CONTRIBUTIONS FROM THE BIOLOGICAL LABORATORY OF THE BUREAU OF FISHERIES
AT WOODS HOLE, MASS.

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INTRODUCTION.

The habits of fishes, like those of most other animals, are inseparably connected with their sense organs. Thus in the matter of feeding, Bateson (1890) has pointed out that probably the majority of fishes seek their food by sight. Many such fishes when kept in confinement are known not to feed at night or even in twilight, though they may be ravenous feeders in daylight. Other fishes, including the eels, skates, sturgeons, suckers, flat-fishes, etc., many of which are bottom fishes and often nocturnal in their habits, seem not to depend upon sight in seeking their food. Their powers of sight are often deficient, and food excites them chiefly through its action on their organs of taste, smell, or touch. As Bateson observed, none of these fishes start in quest of food when it is first put into their tanks, but remain undisturbed for an interval, doubtless until the scent has been diffused through the water. Then they begin to swim vaguely about, and appear to seek the food by examining the whole area pervaded by the scent. The search is always made in this tentative way, whether the food is hidden or within sight, and it is first seized when by accident it is come upon.

Herrick (1903c) has made the interesting discovery that in the cat-fish, which seeks its food in the way just described, the organs of taste pervade the whole skin, and the fish will seize unseen food with great precision, provided only that it is brought near the skin. Thus in this fish the organs of taste largely replace the eye as a means of discovering the food.

From these examples it must be clear how close is the relation between sense organs and habits. The sense organs, in fact, are the usual means of initiating those simple acts which, when taken collectively, constitute what are popularly known as habits, for the sense organs are the avenues through which the external influences enter the animal and excite it to action. How essential, then, in studying the habits of any group of animals, must be a knowledge of their sense organs.

From this standpoint the elucidation of the habits of fish is particularly important, for their sense organs bear close comparison with those of human beings, and their environment withal is so different that they afford a most fascinating field for investigation. It is now fairly well established that many fishes possess in a high functional state the five chief senses of man—taste, smell, touch, hearing, and sight; but it is also known that many fishes possess a sixth set of organs, the lateral-line organs, for which there is no representative in man. As these are well-developed and conspicuous structures in many cases, they may be suspected of playing an important part in the economy of these animals, and it is the purpose of this investigation to ascertain something of their rôle in the ordinary habits of some of our fishes.

HISTORICAL REVIEW.

Every one who is at all conversant with the external markings of fishes is familiar with a line which, in most instances, extends along the side from tail to head. This line, known from its position as the lateral line, consists usually of a row of small pores which lead into an underlying canal, the lateral-line canal. In the head of the fish this canal usually branches into three main stems, one of which passes forward and above the eye, another forward and immediately below the eye, and a third downward and over the lower jaw. These three canals, like the lateral-line canal, open on the surface by numerous pores, and, together with this canal, constitute the lateral-line system.

According to Leydig (1868, p. 3) the pores of these canals were recognized over two centuries ago by Stenon (1664) and by Lorenzini (1678) in elasmobranchs, and by Rivinus (1687) in fresh-water fishes. Subsequently the canals were described by many of the earlier anatomists, particularly by Monro (1785), and an excellent summarized account of them was given by Stannius (1846, p. 49) in his comparative anatomy of the vertebrates. Thus before the middle of the last century the gross anatomy of these organs had come to be fairly well recognized.

All the earlier investigators, so far as their opinions are known to me, seem to have regarded the lateral-line system as a system of glands for the production of the mucus so characteristic of the skins of many fishes. Suggestions contrary to this, however, came from two sources. First, observations on elasmobranchs had shown that this group possesses, in addition to the lateral-line system proper, a set of closely related organs, the ampullæ of Lorenzini. Jacobson (1813) studied the structures of these organs with the view of determining what their probable function was, and concluded from their extensive nerve supply that they were certainly sense organs and probably stimulated mechanically, like delicate organs of touch. Treviranus (1820, p. 146), concurred in Jacobson's opinion that the ampullæ were sense organs, and believed that they probably represented a sense quite distinct from any that we possess. Knox (1825, p. 15) in reviewing the whole subject made the interesting statement that "we can not * * * greatly err in considering these organs as organs of touch, so modified, however, as to hold an intermediate place between the sensations of touch and hearing." Finally, Savi (1841) suggested that in the torpedo they might be organs for the reception of electrical stimuli.

A second body of evidence that suggested the nonsecretory nature of the lateral-line system came from investigations on the vesicles of Savi. These are closed, sac-like organs found in clusters in the anterior part of the head of the torpedo. Like the ampullæ of Lorenzini, they are undoubtedly closely related to the lateral-line system. They were originally described by Savi (1841) as nervous organs, and a sensory function was claimed for them by Wagner (1847). This opinion was subsequently supported by Schultze's discovery (1863, p. 11) that the epithelium of these organs contained an abundance of sense cells. Thus the sensory nature of the vesicles of Savi and of the ampullæ of Lorenzini was clearly in the minds of several of the earlier investigators at a time when the nearly related lateral-line system was regarded as a purely secretory mechanism.

In April, 1850, Leydig (1850a) gave a preliminary account of certain large sense organs found by him in the lateral-line canals on the head of the ruffe (*Acerina cernua*), and later in the same year he (Leydig, 1850b) figured and described these organs in detail not only in the ruffe, but in several other species of fresh-water fishes. Since he could find no reason to suppose that the slime on the surface of these fishes was produced in the lateral-line canals, and since these canals contained large sense organs, he concluded that the lateral-line system was not a set of glands, but a system of sense organs which he believed to be peculiar to fishes (Leydig, 1850b, p. 171). Shortly after this, similar organs were found by Leydig (1851) in certain marine teleosts and by Müller (1852, p. 149) in elasmobranchs; and a few years later Leydig (1857, p. 196) gave in his text-book of histology, an excellent summary of the finer anatomy of these and other closely related structures. Here he briefly discussed the function of the lateral-line organs, and expressed the belief that if they must be placed under one of the five senses as usually defined, they certainly belonged under touch, but in his opinion they were very probably representatives of a new sense especially adapted for life in the water.

A few years later Schulze (1861) showed that on the skin of very young fishes there were sense organs essentially like those described by Leydig from the lateral-line canals of mature fishes. These were so distributed as to foreshadow the lateral-line canals, and they undoubtedly represented the organs which were later to occupy these canals. Schulze further demonstrated a similar system of superficial organs in the water-inhabiting stages of amphibians, and thus showed that these organs occurred in other vertebrates than the fishes, a conclusion subsequently confirmed by Leydig (1868), who, though still holding that the lateral-line organs were closely allied to the organs of touch, regarded them as sufficiently distinct to constitute a sixth class of sense organs. Leydig also suggested the possibility that these organs might be represented in other groups of the animal kingdom than the fishes and amphibians, and went so far as to intimate that certain glandular structures in the skin of the air-inhabiting vertebrates might have been derived from them.

