THE FUNCTIONS OF THE EAR AND THE LATERAL LINE IN FISHES.¹

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ALL vertebrate morphologists are well aware that two of the prominent vexed problems of their science are the history, ontogenetic and phylogenetic, of the ear and that of the system of sense-organs usually called the sense-organs of the lateral line, a structure found in Fishes and aquatic Amphibia, larval or adult. Into the differences of opinion and confusion in this field of research Beard,² in 1884, introduced a semblance of order, and at the same time gave cause for much further contention, by bringing the two organs, or systems of organs, together phylogenetically, and claiming the ear to be nothing more nor less than a modified portion of the system of the lateral line. Since then much has been written upon this phase of the subject, the chief single contribution, perhaps, being that of Professor Ayers,³ who adopted and developed very fully the general idea suggested by Beard.

The chief morphological facts upon which this view is based, are, in brief, the following: —

1. Similarity in ontogeny. — The ear and the lateral line seem to develop from a common ectodermal thickening, which extends forward and backward from the place of origin.

2. Similarity in structure of adult organs. — It is now generally acknowledged by morphologists that the internal ear is not one organ, but a group or system of organs, comprising in the fully developed ear of the fish seven recognizable patches of sensory epithe-

¹ The substance of this article was presented before the Section in Physiology of the British Association for the Advancement of Science at its meeting in Toronto, August 19, 1897.


Functions of the Ear and Lateral Line in Fishes.

The functions of the ear and lateral lines in fishes include the three crista acusticae, contained in the walls of the ampullae of the semicircular canals; the three maculae acusticae, contained in the recessus utriculi, sacculus, and lagena; and the rudimentary macula neglecta, contained usually in the utriculus. The structure of these is well known; in each there is a localized area of sensory epithelium, supplied by special nerve-fibres and consisting of hair- and supporting-cells. The processes of the hair-cells project into a liquid, the endolymph. In addition to these parts, common to both crista and maculae, each macula bears a mass of otoliths, resting upon the sensory hairs. The labyrinthine cavity of the internal ear in the Selachians is more or less freely open to the outside medium through the ductus endolymphaticus.

The sense-organs of the lateral line are numerous, and are either free or contained in canals lying in the skin of the head and the sides of the body. These canals are open at intervals directly to the water of the medium, as are the semicircular canals through the endolymphatic duct. From their position, different portions of the lateral system have received the names supraorbital, infraorbital, mandibular, occipital, and lateral. The structure of the sense-organs closely resembles that of the crista acusticae: in each there is a localized area of sensory epithelium, supplied by special nerve-fibres and consisting of hair- and supporting-cells; the processes of the hair-cells project into a liquid which, when canals are absent, is the water of the medium, and, when canals are present, is this water plus more or less mucus excreted by the cells lining the walls of the canals.

3. Similarity in innervation. — The sense-organs of the lateral line are innervated by nerve-fibres forming well-marked bundles, which run to the periphery usually in company with branches of the fifth, seventh, ninth, and tenth cranial nerves. To speak of them as being innervated by these cranial nerves is misleading; the connection of their nerves with the cranial nerves is secondary. In reality, the nerves of the lateral line form a definite system of their own with a common central origin, which central origin is, likewise, the central origin of the eighth or acoustic nerve.

It must be acknowledged that these facts are of great importance, and seem to warrant the interpretation given to them.

Can physiology throw any light upon this question? A study of function is not usually believed to be capable of elucidating the genetic relationship of organs, and hence most writers have wholly neglected the physiological side. It might have been advantageous if
more had done this, for the physiology that has thus far been introduced is largely speculative, usually lacks an experimental basis, and is at times grotesque. What is needed here, as in all similar cases, is not speculation from morphological facts as to function and the origin of function, but reasoning from physiological facts that are first acquired by rigid and critical experiment. We have here an admirable opportunity to demonstrate not only that the phylogeny of function is worthy of study for its own sake, but that physiology is at times able to present, if not direct, at least valuable circumstantial evidence of the truth of morphological deductions. The evidence that I wish to bring forward has been obtained, unless otherwise stated, by myself from experiments upon fishes at the Marine Biological Laboratory, Woods Hall, Mass., during recent summers. The form chiefly used was the common smooth dog-fish (Galeus canis, Mitchill) of our Atlantic coast.

Some of the results have already been published, but must be mentioned briefly in this connection for the sake of rendering the subsequent work more easily understood. No attempt will be made to discuss the experiments of others upon higher animals, as this for my present purposes would be quite superfluous. The work is not yet completed.

We will consider the functions of the various sense-organs in order.

I. The Ear.

A. The crista acusticae.—The experiments here have been clear-cut, and the results have appeared with a mathematical exactness rarely realized in physiological investigation.

