a few fishes with the view of ascertaining whether or not they showed any evidence of hearing.

At the outset I thought it best to experiment on some common sound-producing species, and for this purpose I did some preliminary work on the swell-fish (*Chilomycterus schœpfi*), the squeteague (*Cynoscion regalis*), and the sea robin (*Prionotus carolinus*). To all of these, practical objections were found, and I was at last obliged to abandon them for fishes that produce no sounds. Among these, three species were found to be especially sensitive to slight vibrations—the king-fish (*Menticirrhus saxatilis*), and the two common species of killi-fish (*Fundulus majalis* and *F. heteroclitus*). Because of the great abundance of *F. heteroclitus*, the ease with which it could be operated upon, and its great hardiness, I chose it for study, and the observations recorded on the following pages, unless otherwise stated, refer to this species.

The ears in Fundulus heteroclitus.—When a tank containing a number of *Fundulus heteroclitus* is struck with the open hand so that the fish can not see the movement of striking, they respond to the vibrations by springing suddenly an inch or so through the water. The question to be considered is whether these vibrations stimulate the fishes through the skin, the lateral-line organs, the ears, or some combination of these. If it could be shown that the ears were not stimulated by the vibrations, it seems to me that we would have evidence pointing to the conclusion that the fishes did not hear. If on the other hand it could be demonstrated that the vibrations did stimulate the ears, the evidence would be conclusive that the animals possessed the sense of hearing. To test these points considerable experimentation was necessary.

Much of the work that has been carried out heretofore has been done with sound generated in air but intended to affect fishes in water. That this method is extremely inefficient I found by trying the following experiment. If a dinner bell is rung in the air by a person standing breast-deep in water, it will, of course, be heard easily by a second person standing in a similar way a yard or two off. If, however, the second person puts his head under the water during the ringing of the bell the sound seems to cease almost entirely and is not again heard clearly by the diver till he emerges. In like manner a bell rung or hit with a stone under water is heard, at best, very faintly by a person standing in the water unless his head is under the surface. In other words, the plane separating air and water is, under ordinary circumstances, an almost impenetrable one for most sounds, whether they are generated on one side or the other of it, and many of the negative results obtained by previous investigators on the sense of hearing in fishes may have been due not so much to the absence of hearing in the animals experimented upon as to their inaccessibility to the sound, or at least to sound of an intensity sufficient to stimulate. This difficulty has been recognized by Kreidl, and in devising apparatus I have profited by his experience and used sound-producing appliances that were in direct contact with the water containing the fishes.

The chief piece of apparatus that I used consisted of an ordinary marine aquarium (pl. 9, fig. 1) with a slate base, two heavy glass sides, and originally two slate ends, one of which, however, I replaced by a piece of deal board free from knots, to serve as a sounding-board. The inside dimensions of the aquarium were as follows: depth, 40 cm. (16 in.); breadth, 37 cm. (15 in.); and length, 87 cm. (35 in.). To the middle of one edge of the sounding-board a stout beam of wood was attached so that it stood out horizontally about 1 meter (40 in.) in the plane of that end (fig. 2). From the free end of the beam a bass-viol string was stretched to the opposite side of the sounding-board. This string could be tightened by a bolt and nut at the free end of the beam, and it was made to pass over a bridge placed near the middle of the sounding-board. The length of the string from the attached end on the sounding-board to the bridge was 25 cm. (10 in.), and from the bridge to the attachment near the free end of the beam 1.15 meters (45 in.). Thus the end of the aquarium might be regarded as something like a large one-stringed bass viol resting sidewise, with the sounding-board for a body and the beam for a neck.

When the string was tightened and plucked or bowed a good tone was obtained, which was transmitted directly through the sounding-board to the water within the aquarium. On keying the string up to a good clear tone, I found by writing off its vibrations on a revolving cylinder that it produced on an average 40 per second, and I retained this pitch by frequent adjustment for the experiments that I subsequently performed. I was led to adopt this low tone since most of the noises that I have heard fishes make were in the nature of low-pitched grunts.

Each time the string was plucked the note began with maximum intensity and then gradually died away. It was, consequently, impossible to get any very significant record of the intensity, but I endeavored to use the apparatus in a uniform way by drawing the string out a constant distance from its position of rest each time I plucked it. The distance usually employed was about 1.5 cm. (0.6 in.). The amount of weight required, when hung at the middle of the longer segment of the string, to depress it 1.5 cm. was found to be about 2.15 kilograms (4.75 pounds), so that each time the string was liberated on being plucked in the usual way, it moved forward with an initial force equal to the pull of 2.15 kilograms, a rough measure of the maximum intensity of the sound produced.

The fishes to be experimented upon were not allowed to swim unrestricted in the aquarium, but they were placed in a small cage (fig. 1) suspended from a cord attached at its ends to the walls of the room. Thus the support for the fish cage was entirely independent of the walls of the aquarium and any vibration that reached the fishes must have done so almost entirely through the water. The cage could be moved in a horizontal direction back and forth on the cord, and thus the fish could be placed at any desired distance from the sounding-board up to 75 cm. (30 in.). The inside measurements of the cage were as follows: Height, 10 cm. (4 in.); length, 20 cm. (8 in.); and breadth, about 10 cm. (4 in.). The bottom of the cage was wood, padded on the inside with cotton wool covered with cloth to provide a deadened surface on which the fishes might rest. The top and three sides were glass; the fourth side was made of coarse netting to retain the fish but to interfere as little as possible with the entrance of sound, and this side was always directed toward the sounding-board. As the fishes averaged about 7 cm. (2¾ in.) in length, the cage gave them ample room for moving about.