In a second paper Schulze (1870, p. 83) pointed out the inaccuracy of this opinion and maintained that the lateral-line organs were strictly limited to fishes and the water-inhabiting stages of amphibians. He also called attention to the important and striking similarity between the sense cells in the lateral-line organs and those in the ear as described by Schultze and by Hasse, a comparison already made by Leydig (1850b, p. 180), and he concluded that the lateral-line organs were stimulated either by mass movements of the water, as when a fish swims through this medium or a current impinges on its body, or by water vibrations whose period is longer than that of the vibrations which stimulate the ear. Notwithstanding this supposed relation to the ear, Schulze agreed with Leydig in regarding the lateral-line organs as organs of touch, though specially modified to meet the requirements of an organism living in the water.

About ten years after the appearance of Schulze's second paper, Dercum (1880, p. 154) called attention to the fact that in many fishes the lateral-line canals were almost if not entirely closed, and that in consequence water could not flow through them, as was supposed by Schulze. Dercum, however, pointed out that since many of the canals were separated from the outer water by only a layer of thin skin applied to the membrane of the canal wall, the system might be said to possess numerous drumheads through which vibrations in the surrounding water could be transmitted to the fluid within the canal, and thus these vibrations could become effective in stimulating the lateral-line organs. Dercum also suggested that the effect of the vibrations might be the more intense the more nearly perpendicular they were to the surface of the canal on which they fell, and in this way it was conceivable that a fish might orient itself in reference to the direction of the vibrations.

These views were in large part accepted by Emery (1880, p. 48), who emphasized the comparison between the lateral-line organs and the internal ear, and thus lead to the opinion subsequently expressed by Mayser (1881, p. 311), Bodenstein (1882, p. 137), and P. and F. Sarasin (1887–1890, p. 54), that the lateral-line organs were accessory ears.

Meanwhile Merkel (1880, p. 55), without knowledge of the contributions made by Dercum and by Emery, showed that it was unlikely that water could be said ever to stream through the canals, and yet he gave very good reasons for supposing that the lateral-line organs were adapted to a mechanical stimulus. From his standpoint there was insufficient ground to consider the lateral-line organs as constituting a sixth group of sense organs, and he was convinced that they were merely tactile-organs somewhat modified for aquatic life.

The opinions thus far presented as to the functions of the lateral-line organs are in no instance based upon experimentation, but upon such indirect evidence as that afforded by the structure of the sense organs and of their surrounding parts.

Previous to the appearance of Fuchs's paper in 1894 very few investigators had made experiments on the lateral-line organs, and such experiments as had been undertaken were of a very simple and tentative character. The earliest of these was the work of Bugnion (1873, p. 302), who showed that a living *Proteus* was not especially sensitive to solutions of alum, salt, or weak acid applied to the lateral-line organs, but that it reacted vigorously when these organs were touched with a needle. Later de Sède (1884, p. 469) reported that fishes in which the lateral line had been cut were less successful in guiding themselves in an aquarium containing numerous obstacles than were normal fish, and he stated that in his opinion the lateral-line organs did not represent a sixth sense but were organs of touch especially concerned with directing the animals. Bateson, some years later (1890, p. 237), stated that he had been unable to get responses from fishes when food substances were tried as stimuli for the lateral-line organs, and lastly, Nagel (1894, p. 191) found no evidence that the lateral-line organs of fishes and amphibians were stimulated chemically; when the lateral-line nerves in *Barbus fluviatilis* were cut on both sides the fish apparently remained normal, but when in certain fish (Schuppfisch) the nerve of only one side was cut, a slight lack of orientation and of muscle coördination could sometimes be observed. These seem to be the only noteworthy experiments on the lateral-line organs that were carried out before the time of Fuchs's work.

Fuchs (1894, p. 467) experimented chiefly on the torpedo, a fish which possesses, in addition to the lateral-line organs proper, the vesicles of Savi and the ampullæ of Lorenzini. Fuchs cut the nerves connected with these two special sets of organs, but without being able to detect any significant change in the subsequent movements of the fish. He then exposed the nerve supplying the vesicles of Savi, and, having placed it in connection with an appropriate electrical apparatus, he found that by pressing lightly on the vesicles a reduction in the current from the nerve could be demonstrated. As this reduction is believed to indicate the transmitting activity of nerves, it follows that the pressure applied to the vesicles was probably a stimulus to them and thereby brought the nerve into action. No such results were obtained from similar experiments on the ampullæ of Lorenzini, but the nerves from the lateral-line system in *Raja clavata* and *R. asterias* also gave evidence of transmission when their terminal organs were pressed. Dilute acids and heat did not stimulate the terminal organs tested, and Fuchs (1894, 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, consisting of the removal of the scales from the lateral line and the destruction of the sense organs under these scales by cauterizing with heat, 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 air bladder.

Richard's conclusions were called in question by Bonnier (1896, p. 917), who pointed out the severity of the operations employed 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 with 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, *Opsanus tau*. When the pectoral and pelvic fins of this fish were removed, so that it 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, on either its side or back, and act as though it had lost its "sense of equilibrium." 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 equilibrium, and in its general behavior closely resembled a normal fish. Moreover, Lee found that the stimulation of the central end of the lateral-line nerve of a dog-fish resulted in perfectly coordinated fin movements, and he therefore concluded that the organs of the lateral line are equilibration organs. How these are stimulated Lee did not attempt to decide, though he suggested (1898, p. 143) that pressure changes in the surrounding medium may be the means of stimulation.

Five years later, in experimenting on the sense of hearing in fishes, I made some observations on the lateral-line organs of *Fundulus* (Parker, 1903a, p. 59; 1903b, p. 197). These led to the conclusion that the lateral-line organs in this fish were stimulated by a very slight mass movement of the water, and they have afforded the point of departure for the present investigation.