One general function is here present, namely, the appreciation of rotary movements of the body, i.e., movements in curved lines. Hence, the semicircular canals with their sense-organs are organs of equilibration.

The methods of arriving at this conclusion were three: turning the normal fish in the planes of the canals and other planes; stimulating separately and in combination the various ampullar branches of the acoustic nerve, which in the fish are separate and very easily reached; and cutting these ampullar branches. The index to the state of the animal's sense of equilibrium was found in the compensating movements of the eyes and the fins. The results obtained by these three methods are entirely harmonious. Thus, turning the normal
animal in a definite plane, either the plane of a canal or a plane between two canals, causes the eyes and fins to make certain definite and constant movements, which indicate a recognition of the body-movement and an attempt to resist or overcome it. If, now, the canals of the corresponding planes be exposed in another animal, and their cristae stimulated artificially, exactly the same compensating movements of eyes and fins are made. The inferences are: first, that the operated fish has the sensation of being turned out of his normal position; and second, that when a normal fish turns in the planes specified, he stimulates the corresponding cristae. This latter inference is corroborated by cutting the nerves supplying the cristae in question, and then turning the animal in the same planes as before. This has not been done for single cristae, and it is quite possible that in such case the others would maintain the compensation; but it has been performed for a functional pair of cristae, and the result is absence of the normal compensating movements pertaining to the canals in question. The harmony of the results of these three methods is striking.

Each canal with its sense-organ has a principal and a subordinate function: the former is the appreciation of rotary body-movements in the plane of the canal and toward its side of the body; the latter is the appreciation of similar movements in the same plane but in the opposite direction. Each canal has a functional opposite, the two lying approximately in the same plane, and the principal function of one being the subordinate function of the other. Such functional opposites are the right anterior and the left posterior, the left anterior and the right posterior, and the right and left horizontal canals. A simple movement of the body in the plane of a canal puts the canal into most complete action; a movement in any other plane may be regarded (from the standpoint of the canals) as a compound movement, and may be resolved into simple movements in the planes of two or more canals. Such compound movements are appreciated by the two or more canals acting as a double organ (functional pair), or triple organ, which likewise possesses its principal and subordinate functions. The action of a functional pair, or double organ, is exemplified in the appreciation of diving movements by the two anterior canals, and in the appreciation of the movement of shooting upward in the water by the two posterior canals.1

1 For a fuller discussion of the functions of the canals the reader is referred to my articles already published. Ueber den Gleichgewichtssinn. Centralbl. f.
B. The maculae acusticae. — Here not so much work has been done, and the results are not as sharp-cut as in the case of the cristae. Artificial stimulation of the maculae has been tried in a large number of cases, but does not appear to give consistent results. Cutting the macular nerves or, perhaps better, removing the otoliths that always cover the maculae, makes a decided general change in the conduct of the animal, which to one familiar with the movements of fishes seems to indicate unmistakably the lack of certain sensory functions. It should be premised that, in the form studied chiefly, the utricular and saccular maculae are very closely contiguous, and the macula of the lagena is simply a small continuation of that of the saccule; hence, so far, it has been impossible to separate the three functionally, and it is very questionable whether the division of labor here is as sharp-cut as with the crista.

Two functions seem to be present, both of which are equilibrating: the appreciation of translatory or progressive movements, or movements in straight lines, and the appreciation of the position of the body in space.

1. Appreciation of progressive movements. — A normal fish has a delicate sense of the distance involved in swimming in a straight line. This is shown by the remarkable skill with which he avoids obstacles; in swimming around his aquarium constantly, he strikes his nose directly against the side of the tank comparatively rarely. This is not so with a fish deprived of all his otoliths or with all his macular nerves severed. Such a fish seems to have little idea of the extent of a forward swim. He is often restless and frequently alters the direction of his progression. In moving along close to the side of a large oblong tank he often swims at his usual rate and with his usual freedom, and appears fairly normal; but, upon reaching the end, it frequently happens that he does not turn, like the normal fish, gracefully to one side and thus avoid the end-wall. On the contrary, he often bumps directly into it. When excited by a stick, he darts about in different directions, irregularly and with awkward,
uncertain, and ill-regulated movements, often shooting far out of the water. Moreover, after swimming into a corner, his movements are awkward and he finds great difficulty in retreating or getting back into open water. If he succeeds in doing this, he may return at once to the same corner and repeat his ungainly attempts at extricating himself. It is easy to draw a hasty inference that the eyesight of such a fish must in some mysterious way be at fault. As a matter of fact, however, a fish deprived of his eyesight, but in other respects normal, does not conduct himself in that way. When left to himself, the blinded fish\(^1\) swims normally in all respects, moving gracefully, easily, and without timidity, and shooting and diving like an uninjured fish. When disturbed by being poked he darts about with great rapidity, but is master of his movements. In the first few hours of his blindness he bumps the end of the tank in progressive swimming, but soon he largely overcomes this, and, probably by his sense of touch, learns to avoid gross contact with such obstacles. He then touches the walls lightly, glides away from them easily, and only when disturbed bumps as at first. When by chance he swims into a corner, he extricates himself easily, gracefully, and with certainty. The compensating movements of his eyes and fins are entirely normal.