My plan was to introduce fishes in various conditions into the cage, and, after they had become accustomed to their surroundings, to subject them to stimulation by sound and observe their reactions. I found it desirable to experiment with three classes of fishes; first, normal ones for a basis of comparison; secondly, fishes from which the ears had been removed; finally, fishes in which the general integument had been rendered insensitive, but in which the ears were intact. The methods of obtaining fishes in these conditions and the responses that they showed will be described for each class of fishes.

Normal fishes.—When a normal fish is first liberated in the cage it swims vigorously about for a few moments, after which it may, sooner or later, come to rest on or near the bottom. The animals are extremely quick-sighted, and, if after they have come to rest the observer makes any sudden movements near the aquarium, they are very likely to begin active swimming anew. It is, therefore, extremely necessary to work in such a way that all movements, and particularly quick ones, are made out of sight of the fish. When the fish is resting on the bottom of the cage, two sets of motions will usually be observed: first, the respiratory movements of the operculum; and secondly, the alternate vibratory movements of the pectoral fins. The opercular movements, as might be expected, always continue, but the movements of the pectoral fins, which seem to be connected also with the respiratory function, often cease entirely.

When a fish has become quiet, except for the respiratory movements, the vibrations from the string may call forth any of four kinds of responses. The first of these is the vibratory movement of the pectoral fins, either a few slight beats, if the fins were previously at rest, or an increased rate or extent of swing if they were previously in motion. The vibration of the string at the intensity ordinarily employed almost invariably called forth this reaction; thus, in ten observations taken from each of ten fishes at a distance of about 25 cm. (10 in.) from the sounding-board there were 96 pectoral-fin responses and 4 failures. Since this response is so readily observed, it has afforded one of the most satisfactory criteria of stimulation.

The second form of response is a change in the rate of the respiratory movements. In a quiescent fish measuring 8 cm. (3.2 in.) in length the respiratory rate was 114 per minute. On stimulating by sound this rate rose suddenly to 138 per minute for some ten or a dozen movements and then fell rapidly to about the former number. This is probably a very usual form of response, perhaps quite as much so as the movement of the pectoral fins, but the shortness of its duration and its inconspicuousness make it less satisfactory as an indication of stimulation than that afforded by the pectoral fins. If the sound from the string is of considerable intensity, the third form of response may appear, a slight motion of the caudal fin, beginning usually at the dorsal edge and proceeding as a wave ventrally. Finally, with strong stimulation, the fish may make a short but quick spring forward.

All these reactions have been obtained from fishes even at 75 cm. (30 inches) from the sounding-board, although the springing movements are more frequently observed when the animals are not so far from the source of sound. One very interesting fact about these reactions is that they can not be repeated rapidly for even a short period. A fish that responds to the first stimulus by a spring, may react to the second or to the third only by moving the pectoral fins, and to the fourth in no observable way. It is only when a considerable period of rest intervenes that the reactions may be repeatedly obtained; and I have found that the minimum period of rest is not far from one minute, though, even then, reactions may sometimes fail to appear.

Earless fishes.—The removal of the ears from a fish is a serious operation, but it is one which, after a little practice, may be accomplished with success and from which the fishes generally recover. These animals are easily etherized by putting them in sea water containing enough ether to give it a strong odor. On being transferred to pure sea water they quickly recover, and an individual that I etherized six times in the course of one afternoon finally recovered without showing any ill effects. The first method I used in operating on the etherized fishes was to open the cranium in the region of the ears and, after cutting the auditory nerves, to remove those nerves and the attached ear-sacs. These parts were easily identified from the fact that the auditory nerve emerges from the medulla almost exactly ventral to the cleft between that organ and the optic lobe, and the ear-sac, which is only partly surrounded by cartilage, lies in the cranial cavity only slightly peripheral to the point where the nerve leaves the medulla (pl. 9, fig. 3). After the operation the fishes were returned to pure sea water and, notwithstanding the exposure of the brain, a considerable number recovered and survived. One of these I kept for more than six weeks, and, though its swimming was characteristically irregular, it was alert and active and, except for a brief intervening period, it fed normally.

From the operation just described about one fish in ten recovered. This proportion was greatly increased by a second form of operation in which the auditory nerve was cut without opening the cranium (fig. 4). After a little practice I found that this could be done with great certainty and about eight out of ten fishes usually recovered. All fishes that had been operated on were kept at least twenty-four hours before they were subjected to experimentation.

Fishes in which the auditory nerves have been cut have very characteristic reactions. When resting or when swimming slowly they behave for the most part as normal fishes do, and, in fact, are often undistinguishable from individuals upon which no operation has been performed. When, however, they are stimulated to rapid locomotion, they swim either in irregular spirals, the same individual revolving sometimes to the right and sometimes to the left, or they turn over and over in irregular circles without accomplishing much real progression. This loss of orientation on attempting rapid locomotion has for some time been recognized as indicative of one of the chief functions of the ears in fishes—i. e., equilibration. It is probable that in resting or in swimming slowly the fish depends upon the eye for orientation, but in quick movements the ears come more into play, and hence after their loss quick movements are accompanied with lack of orientation. The forced movements thus observed may be taken with perfect certainty, so far as my experience goes, as evidence of the successful outcome of an attempt to cut the auditory nerves, for in the few cases where these movements failed to appear, subsequent dissection showed that the nerves had not been cut, and in all instances where the movements were observed and the animals afterwards dissected, the nerves were found severed.