In summarizing this historical review, it is clear that no one has ever brought forward the least reason to suspect that the lateral-line organs are ever normally stimulated by light, heat, or other ether disturbances. It is also very improbable that they are stimulated chemically, for in many instances the covered situation of the organs is not favorable for this form of stimulation, and the direct experiments of Bugnion (1873) on *Proteus*, of Bateson (1890), and of Nagel (1894) on several kinds of fish, and of Fuchs (1894) on *Torpedo* and *Raja* have always given negative results. On the other hand, it is almost universally admitted that the normal stimulus for these organs must be of a mechanical kind, either simple contact, as in touch, or vibratory contact, somewhat as in hearing. It is on this point that the majority of investigations disagree, some maintaining that the lateral-line organs are simply organs of touch (Merkel, de Sède), or of pressure (Fuchs), others that they are organs belonging to an independent class, probably intermediate between touch and hearing (Leydig, Schulze, Dercum, Parker), and, lastly, those that believe them to be accessory auditory organs (Emery, Mayser, Bodenstein, P. and F. Sarasin). That the lateral-line organs were necessary to successful locomotion as organs of equilibration, etc., was first suggested, I believe, by de Sède; and this opinion has received the support of Nagel, Bonnier, and especially of Lee. In attempting to decide between these various views, the first question that arises is: What is the normal stimulus for the lateral-line organs? It is the object of this investigation to find an answer to this question.

MATERIALS AND METHODS.

The experiments about to be described were carried out chiefly on the common mummichog, *Fundulus heteroclitus*, a fish of convenient size, great hardiness, and everywhere abundant in the neighborhood of the biological laboratory of the United States Bureau of Fisheries at Woods Hole, Mass., where the experiments were made. Besides this species seven others were also tested, though not with a full range of stimuli. These additional species were the smooth dog-fish, *Mustelus canis;* the common skate, *Raja erinacea;* the killi-fish, *Fundulus majalis;* the scup, *Stenotomus chrysops;* the toad-fish, *Opsanus tau;* the common flat-fish, *Pseudopleuronectes americanus;* and the swell-fish, *Chylomycterus schœpfi.*

The general method of experimenting was to cut the nerves connected with the lateral-line organs of a number of individuals of a given species, and, after the fish had recovered from the operation, to test them in comparison with normal individuals by subjecting both to a particular stimulus. In this way I expected to ascertain whether with the loss of the lateral-line organs the ability to respond to certain stimuli would disappear. To eliminate the effects of the operation as far as possible I usually tested a third series of fishes in which incisions had been made to reach the nerves, but in which the nerves themselves had not been severed.

In all the fishes, except the dog-fish and the skate, the nerves were cut by the method described in my previous paper (Parker, 1903a, p. 59), i. e., the fishes were etherized by being put for a few minutes in sea water containing a little ether, and the fifth and seventh nerves were then cut by an incision behind the eye, and the lateral-line nerve by an incision just behind the head; the few lateral-line organs between these two incisions were then extripated. In the dog-fish and the skate the operation was similar, except that the fifth and the seventh nerves were more conveniently cut from the roof of the mouth than from the exterior.

The chief objection to this method of operating lies in the fact that in cutting the root of the seventh nerve it is necessary also to cut that of the fifth, so that the tactile sensibility of much of the head, as well as the innervation of the muscles of the jaws, are almost always lost. Notwithstanding the apparent severity of the operations the fishes usually recovered, and even a few hours after the operation began feeding and acted in most respects normally. The majority lived for several weeks, and some of them for over a month. Care was exercised, however, to see that they were properly fed, for the paralyzed state of the muscles of the jaws, though not interfering much with respiration, did make it difficult for the fish to grasp food.

Normal and, as I shall call them, cut fishes were then subjected to the following range of stimuli and their reactions noted: Light, heat, salinity of water, food, oxygen, carbon dioxide, foulness of water, pressure of water, currents, stimuli to equilibrium, vibrations of high frequency (sound), and vibrations of low frequency.

EXPERIMENTS.

Light.—To ascertain whether light was a stimulus for the lateral-line organs the following device was used: An oblong glass aquarium, measuring about 60 cm. in length, 25 cm. in breadth, and 25 cm. in height, was half-covered with opaque cloth, so that one end and the adjacent halves of the top and of the sides were impervious to light. The apparatus was set up in a dark room and illuminated by a 16-candle incandescent electric light, so placed that the light fell across the uncovered half of the aquarium, but without entering the darkened half. The aquarium was filled with sea water and specimens of *Fundulus heteroclitus* were introduced to see if they would assemble in the light or in the dark. It was soon found that these fishes followed one another by sight, and the records finally taken came from experiments in which single fishes were put in the aquarium and their reactions observed. After a fish had become accustomed to its new surrounding, which happened usually in about ten or fifteen minutes, and which was indicated by the fish leaving the bottom of the aquarium and beginning to sport about near the surface of the water, observations were made at intervals of one minute as to whether the fish was in the dark or in the light. It soon appeared that a number of individuals were almost indifferent to the light, being found as commonly in one place as in the other. Others were more generally in the light, and fishes were tested until fifteen such were obtained. These fifteen were tested accurately by being placed individually in the aquarium and by having their positions determined at minute intervals for ten minutes. In 150 observations these fishes were 93 times (62 per cent) in the light.

They were then all operated upon by having the nerves to the lateral-line organs cut. Twelve recovered and were tested as in the first experiment. In 120 observations these fishes were 79 times (66 per cent) in the light. It is therefore highly improbable that the slight tendency to assemble in the light shown by some individuals of this species is in anyway dependent upon the lateral-line organs; in other words, light is not a stimulus for these organs.

Heat.—The stimulation of the lateral-line organs by heat was tested also on *Fundulus heteroclitus.* Five individuals with the nerves to the lateral-line organs cut were compared with five normal individuals by subjecting them to water of different temperatures in cylindrical glass jars 35 cm. high and 23 cm. in diameter.

The temperature of the outside water in which the fishes had been caught was at this time of year (August) about 19.5° C. When the five normal fishes were put in the glass jar filled with water at this temperature, they at once swam to the bottom, and, as is usual with them when first introduced into an aquarium, remained swimming about in the deeper water for some time. Finally, they rose to the surface and sported about in the upper water, remaining there unless frightened by some movement or other disturbance about them, whereupon they would again make a temporary descent. Cut fish acted in all respects like normal ones except, perhaps, that they were not so agile in their movements, but this slight reduction in their quickness of response was not due to the cutting of the nerves of the latteral-line system, for it was observable in fish in which the skin, but not the nerves, had been cut.

In water at 14° C., the reactions of normal and of cut fishes were indistinguishable from those in water at 19.5° C.

At 9° C., much the same was observed as at 14° C., but there was a slight though noticeably greater tendency here to keep in the deeper water than at 19.5° C. This tendency, however, was not pronounced enough to allow one to say that the fish had deserted the top; after having been frightened away from the top they returned less freely than at 14° C. or 19.5° C. In this respect, however, the normal and cut fishes agreed.

Two temperatures higher than 19.5° C. were tried. At 25.5° C. both normal and cut fishes swam down, and for the most part stayed in the deeper water. Now and then an individual would swim to the top, but it almost always quickly returned to the bottom. In these respects normal and cut fishes were indistinguishable.