It is thus seen that the fish deprived of retinal sensations and the fish deprived of macular sensations act very differently. The conclusion that in the latter animal the appreciation of progressive movements is dulled or largely eliminated seems quite sufficient to explain the phenomena.

We thus find experimental proof — and the first thus far reported in animals lower than man, if I am not mistaken — of the presence in the otolithic parts of the ear of a power to appreciate progressive movements. That such a function must exist there was ably advocated by Breuer,\(^2\) who gave reasons for the probability “that the perception of rectilinear movements is sharper in Fishes and Birds than we find it in observations on ourselves.”


\(^1\) In blinding, the contents of the eyeballs, including the retinas, were removed; the sclerotic coats with their muscular attachments were left in situ.
in any other position than that with the back upward and the belly downward. He not only resists with all his powers being turned over (this movement is appreciated by the semicircular canals), but with equal energy he resists being compelled to remain out of his customary position; and, when put out of the latter and then left to himself, he at once assumes his normal attitude.

It is not so with a fish from which the otoliths have been removed, or in which the macular nerves have been cut. If either of these operations be done upon one side only, the eyes and fins are placed in abnormal positions; in reclining, the operated side is usually slightly downward; normal swimming is possible, but here usually the operated side is depressed; when disturbed, the fish usually darts off with that side downward; and in coming to rest he often loses his balance and sinks down flat upon that side, never upon the other. If the operation be performed on both sides, the fish seems to have largely lost his sense of upness and downness. While preferring usually the normal attitude, it is not difficult to make him remain lying on his back or side; and not rarely he is found in such abnormal positions, having assumed them himself. He swims at times upon his side, and occasionally upon his back. He seems not to appreciate at all clearly his position in space.\footnote{1}

I have found no reason to disbelieve that the same otolithic parts of the ear appreciate both progressive movements and position in space, which is not in accordance with the doctrine of specific energy in its extreme form. The view of Breuer,\footnote{2} however, seems wholly reasonable, namely, that changes in the pressure of the otoliths are appreciated as changes of position in space when they are accompanied by sensations (ampullar) of rotary movements, and as progressive movements when not so accompanied.

It is evident that there is a close functional connection, through the central nervous system, between the sensory organs of the ear, the cristae and maculae, and the locomotor organs of the body. A reflex arc with the evident function of equilibration is thus established. The idea that the cristae and maculae are sensory organs of this function does not preclude acceptance of the well-established fact that other

\footnote{1} For a fuller discussion of this statical function of the maculae, the reader is referred to the author's articles in the Centralblatt für Physiologie, 1892, vi, p. 508, and the Journal of physiology, 1893, xv, p. 311.

\footnote{2} Breuer, \textit{loc. cit.}
sensory organs, such as the eyes, are similarly connected by reflex arcs with the locomotor organs, and similarly function as sensory organs of equilibration. In these latter organs equilibration is accessory to other chief functions, as in the eyes to sight; in the cristaæ and maculae it is the chief, and perhaps the only, function.

The functions of the ear of the fish so far considered may be put in convenient tabular form as follows:—

I. Dynamical functions, in recognition of
   1. Rotary movements, mediated by cristaæ acusticae.
   2. Translatory movements, mediated by maculae acusticae.

II. Statical functions, in recognition of
   3. Position in space, mediated by maculae acusticae.

As to the manner of stimulation, it is evident that both the cristaæ and the maculae belong to the category of pressure-organs. This is most evident in the macula, in which the pressure of the otolithic mass upon the delicate sensory hairs affords a constant stimulus which varies in intensity with the position of the animal in space, or with the force of the progressive movement.