A second feature of interest that generally characterized fishes with severed auditory nerves was the color that they finally assumed. Under ordinary circumstances the color of this species is a light greenish-gray. When etherized the fishes become very dark, with a mottling of blue-green on the sides and belly. After recovery from cutting the auditory nerves, the dark coloration disappears and the fish assumes a tint even paler than that of a normal individual. This tint is retained throughout life. Etherizing probably influences the chromatophores of the skin directly, but cutting the auditory nerves introduces changes that are probably dependent upon the nervous control of the chromatophores.

When the earless fishes were tested in the sounding apparatus, they yielded very interesting results. Unlike the gold-fishes experimented on by Kreidl (1895), they differed markedly from normal fish. In an extended series of observations on over 20 fishes I never once observed with certainty the springing reflex as a result of sounding the bass-viol string. The fishes were usually very active, and I was never able to ascertain with certainty whether they showed a change in the respiratory rate on stimulation. The pectoral-fin movements, however, were observed with much certainty. On 10 earless fishes I succeeded in getting 10 observations each to sound stimuli at about 25 cm. (10 inches) from the sounding-board. The total result was that in 82 observations there were no reactions and in the remaining 18 the reactions were at best slight ones. As the fishes often moved the pectoral fins without apparent cause, some of the 18 reactions may have been accidental coincidences, but others were so precise and typical that I am convinced they were due to stimulation. Earless fishes, therefore, differ from normal ones in that their pectoral-fin responses to vibrations from the bass-viol string are enormously reduced, though not entirely obliterated.

Fishes with insensitive skins.—For reasons already given it is imperative, before drawing conclusions from the condition of earless fishes, to examine the evidence afforded by those whose general surface has been rendered insensitive. In this way it is possible to ascertain what part the integument plays in the reception of sound vibrations. I had hoped that the integument of *Fundulus heteroclitus* could be rendered insensitive by immersing the fish for a short time in a solution of cocaine, but all attempts in this direction proved failures, since the drug acted much more vigorously as a poison than as an anæsthetic, and I was finally obliged to abandon this method altogether and resort to nerve-cutting.

The following operation performed on etherized fishes insures an almost complete insensibility of the surface. The fifth and seventh cranial nerves can be cut just posterior to the eyeball (pl. 9, figs. 3 and 4), the lateral-line branch of the tenth nerve can next be cut at the posterior edge of the pectoral girdle (fig. 5), and finally the spinal cord can be severed at the fourth or fifth vertebra. Severe as this operation is, almost all fishes recover from it and respire and feed normally, though they seldom live beyond two weeks after the operation.

Fishes that have recovered from this operation show certain well-marked characteristics. The integument, particularly that of the dorsal surface, is unusually dark, as a result of the expanded condition of the chromatophores. The fish's mouth is gaping and motionless in consequence of the motor portion of the fifth nerve having been cut. This condition, however, does not interfere with respiration or with the sucking in of pieces of food, an act which the fish performs with avidity. Since in cutting the fifth and seventh nerves, the three small nerves to the muscles of the eyeballs, the third, fourth, and sixth, must also be cut, the eyes are motionless and usually protrude somewhat. Finally, as a result of cutting the spinal cord, the whole trunk of the animal is, as a rule, passive and is drawn after the head, the swimming being performed by the pectoral fins. Since the greater part of the cord is intact, a more or less vigorous stimulus applied to the trunk is followed by movements in the dorsal, anal, and caudal fins, or even by a locomotor response of the whole trunk, but such movements are made only after special stimulation, and the trunk is ordinarily carried passively, like a paralyzed appendage. As a result of having so little of the normal locomotor apparatus intact, the fishes often swim ventral side up, for the action of the pectoral fins is not always sufficient to overcome the physical effects of the specific gravity of the fish's body.

Fishes that have recovered from the operation just described have intact the ears, the central nervous organs from the anterior end of the brain caudad to the fourth or fifth vertebra, and the sensory and motor apparatus for the region of the gills and the pectoral fins. Excepting in these two rather restricted regions, the whole integument is insensitive, at least so far as its capacity to originate impulses to movements in the gills or pectoral fins is concerned. Such fish, therefore, are in a condition to receive stimuli through the ears and to respond by respiratory or pectoral-fin movements.

The reactions that these fishes showed to the sound apparatus were surprisingly clear and decisive. From the nature of the operation one would not expect them to be able to give the sudden spring that the normal fishes often showed, and, as a matter of fact, such responses were never observed. Were the skin of the trunk sensitive, it is conceivable that the caudal-fin reaction might occur, for the cord, though severed from the rest of the central nervous organs, was in itself intact. Caudal-fin reactions were, however, also never observed. The respiratory reactions and the pectoral-fin responses occurred with great regularity. When the bass-viol string was made to vibrate, the respiratory rate increased for a very brief period. In a fish 7 cm. (2¾ inches) long the rate previous to stimulation was 120 per minute; immediately after stimulation it was 156. The reactions of the pectoral fin were also well marked. In ten observations on each of ten animals at a distance of about 25 cm. (10 inches) from the sounding-board the pectoral-fin responses occurred 94 times in the total hundred. This is in close agreement with the normal fishes and in strong contrast with the earless ones. So far, then, as reactions to the vibrating chord are concerned, these fishes show the essential characteristics of normal individuals.