At 30.5° C., both normal and cut fishes swam to the bottom of the vessel and stayed there persistently. In the course of fifteen minutes not a single fish came to the surface, whereas at 19.5° C. all fishes returned to the surface usually in three to four minutes. Moreover, the fishes continually nosed about on the bottom of the jar as though they were seeking still deeper water.

Since in all these temperature experiments the normal fish and the cut ones reacted in essentially the same way, I conclude that heat is not a stimulus for the lateral-line organs. This is in agreement with Fuchs's results (1894, p. 473) on the vesicles of Savi which were stimulated by pressure but not by heat.

The reactions of *Fundulus* to heat, though of negative value so far as the purposes of this paper are concerned, have an interesting biological bearing. It appears from the experiments given that at a temperature of 19.5° C. (corresponding to that of the outside water from which the animals had been taken), or at lower temperatures down to 9° C., the fish remain, when otherwise undisturbed, near the top of the water; but at temperatures above 19.5° C., particularly about 30° C., they seek the deeper water and remain there. In other words, they are negatively geotropic in the cooler water (9° to 19.5° C.), and become positively geotropic in the warmer water (25.5° C. to 30.5° C.), the increase of temperature causing a reversal of the sense of geotropism. This change is just the opposite of that recently pointed out by Torelle (1903, p. 475) for the frog. This animal remains near the surface of the water at high temperatures, and goes to the bottom at low temperatures, the turning point being at about 10° C. Probably these reactions, though reversed in the two instances, are not without significance for these two species. The frog may be thus protected from severe cold and the mummichog from overheated surface water.

Salinity.—Near the shore, and particularly near the mouths of rivers, the salinity of the sea water is subject to much variation, and it is not impossible that differences in this respect might be responded to by fishes through their lateral-line organs. Tests in this direction were made upon *Fundulus heteroclitus* by subjecting normal and cut individuals to the action of sea water variously diluted or concentrated. The sea water at the end of the government wharf at the Woods Hole laboratory is well mixed by the tides, and has the usual specific gravity of about 1.025. Water taken from this source was diluted with tap water to decrease the salinity, or concentrated by boiling to increase it. Care was taken after the boiled water had been cooled to aerate it thoroughly before it was used in experiments.

Normal and cut fishes were placed first in glass jars containing ordinary sea water and then in jars containing the diluted sea water. The fishes showed no characteristic reactions to mixtures containing 90 per cent, 80 per cent, 70 per cent, or 60 per cent of sea water. In the mixture containing half sea water and half fresh water a decided reaction was obtained in that the fishes swam about in an excited way, often with darting movements, and were as frequently found in the deeper water as near the top. Very slight evidence of this condition could at times be detected in the 60 per cent and 70 per cent mixtures, but the reactions were most decided in the 50 per cent mixture. Since the normal and the cut individuals were indistinguishable in respect to these reactions, there was no reason to suppose that the diminished salinity of the water was a stimulus for the lateral-line organs.

Both classes of fishes were put into sea water concentrated by boiling to three-fourths its original volume (the specific gravity was something over 1.030). In this water the fishes swam and respired normally, though it was evident that they were buoyed up by the greater density. Normal and cut fishes were again indistinguishable, and there was therefore no reason to suppose that the increased density had any stimulating effects on the lateral-line organs. In this respect my results agreed with those of Bugnion (1873, p. 302), who experimented with salt solutions upon the lateral-line organs of *Proteus*.

Food.—The normal stimulus for taste in animals, as in the human being, is the dissolved material in their food. Judging from the aquarium habits of some fishes, they seek their food chiefly by the eye, but it is also possible that the juices of the food may excite them. To ascertain whether the lateral-line organs are thus stimulated, I placed a single individual of *Fundulus heteroclitus* in a small vessel of sea water and, after it had become quiet, endeavored to discharge from a capillary tube some mussel juice on the lateral line of the body, the substance of *Mytilus edulis* being a favorite food of this fish. The extreme activity of the fish made such an experiment rather difficult, but after frequent trials on several individuals I got no results that could be said to indicate that the lateral-line organs were stimulated.

In a second set of experiments I etherized the fishes and cut the spinal cord just behind the head. After recovery, such fishes act as though the trunk muscles were paralyzed and swim about slowly by the pectoral fins. If properly fed they live for a week or more. They often rested on the bottom of the vessel in which they were kept, and when quiet afforded an excellent opportunity for testing the lateral-line organs. But even under these circumstances I never obtained reactions from these fishes that led me to conclude that the sea water decoction of mussel discharged on their lateral lines ever stimulated these organs. In this respect my results agreed with those of Bateson (1890, p. 237), and I conclude that the lateral-line organs are not stimulated by food.

Oxygen.—The oxygen dissolved in sea water is essential for the life of marine fishes, and as the amount varies in different parts of the sea, it is possible that this substance may serve as a stimulus to the lateral-line organs. To test this possibility, specimens of *Fundulus heteroclitus*, normal and cut, were introduced into sea water that had been boiled to expel the dissolved gases and then cooled with as little exposure to air as possible. When the fish were introduced they swam rapidly throughout the whole vessel, and their respiration was characterized by rapid and deep swallowing movements. These features disappeared very quickly on transferring the fish to ordinary sea water. Since normal and cut fishes acted alike in this experiment, there was no reason to suppose that lack of oxygen was in any way a stimulus for the lateral-line organs.

Carbon dioxide.—As carbon dioxide is one of the most extensive waste products from animals' bodies, it might be regarded as a possible means of polluting water, and the lateral-line organs might serve to detect this pollution. To ascertain whether carbon dioxide was a stimulus for these organs, normal and cut individuals of *Fundulus heteroclitus* were introduced into sea water through which carbon dioxide gas had been bubbling in minute streams for over half an hour. Both classes of fishes acted as though they were in ordinary sea water, and there was no reason to conclude that carbon dioxide had any effect upon the lateral-line organs.

Foulness of water.—A quantity of foul water taken from a vessel in which marine animals and plants were decaying was mixed with sea water and cut and normal individuals were introduced into it and their reactions observed. Although this mixture had a most offensive odor to the experimenter, the two sets of fishes behaved as though they were in ordinary sea water, and hence the general condition of foul water could not be said to afford a stimulus for the lateral-line organs.

Salts, food substances, oxygen, carbon dioxide, and the materials in foul water would probably all act as chemical stimuli on the lateral-line organs, if they acted at all, but since none of them appear to be stimuli for these organs, the observations of Bugnion (1873), Fuchs (1894), and Nagel (1894) to the effect that the lateral-line organs are not stimulated chemically, were confirmed. This view of the nonchemical reactiveness of the lateral-line organs has been clearly maintained from a morphological standpoint in two recent papers by Herrick (1903a, 1903b.)