Discussion of the results of the experiments.—It is clear from the experiments described in the preceding sections that fishes whose ears were rendered functionless, but whose skins were normally sensitive, reacted only slightly to the stimulus from the sound-producing apparatus, whereas those with insensitive skins but functional ears responded to this stimulus, as far as their conditions would permit, almost exactly as normal fishes did. It might be assumed that the failure to respond on the part of earless fishes was due not to the loss of the ear, but to the shock of the operation they had undergone. This, however, does not seem to be the case, for, after the fishes had recovered from the immediate effects of the operation, they were active, fed well, and sometimes lived many weeks. Moreover, if the operation were as severe as is implied in the above assumption, one might expect some indications of this in fishes in which only one auditory nerve had been cut. As a matter of fact, immediately after this operation fishes with only one ear intact did swim irregularly, but in from six to eight hours this tendency disappeared entirely, and the fish in its quickness, precision, and normality of response became, so far as my observations went, absolutely indistinguishable from a normal individual. Further, fishes with the fifth, seventh, and lateral-line nerves and spinal cord cut have without doubt suffered a more severe shock than those that have had only the eighth nerve cut, and yet the pectoral-fin reactions of the former were essentially normal. It therefore seems to me that the great reduction in the number of pectoral-fin reactions of earless fishes is due to the loss of the ear as a sense organ and not to secondary complications accompanying the operation.

Although some of the observations recorded on the preceding pages make it certain that in these fishes the ears are stimulated by disturbances such as those set up in the water by the sounding apparatus, it may still fairly be asked whether these disturbances are in the nature of sounds. When the bass-viol string attached to the aquarium was plucked, a series of sound waves of diminishing intensities was delivered to the water. To ascertain something of the nature of this sound I immersed my head in the water of the aquarium and had an assistant pluck the string in the usual way. The sound that I thus heard was, so far as I could judge, of nearly the same pitch as that which the string gave to the air and of only slightly greater intensity. This sound certainly reached the fishes.

The sounding apparatus, however, did more than give rise to this sound. When the string was plucked two things besides the production of sound certainly happened: First, the whole aquarium, including its supporting table, trembled slightly, and, probably as a consequence of this, ripples started from the ends and sides of the aquarium and proceeded toward the center. These ripples, though chiefly surface effects, indicated a wave motion that penetrated the water to some extent, and that was doubtless the cause of the very slight swaying movement of the fish cage occasionally noticed after the string had been vigorously plucked. Moreover, a distinct tremor could be felt in the water when the hand was held 5 to 8 cm. (2 to 3 inches) from the sounding-board and the string was plucked. The question naturally arose whether the fishes did not respond to the movement of the aquarium as a whole or to the wave movement indicated by the ripples rather than to the true sound waves.

To answer this question, at least so far as the ripple movement was concerned, I was led to study the reaction time of the fishes. Unfortunately circumstances prevented me from reducing this to a very accurate process; but, by listening to the beat of a chronometer and at the same time watching the fish, I am confident that the fin reactions occurred in less than 0.2 second after the string had been plucked. The sound waves and ripples mentioned above traveled from the sounding-board toward the fish at very different rates. The sound waves must have passed over the 25 cm. of water between the sounding-board and the fish almost instantly. The surface ripple traveled much less rapidly and its rate could be easily measured. This proved to be a meter (39⅜ inches) in 4.8 seconds; hence, to traverse 25 cm. (10 inches) the ripple required about 1.2 seconds. Since the fishes responded in less than 0.2 second, they must have reacted to something other than the disturbance indicated by the ripples.

Having eliminated the ripples as the initial stimulus for the fishes, it remained to be shown whether this stimulus was the movement of the whole aquarium or the sound waves proper. I succeeded in doing this by substituting an electric tuning-fork for the bass-viol string. The tuning-fork was placed so that its base was within about a millimeter ($\frac{1}{25}$ inch) of the sounding-board. The iron frame holding the fork rested on supports made of rubber bottle-stoppers. These flexible supports allowed the fork to be moved enough to bring its base into contact with the sounding-board without moving the supports over the surface on which they rested. As this could be done without any initial jar, it was possible to communicate to the water in the aquarium a sound of uniform intensity and pitch without moving the aquarium as a whole and also without producing any ripple. The fork, moreover, produced a tone much purer than that obtained from the string. It had a pitch of 128 vibrations per second.

Earless fishes, when subjected to sound waves from the tuning-fork, showed nothing that I could identify as a reaction. Normal fishes and fishes with normal ears but insensitive skins very usually reacted by pectoral-fin movements. The occasional failure to respond was attributed by me to the faintness of the vibrations, for the most intense sound obtained from the fork was much less than that produced by the bass-viol string. That the fishes, however, always did react, even to this relatively faint tone, was pointed out to me by my friend Dr. F. S. Lee, who while watching one of the experiments thought he detected an increase in the respiratory rate even when no pectoral-fin reaction occurred. Subsequent study showed this to be entirely correct, for, irrespective of pectoral-fin responses, at each sounding from the tuning-fork an increase of the respiratory rate did take place for a very short period. There is, then, no question but that these fishes respond to sound waves, and, since this response is through the ear, I conclude that *Fundulus heteroclitus* may be said to hear. Since I never succeeded in getting reactions of any kind to the tuning-fork from earless fishes with skins and lateral lines intact, I have no reason for believing that these parts are stimulated by true sound waves, and I attribute the responses that earless fishes occasionally showed to the vibrating bass-viol string not to the action of its sound waves on the skin or the lateral-line organs, but, as will be shown later, to the influence of the accompanying movement of the whole aquarium and its contained water on these parts.

Although the experiments already described remove every reasonable doubt from my mind as to the ability of these fishes to hear, the objection may still be raised that the conditions under which they were carried out were so artificial that they may be said to have almost no bearing on the ordinary habits of *Fundulus*, and it must be admitted that the relatively small volume of water in the aquarium and the character of its walls as reflecting surfaces for sound, may possibly have introduced factors to which the fishes, in their natural surroundings, were not accustomed. To ascertain how much weight should be given to this objection the following experiment was tried. The sounding apparatus, consisting of the sounding-board and the bass-viol string, was taken from the aquarium and set up in the open water of the outer pool at the Fish Commission wharf. The fish cage was hung at a distance of 50 centimeters (20 inches) from the sounding-board and toward the center of the pool, which is about 100 feet wide. The sound, therefore, was as unrestricted as that which naturally reaches these fishes. On experimenting with normal fishes, fishes without ears, and those with insensitive skins, results were obtained essentially like those observed in the aquarium, and I therefore concluded that the restriction of the water in the aquarium played no essential part in the results obtained from that apparatus. There is, thus, good reason to believe that *Fundulus heteroclitus* not only hears, but that for it hearing is a normal process.

Having determined that hearing was one of the normal functions of the ears in *Fundulus*, I had hoped to be able to ascertain by experiment the particular part of the ear, if such there be, that was concerned with this sense. The internal ear in *Fundulus heteroclitus* is like that in most teleosts. It consists of the usual three semicircular canals and a large sacculus, at whose posterior end a well-developed lagena is present. The sacculus is a thin-walled chamber, vertically flattened and containing a thin, flat otolith of considerable size. Sometimes this otolith is represented by two pieces—a small one at the anterior end of the sacculus and a much larger one occupying the more central part of this chamber. The lagena, which is well separated from the sacculus, also contains an otolith. On the median face of the sacculus is an extensive macula acustica sacculi, formed by the termination of the major part of the eighth nerve. There is also a well-developed papilla acustica lagenæ, as well as the usual three cristæ acusticæ ampullarum. I am unable to state whether other sensory patches, such as the macula acustica neglecta, occur here or not.

Having made a preliminary study of the anatomy of the internal ear, I had hoped to be able to cut in different individuals different branches of the eighth nerve, and, by further experimentation on fishes thus prepared, to determine the functions of the several sense organs of the internal ear. After numerous unsuccessful attempts I was at last obliged to abandon this plan because of the small size of the branches and their somewhat intricate relations, and I am, therefore, in possession of no observations that show which part or parts of the internal ear are concerned in hearing.

THE LATERAL-LINE ORGANS AND THE SKIN.

Introductory.—The lateral-line canals were regarded by most of the earlier investigators as glands for the production of the mucus so characteristic of the skins of fishes. About the middle of the last century Leydig (1850, p. 171) discovered the numerous sense organs contained in these canals, and declared that the whole system represented a sensory apparatus peculiar to fishes. Subsequently Leydig (1868, p. 2) expressed the opinion that these organs implied the possession of a sixth sense, one in addition to the five usually attributed to vertebrates, though he admitted that this sense was probably closely related to touch. Two years later the lateral-line organs were investigated by Schulze (1870), who demonstrated that true lateral-line organs were found only in the water-inhabiting vertebrates. From a study of their structure Schulze (1870, p. 86) was led to the belief that they were stimulated by the mass movement of the water, as when a current passes over the surface of a fish or when the fish swims through the water. He further believed that they were stimulated by sound waves whose length was greater than that of waves to which the ear was adapted. In this respect they were organs somewhat intermediate in character between those of touch and of hearing. These opinions were opposed by Merkel (1880, p. 54), who pointed out the inaccessibility of the organs to moving water in many cases, and who regarded them merely as organs of touch. The opposite extreme was taken by P. and F. Sarasin (1887–1890, p. 54), who designated them accessory ears, a view suggested some years previously by Emery (1880, p. 48).

The opinions thus far given were based for the most part on an interpretation of the anatomy of the lateral-line organs, and not upon any positive experimental evidence as to the function of these parts. Fuchs (1895, p. 467) seems to have been the first to attempt work in this direction. His experiments were made chiefly on the torpedo, a fish in which, in addition to the lateral line proper, two other sets or organs, the vesicles of Savi and the ampullæ of Lorenzini, may be regarded as parts of the lateral-line system. In an active torpedo Fuchs cut the nerves connected with these two special sets of organs without, however, being able to detect any significant change in the subsequent movements of the fish. He then exposed the nerve innervating the vesicles of Savi, and having placed it in connection with the appropriate electrical apparatus, he found that on pressing lightly upon the vesicles a negative variation in the current from the nerve could be detected. As this negative variation is evidence of the momentarily active condition of the nerve, it follows that pressure differences may be assumed to be a means of stimulating the vesicles of Savi. No such results were obtained from the nerves distributed to the ampullæ of Lorenzini, but the nerves from the unmodified lateral-line organs in *Raja clavata* and *R. asterias* showed negative variations when their terminal organs were subjected to pressure. Dilute acids and changes of temperature were not stimuli for any of the terminal organs tested, and Fuchs (1895, p. 474) concluded that pressure was the normal stimulus in the skate for the lateral-line organs, and in the torpedo for the vesicles of Savi, but not for the ampullæ of Lorenzini.