Pressure of water.—Fuchs (1894, p. 474) suggested that changes in the hydrostatic pressure might be the means of stimulating the lateral-line organs. In testing this proposition normal and cut individuals of *Fundulus heteroclitus* were subjected to diminished hydrostatic pressure in a cylindrical glass museum jar three-fourths full of water. The jar was about 80 cm. high and 25 cm. in diameter, and was provided with an air-tight top. By means of a small hand pump air contained after the jar was closed was removed until the pressure was reduced from the usual 15 pounds per square inch to about 5 pounds.

When the fish were first put into the jar they all descended, as is usual, to the bottom, but after the removal of air had continued for some time they came to the top of the water, and when the pressure had fallen to about 5 pounds, it was evident that they were unable to keep below the surface of the water without vigorous and continuous swimming. Since they possess air-bladders, it seemed likely that the reduced pressure had caused such an enlargement of these organs that the fish were carried to the top of the water by their own buoyancy, and this explanation was tested by inserting capillary glass tubes into the sides of several, so that as the pressure was reduced the air could escape from the bladder. When the fish were subjected to diminished pressure under these conditions, air was seen to escape from them, and they remained quietly swimming at the bottom of the jar. Evidently the first set of fish were kept near the top of the water through their altered specific gravity. Normal and cut fishes reacted in essentially the same way in these experiments, hence there was no reason to suppose that a diminished hydrostatic pressure was a stimulus to the lateral-line organs.

In a similar way normal and cut fishes were put in a water-tight jar in which the pressure could be raised from 15 to 22 pounds on the square inch. When first introduced the fishes went to the bottom, and after the pressure was put on they remained there with the exception of short intervals, when by vigorous swimming they could get into the upper part of the jar. From such situations, however, they would often almost drop to the bottom. As in the experiments with reduced pressure, so here the air-bladder doubtless played a controlling part; for when it was punctured so that with increased pressure water could enter it, the fish swam much more freely. The increased pressure, nevertheless, stimulated the fishes, for they never seemed to come into a restful state in the fifteen minutes or so during which they were under pressure. Since the reactions of the normal and cut fishes were indistinguishable, however, there was no reason to suppose that increased hydrostatic pressure is a stimulus for the lateral-line organs.

These observations make it appear improbable that changes in hydrostatic pressure, as suggested by Fuchs (1894, p. 474), are stimuli for the lateral-line organs. Nor in fact do the observations made by Fuchs really lend much support to this hypothesis. He found that when he pressed on the lateral-line organs of *Raja*, the electrical changes in the nerves connected with them indicated that the organs had been stimulated. But the pressure thus exerted was without doubt of a very different kind from increased or decreased hydrostatic pressure; it was very probably a *deforming* pressure and not one that exerts its influence in all directions equally. It is well known that for the stimulations of the tactile organs of the human skin a deforming pressure is vastly more effective than such a pressure as is obtained by putting the hand deep in water. Under such circumstances the tactile sensations are not strongest from the parts under greatest pressure but from the region of greatest deformation, i. e., where water and air meet. It seems to me, therefore, that Fuchs's experiments demonstrate that the lateral-line organs can be stimulated by a deforming mechanical influence, but since hydrostatic pressure does not deform to any great extent, there is no reason to suppose that it stimulates these organs. Hence I do not think that my observations are at variance with those of Fuchs, but that he drew a wrong inference from what he observed.

Currents.—From the time of Schulze's second paper on the lateral-line organs (1870), water currents have been regarded with more or less favor as stimuli for the lateral-line organs. To ascertain whether currents do stimulate these organs, I have experimented on *Fundulus heteroclitus*, *F. majalis*, *Stenotomus chrysops*, *Pseudopleuronectes americanus*, *Mustelus canis*, and *Raja erinacea*. All these fishes when introduced into running water swim against the current, i. e., they are strongly rheotropic.

I tested the smaller species (*Fundulus heteroclitus*, *F. majalis*, *Stenotomus chrysops*, and *Pseudopleuronectes americanus*) by exposing them in a large open trough to a gentle flow of water. The trough, which was about 50 cm. wide, always contained a depth of at least 10 cm. of water and was about 3 meters in length. An inlet was established at one end and an outlet at the other, and a gentle current of water was kept flowing through the trough. A normal *Fundulus heteroclitus* when put in this trough immediately turned its head against the current and swam toward the source, often making its way actually into the open end of the inlet tube. If in its progress the fish was swept into the adjacent and more quiet water near the side of the trough, it would often sport about there for a while, but on returning to the current it would take up again its course toward the inlet. At times when the current was strong there would form on the sides of the trough small backset currents, and it was instructive to observe how quickly the fish reversed its direction when by any accident it was carried from the main current into a backset. In all the many fishes tested, irrespective of illumination, etc., they swam against the current.

Individuals in which the nerves to the lateral-line organs had been cut proved to be absolutely indistinguishable from normal fishes under these conditions. In agility and certainty of response there was no difference between the two sets. Hence I was led to conclude that the lateral-line organs were not essential to the fish in swimming against a current, and that therefore a current was probably not a stimulus for these organs.

Similar experiments were made with *Fundulus majalis* and *Stenotomus chrysops*, both of which gave results identical with those obtained from *Fundulus heteroclitus*. *Pseudopleuronectes americanus*, normal and cut, also swims against the current, but often takes hold of the bottom of the trough by a sucker-like action of the whole body. This temporary anchoring, however, was as characteristic of the cut fishes as it was of the normal ones, and there is no reason to suppose that the lateral-line organs were involved.

The larger fishes, *Mustelus canis* and *Raja erinacea*, were tested not in the trough but at one of the tide openings on the wharf outside the laboratory. Here at certain tides a steady broad current maintains itself, and in this it was comparatively easy to experiment with these fishes. Normal and cut individuals were put into a simple harness made of twine and to which a cord was attached so that they could be conveniently restrained. By this means they could be placed in the current where desired and their reactions noted. Both the dog-fishes and the skates swam vigorously against the current, and this happened irrespective of the condition of the lateral line. In fact it was impossible to tell from the reactions of the fish in the water whether the nerves to the lateral-line organs had been cut or not. My own experiments, therefore, confirm the opinion of Tullberg (1903, pp. 13, 15) that the lateral-line organs are not concerned with swimming against a current.

Stimulus to equilibrium.—The ability of a fish to keep its equilibrium at rest or in motion has, from time to time, been stated to be dependent at least in part on the lateral-line organs. So far as I am aware, the first investigator to make suggestions in this direction was Richard (1896, p. 131), who supposed that the lateral-line organs were at least indirectly connected with the equilibrium of a fish in that they influenced the amount of gas in the air bladder. Lee (1898, p. 144), however, first clearly expressed the belief, based upon extended observations on the toad-fish and the dog-fish, that the lateral-line organs were primarily organs of equilibration. Because of the growing favor in which this view has been held, I felt that it was desirable not only to make new observations in this direction, but also to repeat carefully the experiments of those who had already advocated this theory, with the view of gaining a critical insight into the present standing of the question. For these reasons I have carried out experiments on the equilibration function of the lateral-line organs in *Fundulus heteroclitus*, *Stenotomus chrysops*, *Opsanus tau*, and *Mustelus canis*.

When the nerves to the lateral-line organs in the species of fishes just mentioned were cut by the methods already described, and the fishes were allowed to recover from the shock of the operation, it was remarkable how little changed they seemed to be. So far as their ordinary movements were concerned they were often indistinguishable from normal fishes. They swam with agility and kept their equilibrium perfectly. My own observations entirely support Lee's statement (1898, p. 140) that the destruction of all the lateral-line organs "does not seem to interfere much, if any, with the animal's equilibrium." I usually found it impossible to bring a cut fish to rest on its side or back, for when displaced from its usual upright position it reacted as a normal fish by struggling to return to that position.

Those fishes that possess air bladders, such as *Fundulus* and *Stenotomus*, had no difficulty after the operation in keeping below the surface, and I found no reason to suppose that the lateral-line organs had any influence on the amount of gas contained in the air bladder, as conjectured by Richard (1896). In fact, all my observations supported Bonnier's opinion that Richard's results were due to the severity of his operations and not to the loss of the lateral-line organs, and since many fishes with well-developed lateral-line systems have no air bladders, it seems to me highly improbable that these sense organs are directly concerned with the state of the bladder.

I next repeated Lee's experiments on the toad-fish, *Opsanus tau*, and the dog-fish, *Mustelus canis*. Lee (1898, p. 140) states that after the removal of the pectoral and pelvic fins from the toad-fish, the natural means for support for the resting animal, and the destruction of the lateral line organs, there were "decided evidences of a lack of the sense of equilibrium." The fishes were unsteady in their movements and would lie quietly upon the side or back, in this respect being in strong contrast with individuals whose fins and skin had been cut to an equal extent, but whose lateral-line systems were still intact. These, according to Lee, were active and certain in their movements, showed no lack of equilibrium, and in general closely resembled normal individuals.

My own observations on *Opsanus* do not support those of Lee. I prepared six toad-fish by cutting off the four fins as Lee did and then severing the nerves to the lateral-line organs. This operation was easily carried out by following the careful topographical account of the lateral-line system given for this species by Clapp (1898). Of the six fishes operated upon one died shortly after the operation but the remaining five all lived over five days and one over a week. These I carefully compared with five other fishes from which the four fins had been removed and the skin, but not the nerves to the laterial-line organs, had been cut. So far as the retention of equilibrium was concerned, I found it impossible to distinguish one set from the other. Both, though rather irregular in their locomotion, retained fairly upright positions, and none ever showed the characteristic disturbances seen in the locomotion of many fishes from which the ears have been removed. Occasionally individuals could be found that would lie quietly often for some time on the side or back, as described by Lee, but these always proved to be moribund and usually died within a day or so after this symptom appeared. Since cases of this kind occurred among those fishes in which the lateral-line organs were intact, as well as among those in which the nerves had been cut, I concluded that the loss of equilibrium seen in these instances was not due to the exclusion of the lateral-line system, but to general weakness preceding death. I therefore do not believe, as Lee does, that the loss of the lateral-line organs in *Opsanus* is accompanied with any special disturbance in equilibrium.

Lee (1898, p. 142) also experimented upon the dog-fish by exposing the lateral-line nerve and stimulating its central end, whereupon he obtained well coordinated muscular movements like those seen on stimulating the ampullar organs of the internal ear. I have repeated this experiment on *Mustelus canis* and can confirm Lee's statements even to detail. I have worked with care only on the pectoral-fin reactions, but these will suffice to give a clear insight into the nature of the response. When, as Lee states (1898, p. 142), the left lateral-line nerve is stimulated centrally, the left pectoral fin is elevated and the right depressed. Since this reaction, which is always very marked and clear, is of a kind to restore equilibrium, one might conclude with Lee that the lateral-line organs are organs of equilibration, but exactly the same reaction can be called forth by touching the skin with the electrodes. If the lateral-line nerve is cut on one side of the body and the electrodes are applied on that side and at a point posterior to the cut, the pectoral-fin reactions that occur are the same as those seen when the lateral-line nerve is stimulated centrally. Since the pectoral-fin reactions thus obtained disappear when the spinal cord anterior to the region of stimulation is cut, there can be no doubt that the general cutaneous terminations of the spinal nerves are the recipients of the stimulus. Hence Lee's conclusion that the lateral-line organs are organs of equilibration must be qualified by the statement that there is no reason to suppose that these organs are more concerned with this function than is the integument. This opinion is supported by certain observations made by Lyon (1900, p. 79) to the effect that when the tail of a dog-fish is turned laterally, compensating movements of the eyes can be observed even though the second and eighth nerves are cut. Since these movements disappear on cutting the spinal cord, Lyon concludes that the afferent path is from the sensory nerves of the skin or muscle.

So far as equilibration is concerned, the lateral-line organs are certainly much inferior to the ear and even the eye. Thus if the nerves to the lateral-line organs of a dog-fish are cut, the animal will continue to swim as a normal individual does. If the eyes are covered, normal swimming still continues. But if the eighth nerve of a dog-fish is cut, and the animal is made to swim rapidly, it will usually lose its equilibrium even with the whole lateral-line system intact, and if the eyes are covered it invariably does so. Thus while the eye may in part supplement the ear in orientation, the lateral-line organs seem to be of no significance in this respect, and our only reason for supposing that they are of value in equilibrium is the fact that on stimulating the lateral-line nerve, fin movements, etc., occur such as are produced by stimulating the ampullar organs of the ear; but this does not raise them as organs of equilibration to an order higher than that of the skin. Since in this respect they are much inferior to the internal ear, it is misleading to designate them as special equilibration organs.

Vibrations of high frequency (*sound*).—The suggestion made by Emery (1880), Mayser (1881), Bodenstein (1882), and others, that the lateral-line organs may be accessory ears, calls for a test of these organs by sounds. To carry out this I used the same apparatus that I had formerly employed to test the sense of hearing in fishes (cf. Parker, 1903a, 1903b). This consisted of a marine aquarium, one end of which was made of wood and in which was hung a smaller glass aquarium closed at one end (that next the wooden end of the large aquarium) by a silk net of coarse mesh. Thus the fish could be restrained in the smaller aquarium and yet be subjected to sound from the sounding-board at the end of the larger one. As a source of sound I used a tuning fork driven by electricity and giving out 100 vibrations per second. It was placed on an isolated base so near the sounding-board that a very slight movement was sufficient to bring it into contact with the board, and thus the sound could be conveyed to the water. Experiments were made on *Fundulus heteroclitus*, *F. majalis*, *Stenotomus chrysops*, and *Mustelus canis*.