Apparently without knowledge of the work done by Fuchs, Richard (1896, p. 131) performed some experiments on the gold-fish. These consisted in the removal of the scales from the lateral line and the destruction of the sense organs under these scales by cauterizing with heat, silver nitrate, or potassic hydrate. After this operation some of the fishes were unable to keep below the surface of the water, and though they soon died, Richard (1896, p. 133) believed that he had evidence enough to show that the lateral-line organs were connected with the production of gas in the hydrostatic apparatus.

Richard's conclusions were called in question by Bonnier (1896, p. 917), who pointed out the severity of the operations employed by the former and intimated that the results were more probably dependent upon the excessive amount of tissue removed than upon the destruction of the lateral line. Bonnier (1896, p. 918) further recorded experiments of his own in which the lateral-line organs were destroyed by electro-cautery. Fishes thus operated upon showed two characteristics—they could easily be approached by the hand and even seized, and they failed to orient themselves in reference to disturbances caused by bodies thrown into the water. Bonnier concluded from his experiments that the lateral line, in addition to other functions, had to do with the orientation of fishes in reference to centers in the water from which shock-like vibrations might proceed.

Lee (1898, p. 139), whose experimental methods were much the same as those used by Bonnier, obtained some significant results, particularly with the toad-fish, *Batrachus tau*. When the pectoral and pelvic fins of this fish were removed, so that the animal might be said to be without its usual mechanical support, and the lateral-line organs were destroyed by thermo-cautery, the animal would lie quietly for some time, either on its side or back, and acted as though it had lost its "sense of equilibration." That its condition was not due to excessive injury was seen from the fact that a finless fish in which an equal amount of skin had been cauterized, but in which the lateral-line organs were intact, showed no lack of equilibration, and in its general behavior closely resembled a normal fish. Moreover, stimulation of the central end of the lateral-line nerve resulted in perfectly coordinated fin movements, and Lee (1898, p. 144) therefore concluded that the organs of the lateral line are equilibrating organs. How these are stimulated Lee does not attempt to decide, though he suggests (1898, p. 143) that pressure changes in the surrounding medium may be the means of stimulation.

From this brief historical résumé it must be evident that there is still very little unity of opinion as to the functions of the lateral-line organs.

The lateral line in Fundulus heteroclitus.—The lateral-line system in *F. heteroclitus* presents a condition typical for teleosts. Its sense organs are contained in canals that open by pores on the surface of tho skin. A lateral-line canal as indicated by its pores (pl. 9, fig. 5) extends along the side of the trunk from near the tail forward to the head. Here the arrangement of the pores (figs. 4, 5) gives evidence of a mandibular, a suborbital, a supraorbital, and an occipital branch. By cutting the fifth and the seventh nerves behind the eye (fig. 4), and the lateral-line nerve near the pectoral girdle (fig. 5), the innervation of this whole system, except a small tract above the gills, can be rendered inoperative; the sense organs in the small tract can be easily excised. Fishes that have undergone this operation recover almost invariably and in a very short time; the integument of their heads is insensitive owing to the necessity of cutting the fifth as well as the seventh nerves; but that of their trunks, which is of course innervated from spinal sources, retains its normal sensitiveness, except so far as the lateral-line organs are concerned. In seeking for evidence as to the function of the lateral-line organs, I compared carefully the reactions of normal fishes with those in which the nerves of the lateral-line organs had been cut.

When a normal fish is liberated in an aquarium, it swims at once to the bottom. Here it may move about excitedly for some minutes, after which it usually begins to make upward excursions. At first it will swim only part way to the top, returning each time quickly to the bottom. Eventually it may make several quick excursions to the upper surface of the water, and ultimately may remain there playing about close to the top. If now any disturbance is made the fish will again swim at once to the bottom, and only after some time will it return to the top, in the same cautious way as before. Almost any disturbance seems to drive the fish to the bottom—a flash of light on the water, a quick but noiseless movement of the observer, or an unseen blow on the aquarium, conditions all of which suggest that the movements of the fish are of a protective nature.

To one form of disturbance the fishes were particularly sensitive, and this was the slight movement of the whole aquarium that occurred whenever the bass-viol string was plucked. This movement could be produced without the accompanying sound by giving a slight vibratory motion to the beam attached to the sounding-board on the aquarium (fig. 2). It was remarkable how accurately the fishes responded to this stimulus. If the fish was playing at the top of the water, the slightest movement of the aquarium as a whole would cause it to descend immediately to the bottom; if it was on its upward course, it could be checked and made to descend at any point; and if it was near the bottom, it could be kept there as long as the movement continued. In all of the several hundred trials of this kind that I made, I never found a normal fish that would remain high in the water or swim upward while such movements were being imparted to the aquarium. Whenever the fish was above the bottom, the response was an instantaneous downward course.

With fishes in which the nerves to the lateral-line organs had been cut, the reactions were totally different. Such fishes, when left to themselves in an aquarium, were scarcely distinguishable from normal ones. As with the toad-fishes observed by Lee (1898, p. 140), the loss of the lateral-line organs seemed to interfere in no essential respects with the movements of the animals; they were active and quick, returned at once to a normal position when displaced, and oriented with accuracy, so far as I could see, in that they at once swam away from such centers of disturbance as come from dropping a stone in the water. In this last particular they were very unlike the fishes reported on by Bonnier (1896, p. 918). In one important point they differed absolutely from the normal fishes; they would swim upward and remain near the top during even a considerable agitation of the whole aquarium, though they would dart downward at any sudden movement on the part of the observer. Hence these fishes must have lost their capacity to be stimulated by the mass movement of the water, and since this defect was observed only after the lateral-line organs had been rendered inoperative, I concluded that the normal stimulus for these organs was a very slight mass movement of the surrounding water. Since such movements always accompanied the sound produced by the bass-viol string, it follows that the disturbances set up by this string must have acted as a stimulus for the lateral-line organs as well as for the ears, and it is therefore not surprising that earless fishes sometimes reacted when the string was plucked.