My experiments on *Fundulus heteroclitus* confirm my results of a year ago (Parker, 1903a, p. 56; 1903b, p. 199). When normal individuals of this species were stimulated by sound they often responded by pectoral fin movements and almost invariably by an increase in their respiratory rate. This continued to be true even after the nerves to the lateral-line organs had been cut, and I therefore concluded that the lateral-line organs were not essential to these responses. Since the pectoral fin and the respiratory reactions disappeared in individuals whose eighth nerves had been cut, but whose lateral-line organs were intact, it was evident that while in this species these sounds were effective stimuli for the ear they were not so for the lateral-line organs.

Fundulus majalis reacts in many respects like *F. heteroclitus*. Its movements, however, are often more sudden and darting than in the other species. To vibrations of the tuning fork the animals usually spread the fins and often gave a short dart forward. This continued after the nerves to the lateral-line organs had been cut, and ceased only with the cutting of the eighth nerve; hence I conclude that also in *F. majalis* sound is a stimulus for the ear but not for the lateral-line organs.

Although I tested a considerable number of *Stenotomus chrysops* and *Mustelus canis*, both in normal condition and with their lateral-line nerves cut, I was unable to elicit from them any unquestionable reactions to the sound from the tuning fork. This stimulus certainly did not act on the lateral-line organs of these two fishes, and from the experiments on the two species of *Fundulus*, I conclude that there is no reason to suppose that a sound of 100 vibrations per second is a stimulus for the lateral-line organs, though it may be for the ear.

Vibrations of low frequency.—When a slow but noiseless vibration was given to the aquarium containing *Fundulus heteroclitus*, the fishes, as I have elsewhere stated (Parker, 1903a, 1903b), were vigorously stimulated. The stimulus that affects them seemed to proceed from a movement of the body of water in the aquarium as a whole, for the most convenient way to produce this stimulus was to make the aquarium and the supporting table vibrate slightly by drawing the aquarium a little to one side, thus straining the table slightly, and then letting it go. The motion thus produced, when written off on a moving surface, was found to consist of a series of vibrations very close to six per second, and each time the aquarium was made to vibrate, about forty such vibrations were accomplished before the apparatus came to rest again.

I have nothing to add to my former statements (Parker, 1903a, p, 59; 1903b, p. 199) about the reactions of *Fundulus heteroclitus* to this stimulus. When normal individuals are first introduced into an aquarium they swim at once to the bottom, and only after some time and numerous cautious attempts do they come to swim at the surface. As I have already noted, any slight disturbance, such as a quick movement of the observer or a slight jar given to the aquarium, is sufficient to cause them to descend at once. If, by means invisible to the fishes, the slow vibration already described is given to the aquarium, they dart at once to the bottom and remain there some time before returning to the surface. When the fish again begin to swim upward toward the surface, their progress may at any moment be stopped by causing the aquarium to vibrate, for they will again descend. Under no circumstances will the normal fishes rise and stay at the surface while the aquarium is in vibration. These reactions are in my experience practically invariable.

When individuals with the nerves to the lateral-line organs cut are subjected to similar tests, the contrast with normal fishes is striking. Cut fishes will continue to sport about near the surface, or even swim upward from below, while the aquarium is in vibration. In fact the vibration seems to have no effect upon them except in that it produces ripples on the top of the water, and when they come under the influence of these they usually descend a few inches into water which, so far as one can judge from the particles of silt contained in it, is not in motion from the surface ripples. Here they will remain and sport about during the vibrations, though this region would be immediately deserted by a normal fish. Hence I conclude that a body of water vibrating at a relatively slow rate, six per second, is a stimulus for the lateral-line organs in *Fundulus heteroclitus*.

The reactions of *Fundulus majalis* to vibrations of low frequency, except for the darting movements already mentioned, were almost identical with those of *F. heteroclitus*. Normal individuals reacted to the vibrations usually at once by descending; cut ones gave no evidence of being stimulated. In one set of the normal fishes that were being tested preparatory to operations two were found that could not be said to respond to the vibrations. Such conditions were never met with in *F. heteroclitus*, and they were so rare in *F. majalis* that they constitute an unimportant exception to the statement that the two species in their lateral-line reactions are essentially alike.

Stenotomus chrysops when put in the aquarium usually swam down to the bottom and remained in the deeper water, sometimes with the lower fins in contact with the floor of the aquarium, sometimes a few inches above this. In all tests of vibrations made with these fishes, care was taken that the stimulus should be applied only when the fishes were not in contact with any solid body, i. e., when they were suspended somewhat above the bottom of the aquarium. Under such circumstances a noiseless vibration almost invariably called forth a very characteristic reaction. When quietly suspended in the water the fish usually rests with its head pointed obliquely downward and its tail up. On stimulating it with a vibration it almost invariably sets its fins and changes the direction of its axis so that its head points obliquely upward. This was observed clearly in six out of seven normal fishes. These six were then operated upon by cutting the nerves to the lateral-line organs. Five recovered, and none of these reacted to the vibrations of low frequency unless the aquarium was made to vibrate very considerably. Under such circumstances occasional, but unquestionable, reactions, precisely like those just described, were observed. Since these reactions are not interfered with by cutting the eighth nerves, and occur when the literal-line organs are excluded, it is probable that they result from a stimulation of the general cutaneous nerves. Thus in *Stenotomus chrysops* one form of stimulus is probably effective for two sets of sense organs, those of the skin and those of the lateral-line system.

In testing the smooth dog-fish, *Mustelus canis*, for reactions to vibrations of low frequency, I found the ordinary individuals too large for work in the aquarium, and I therefore experimented on young animals not over a foot and a half in length. As already noted, none of the specimens I tested gave any response to the tuning fork at 100 vibrations per second. To the slower vibrations, six per second, all fishes tested were very responsive and reacted usually in a very uniform way. In seven young fishes that were tested all raised the tail when the aquarium was made to vibrate, and if the fishes were high in the water they usually swam to the deeper situations. These reactions, particularly the elevation of the tail, were unusually regular. I noticed no change in the respiratory rate. It was with difficulty that even these young fishes were tested, for, since they were relatively large, it was only now and then that they were not in contact with solid parts of the acquarium, and consequently in position for satisfactory stimulation. Notwithstanding this difficulty, however, enough unquestionable reactions were obtained to place beyond doubt the statements made above.