If the lateral-line organs are stimulated by a slight mass movement of the water, it occurred to me that I ought to be able to separate, in a mixed school of fishes, those with lateral-line organs intact from those in which the nerves to the organs had been cut, by simply imparting a slight mass movement to the water. Under such conditions the normal fishes ought to swim to the bottom, leaving the defective ones above; but on trying the experiment I found that the fishes were so accustomed to form a school that when the normal ones started for the bottom the others did the same, and I was entirely unable by this means to separate the normal from the defective individuals. But I finally succeeded in doing this by modifying the experiment, in that I used only two individuals, one normal and one defective, and agitated the aquarium only when they were widely separated. The result was very decisive in that the normal one invariably took the initiative in descending, and in fact was often not followed by its defective companion.

Having found the conditions under which the lateral-line organs were stimulated, it is natural to inquire as to the exact nature of the stimulus. Ordinarily the fishes were induced to react by making the whole aquarium swing at about ten vibrations per second; but a like reaction was obtained from the normal fishes when a single swing, or what was as near as possible a single swing, was given to the aquarium. The stimulus therefore is not necessarily of a vibratory kind, but consists in a slight movement of the body of water as a whole. It might be supposed that since the fish was suspended in the water, the motion of the aquarium as a whole could have no influence on it. But it must be remembered that the fish was somewhat heavier than the water, and that each time the aquarium was moved the fish, from its inertia, must have lagged a little behind or, once set in motion, moved a little ahead, and it is this slight difference in the rate of movement of the fish and of the adjacent water that, in my opinion, induces stimulation. I am not prepared to say how this affects the sense organs in the lateral-line canals; but it is not impossible, as Schulze (1870, p. 85) suggested, that slight currents are thereby set up that move and thus stimulate the bristle cells of the lateral-line organs.

The extreme sensitiveness of animals to slight motions of this kind has already been pointed out by Whitman (1899, pp. 287 and 302) in the leech and salamander, and I suspect that the sensitiveness of the blind fish, as observed by Eigenmann and quoted by Whitman (1899, p. 303), may also be in the nature of a lateral-line response.

Having reached the conclusion that the downward swimming of the fishes could be brought about by stimulating the lateral-line organs through slight mass-movements of the water, I next attempted to ascertain the relative importance of different parts of the lateral-line system in this reaction. I prepared one set of the fishes in which the lateral-line nerves were cut close to the pectoral girdles, thus rendering ineffective the lateral-line organs of the trunk while those of the head were left intact. These individuals responded in all respects, so far as I could see, as normal fishes did, and I therefore concluded that the lateral line proper was not an essential part of this system of sense organs.

In the second set of fishes I cut the fifth and seventh nerves of both sides, thus preventing the lateral-line organs of the head from acting. These animals always descended when the aquarium was shaken, but with noticeably less precision than in the cases of normal individuals. It therefore seemed probable to me that the portion of the lateral-line system on the head was more effective than that on the trunk, but as this experiment involved cutting the general cutaneous nerves of the head as well as the lateral-line nerves, the experiment is not wholly conclusive.

Finally, in a third set of fishes, I cut the lateral-line nerves and the fifth and seventh nerves of the right sides only, leaving the left sides intact. These fishes, though a little sluggish, reacted in an essentially normal way. From these three sets of experiments I conclude that the lateral-line organs may be considerably reduced without seriously impairing the action of the system as a whole, though the portion of the system on the head is less easily dispensed with than that on the trunk.

The skin in Fundulus heteroclitus.—While I was experimenting on fishes in which the lateral-line organs had been rendered inoperative I was at times puzzled by getting reactions that seemed contradictory to the general conclusion that such fishes were not stimulated by a slight movement of the whole mass of water. Occasionally on making the whole aquarium move slightly a fish without lateral-line organs would swim rapidly to the bottom. On watching for instances of this kind I soon found that they occurred only when the fishes were close to the top of the water, and in fact were within the range of wave action. When the whole aquarium was moved, even only slightly, the upper surface of the water was thrown into small waves. These waves, as could be seen by the motion of small suspended particles, extended only a few centimeters below the surface of the water, but they established a region into which the fishes without lateral-line organs would not ascend, and from which, if overtaken by the waves there, they immediately escaped by swimming downward. As fishes without ears as well as without lateral-line organs were stimulated by these surface waves, I concluded that in this instance the motion of the water must affect the general cutaneous nerves (touch).

If the motion of surface waves is a stimulus for the general cutaneous nerves, it would seem probable that currents in the water would also affect these nerves and that the ability of a fish to head up a stream might depend rather on the stimulation of its skin than, as Schulze has implied, on the stimulation of its lateral-line organs. *Fundulus* is in a marked degree rheotactic, i. e., it swims vigorously against a current, and I therefore resolved to test this fish to ascertain whether its rheotaxis depended on its lateral-line organs or not. Six specimens, in which the nerves to the lateral-line organs had been cut, were placed one after another at the open end of a large glass tube through which a moderately strong current of sea water was flowing. All swam energetically up the tube, and, so far as this reaction was concerned, they were in no observable respect to be distinguished from normal fishes. Their rheotaxis certainly did not depend upon their lateral-line organs, but was undoubtedly the result of cutaneous stimulation. Unfortunately I was unable so to operate on other individuals that I could obtain active specimens whose cutaneous nerves were severed but whose lateral-line systems were intact, and hence the only conclusion I can draw is that the general cutaneous nerves are stimulated by wave and current action and that this is sufficient to account for rheotaxis, but I can not state whether or not the lateral-line organs are also stimulated by these means.

Conclusions concerning the lateral-line organs and the skin.—The observations on *Fundulus* recorded in the preceding pages give no support to the view of P. and F. Sarasin that the lateral-line organs are to be regarded as accessory ears, for individuals in which the eighth nerves had been cut and in which the lateral-line organs were intact did not respond to the sound-waves from a tuning-fork to which fishes with ears reacted with certainty. I have also seen no reason to suppose that the lateral-line organs are especially connected with the production of gas in the air-bladder, as suggested by Richard, or that they are particularly concerned with equilibration, as advocated by Lee. Since they are stimulated by slight disturbances in the water that do not affect the general cutaneous sense organs, I can not agree with Merkel in classing them as tactile organs. Their appropriate stimulus is a slight mass-movement of the water, which may or may not be vibratory, and which induces the fish to swim into deeper regions. This form of stimulus is of precisely the kind that was attributed to these organs by Schulze (1870), but I have not been able to confirm Schulze's further opinion that current and surface wave movements stimulate these parts. Such stimuli certainly do affect the general cutaneous sense organs, but whether or not they influence the lateral-line organs I am unable to say.

GENERAL REACTIONS OF OTHER FISHES.

Although my studies were made almost exclusively on *Fundulus heteroclitus*, I tested, as opportunities offered, other species of common fishes. These were placed without being operated upon in the aquarium with the bass-viol string as a means of producing sound. Because of the mixed character of the stimulus produced by this apparatus and also because of the fact that the fishes were not operated upon in any way, the results are significant in only one or two instances.

Young mackerel, while swimming in the aquarium, always moved downward when the string was vibrated. The same was found true of adult mackerel, but whether this reaction was an ear or a lateral-line response was not determined.

Menhaden, after they became somewhat accustomed to the aquarium, gave a sudden leap each time the string vibrated, but showed no tendency to descend. In this instance, too, no clew was obtained as to the organs stimulated.

Three specimens of smooth dog-fish, each about 18 inches long, were tested. When these fish were resting quietly on the stone bottom of the aquarium, the vibration of the string would cause them to move their pectoral and pelvic fins, or even begin swimming, but when they rested on some 3 inches of cotton wool covered with a cloth to afford a deadened surface on the bottom of the aquarium, no reaction of any kind was ever obtained. Apparently the ears, lateral-line organs, and skins of these fishes are not open to any of the stimuli produced by the vibrations of the bass-viol string and transmitted through the water, and they thus differ markedly from the other fishes examined.

These few notes serve to show that different species respond very differently to the same forms of stimuli and emphasize the importance of refraining from generalizations on the functions of the lateral-line organs and the ears in fishes before a considerable number of species have been fully examined.

SUMMARY.

1. Normal *Fundulus heteroclitus* reacts to the sound waves from a tuning-fork of 128 vibrations per second by movements of the pectoral fins and by an increase in the respiratory rate. It probably also responds to sound waves by caudal-fin movements and by general locomotor movements.

2. Individuals in which the eighth (auditory) nerves have been cut do not respond to sound waves from the tuning-fork.

3. The absence of responses to sound waves in individuals with severed eighth nerves is not due to the shock of the operation or to other secondary causes, but to the loss of the ear as a sense organ.

4. *Fundulus heteroclitus* therefore possesses the sense of hearing.

5. The ears in this species are also organs of prime importance in equilibration.

6. Normal *Fundulus heteroclitus* swims downward from the top of the water and remains near the bottom when the aquarium in which it is contained is given a slight noiseless motion.

7. Individuals in which the nerves to the lateral-line organs have been cut will swim upward or remain at the top while the aquarium is being gently and noiselessly moved.

8. The lateral-line organs in this species are probably stimulated by a slight mass movement of the water against them. They are not stimulated by sound waves such as stimulate the ears.

9. Individuals in which the nerves to the lateral-line organs have been cut swim downward and thus escape from regions of surface wave action. They also orient perfectly in swimming against a current. Since surface waves and current action stimulate fishes in which the nerves to the lateral-line organs and to the ears have been cut, these motions must stimulate the general cutaneous nerves (touch).

10. The vibrations from a bass-viol string when transmitted to water stimulate the ears and the lateral-line organs of *Fundulus*. They also stimulate mackerel and menhaden, but not the smooth dog-fish, which responds only when in contact with solid portions of an aquarium subjected to vibrations.

The work recorded on the preceding pages was done at the biological laboratory of the United States Fish Commission at Woods Hole, Mass., and I take this opportunity of expressing my indebtedness to the Director, Dr. Hugh M. Smith, and to his assistants for much help rendered me. I am also under obligations to Prof. W. C. Sabine, of Harvard University, for advice and assistance in connection with the sound-producing apparatus, and to Prof. F. S. Lee, of Columbia University, for friendly criticism and many suggestions.

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