After the nerves to the lateral-line organs were cut, both the elevation of the tail and the downward swimming ceased. To ascertain how much of the loss of response was due to the cutting of the skin, etc., I made the necessary skin apertures for cutting the nerves in one individual, but did not sever the nerves, and then tested the animal. It still elevated the tail with great regularity on stimulation. On cutting the nerves this reaction entirely disappeared. Hence I believe the loss of reactiveness is due to the elimination of the lateral line organs and not to the shock of the operation. Six of the seven dog-fishes operated upon recovered, and most of them lived for two or three weeks after the operations. When tested toward the end of this period they were as characteristic as they were a short time after recovery.

I attempted similar experiments with small skates, *Raja erinacea*, and succeeded in getting on stimulation excellent tail reactions like those described for the dog-fish, but since these fishes were always in contact with the solid bottom of the aquarium it was impossible to say with certainty that they were not directly stimulated through their tactile organs. On cutting the nerves to the lateral-line organs, however, these tail reactions disappeared. Although I believe it would be hazardous to draw any conclusion from the experiments on the skate just recorded, the records on the four other species of fishes tested show beyond a doubt that the lateral-line organs are stimulated by water vibrations at the rate of 6 per second, though they are not stimulated when the rate reaches 100 per second.

DISCUSSION OF RESULTS.

From the foregoing experiments I conclude that the lateral-line organs of the species of fishes experimented upon are not stimulated by light, heat, salinity of water, food, oxygen, carbon dioxide, foulness of water, pressure of water, currents, and sounds. They are stimulated by vibrations of low frequency, as surmised by Schulze (1870), and these may be of service to the fishes in their orientation and equilibration reflexes, as suggested by de Sède (1884), Bonnier (1896), and especially by Lee (1898). There is, however, no reason so far as I can discover, for designating these organs as special organs of equilibration such as the ear, for in this respect they are of no higher value than the skin, and they are certainly inferior to the eye.

The stimulus for the lateral-line organs (a water vibration of low frequency) is a physical stimulus intermediate in character between that effective for the skin (deforming pressure of solids, currents, etc.) and that for the ear (vibrations of high frequencv), and indicates that these organs hold an intermediate place between the two sets of sense organs named. This opinion, even from an actual genetic standpoint, has already been urged by many observers. Leydig (1850 b, p. 180) long ago pointed out the histological similarity between the sense organs of the internal ear and those of the lateral-line system; and Schulze (1870) emphasized this relation and brought into strong contrast the histological differences between the organs of the ear and the lateral-line system and those of the sense of taste, a contrast strengthened by the recent work of Herrick (1903a, 1903b, 1903c).

The innervation of the lateral-line organs and of the ear also supports the belief in the genetic relations of these parts. Mayser (1881, p. 311) first pointed out the interesting fact that the nerves from the lateral-line organs and from the ear all terminate in one central structure, the so-called tuberculum acusticum, and this observation has been confirmed and its significance admitted by almost all subsequent investigators.

The development of the ear and of the lateral-line organs has led to still more important results, however, for in this way it has been shown that both sets of organs are derived from the skin, and that the relations of the ear to the lateral-line organs are such that, as Beard (1884, p. 143) declared, the ear may be regarded as a modified part of the lateral-line system. This opinion was accepted by Ayers (1892, p. 306) in his interpretation of the work of Allis (1889), and has been maintained recently by Cole (1898, p. 197) as now fully established, notwithstanding the fact that in some fishes, like *Amia*, the ear and lateral-line organs develop separately (Beckwith, 1902).

Finally, the physiological evidence shows that these organs are intermediate in character between the skin and the ear, and support the conclusion elsewhere expressed (Parker, 1903b, p. 198), that together these sense organs represent what may be figuratively spoken of as three generations, in that the skin represents the first generation, which gave rise to the lateral-line organs, from which in turn came the ear. Thus the organs of touch, of the lateral-line system, and of the ear form a natural group, genetically connected as just indicated.

It may well be asked what disturbances in the water under natural conditions give rise to stimuli for the lateral-line organs. To determine this I tried some experiments with normal and cut *Fundulus heteroclitus*. It seemed to me probable, since the vibratory stimulus for the lateral-line organs was usually accompanied by ripples on the surface of the water, that by blowing on the water and producing strong ripples a movement might be induced in the deeper water sufficient to stimulate the lateral-line organs. This was tested by putting normal fish one at a time in an aquarium about a foot deep and blowing on the surface of the water till strong ripples were produced. All the fishes invariably went to the bottom and stayed there while the water remained agitated. These fishes were then cut, and after recovery again tested. While none of them would stay in the superficial water obviously in motion, as, in fact, was to be expected, none sought the bottom as they formerly had done, and there was no doubt left in my mind that when wind blows upon the surface of water it causes a motion of the deeper water, which stimulates the lateral-line organs. If this be true it follows that the more active fishes should have better developed lateral-line organs than the more sluggish bottom ones, and, at least so far as sharks and rays are concerned, this has been claimed to be so by Garman (1888, p. 65) and by Ewart (1892, p. 81).

I also tried the effects on normal and cut *Fundulus heteroclitus* of dropping unseen objects into the water. This was done with as little noise as possible, and almost always was followed by a sudden spring on the part of a normal fish generally away from the center of disturbance, so that I am led to conclude that the disturbances set up by such an object as a stone falling into the water stimulate the lateral line organs and with more or less directive effect, as surmised by Bonnier (1896).

That the movements generated in the water by the male *Polyacanthus* when mating are stimuli for the lateral line organs of the female, as suggested by Stahr (1897), may be true, but is unsupported by any proof.

So far as these observations go they show that surface wave movements, whether produced by moving air on the water or solid bodies falling into the water, are accompanied by disturbances which are stimuli for the lateral-line organs. This doubtless is the most usual form of stimulus for these organs in surface fishes, for I have shown that currents and direct wave action are probably not effective in this respect.

SUMMARY.

1. The lateral-line organs are not stimulated by light, heat, salinity of water, food, oxygen, carbon dioxide, foulness of water, water pressure, water currents, and sound.
2. The lateral-line organs are stimulated by water vibrations of low frequency—six per second.
3. The lateral-line organs may be of service to the fish in orientation, but they are of no more significance in equilibration than the skin, and are inferior in this respect to the eye and the ear.
4. Waves on the surface of the water produced by air currents and the disturbances made by bodies falling into the water produce vibrations in the deeper water that stimulate the lateral-line organs.
5. The skin, the lateral-line organs, and the ear form a natural group of sense organs whose genetic relations are such that the skin (organs of touch) may be said to be the first generation from which the lateral-line system has been derived, and this in turn has given rise to the ear.

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