In the cristaæ, the most reasonable mode of stimulation appears to me to be that due to the inertia of the endolymph as the hair-cells are moved through space along with the body. The result is a greater pressure upon one side of the hairs than upon the other, and hence a stimulation of the sensory cells by pressure.¹

¹ In a recent article E. v. Cyon (Bogengänge und Raumsinn. Experimentelle und kritische Untersuchung. Archiv für Physiologie, 1897, p. 29) appears in the light of a sceptic regarding the results obtained in my experiments on dog-fishes, apparently because of their exactness and completeness. Among other things he reproaches me with the fact that “Lee hat . . . immer alles bestätigt gefunden, was die Hypothese erheischt.” This fact will occasion no surprise, when it is borne in mind that the great majority of my results were obtained long before the “hypothesis” as formulated by myself was made (cf. Lee: Journ. of physiol., 1893, xv, p. 321), and long before I was acquainted with the work of Breuer. The theory as formulated in my chief Paper was a direct induction from the facts obtained by myself; I took pains to keep it within the limits of those facts, and thus it was that I “always found what the hypothesis demanded.” In a subsequent Paper (Lee: ibid., 1894, xvii, p. 102) I aimed “to fill in certain gaps that were left in the previous series, to make the proof of certain points more logically complete, and experimentally to verify certain inferences and prophecies resulting from the theory formerly stated.” As regards the exactness of my results, I have often felt and expressed surprise similar to that which Cyon apparently feels. Yet I have endeavored accurately to chronicle the phenomena...
C. The question of hearing. — We thus appear to have found a function for all of the sensory organs of the ear of the fish. But the question naturally arises — does not the fish possess audition? In higher vertebrates, of course, this is present, and we can add to the above scheme:

111. Auditory functions, in recognition of

4. Vibratory motions, mediated by papilla acustica basilaris.

This exhausts all possible cases of mechanical (i.e. visible) motions in matter. It is interesting that the ear is the sense-organ that appreciates all kinds of visible motion.

Wherever among vertebrates undoubted audition exists, there is present an additional group of sensory end-organs, the papilla acustica basilaris. This does not exist in Fishes, but appears first in the Amphibia as an offshoot from the lagena, and in higher vertebrates constitutes the nervous portion of the organ of Corti of the cochlea, actually observed under the circumstances of the many and widely varied experiments.

Cyon further seems to regard the integrity of the sense of sight as necessary to the performance of the compensating movements of the eyes, and makes the astonishing statement that "... der Dogfish (Galea canis) tagesblind ist, wie Beer unzweifelhaft bewiesen hat." On the contrary, Beer (Die Accommodation des Fischauges. Arch. f. d. ges. Physiol., 1894, lviii, p. 577) has neither stated nor attempted to prove such a thing. He says: "Wir haben einen Grund anzunehmen, dass die Pupille der in Freiheit lebenden Fische wegen der relativen Dunkelheit grosserer Tiefen noch etwas weiter sein wird, als bei den Thieren in den gewöhnlichen Versuchsbasins, die in einer für sie vielleicht blendenden Helle leben. Bei vielen Haifischen und Rochen tritt sogar in den dunkleren grossen Aquarien der Station tagsüber eine so starke Miosis ein, dass die Pupille — die Nachts, resp. im Dunkeln sehr weit ist und dann auch hier den Linsenrand sehen lässt — fast gar nicht sichtbar, sondern ... verschlossen wird; die Thiere benehmen sich auch wie blind," etc. As a matter of fact, under the circumstances of my experiments, the pupils of Galeus canis varied greatly in size, from being wide open to being partially closed. But I do not now recall a single instance of their being wholly closed, nor have I ever seen an uninjured individual of this species behaving during the daytime like a blind fish. In an experience of three summers this species has not exhibited himself as "blind in daylight." This question is, however, of minor importance, since, as stated above, the eyeballs from which the contents, including the retinas, are removed, perform the normal compensating movements. Cyon appears not to comprehend the fact accented above, namely, that the movements of the eyes are reflex movements, the afferent stimulus to which comes from the crista acusticae. This does not preclude the further undoubted fact that under normal circumstances the movements are accompanied by sensations of sight.
At first sight the presence of the "ear" in Fishes presupposes a sense of hearing; but the absence of the papilla acustica basilaris argues against it. The fact that fishes, with comparatively few exceptions, are dumb seems to me strong evidence against the possession by them of a sense of audition. It would seem that the primary purpose of the power of emitting sound by an organism is communication with other individuals of its own species. Similarly, the primary purpose of a sense of hearing is apparently the gaining of information regarding the presence of other individuals of one's own species. In each case the employment of the function for other purposes would be secondary. If this be so, we should expect the two powers of emitting sound and of hearing sound to be developed in the same individuals and developed more or less pari passu. A survey of the various groups of animals shows this to be the case. Further, it is difficult to conceive upon any grounds the object or usefulness of the possession by Fishes of the power to hear in the sense in which the term is ordinarily used. The depths of the sea are silent, the sounds of the waves probably penetrate only the most superficial layers of the water, and aquatic animals, with comparatively few exceptions, are dumb. Along the shores some outside sounds might penetrate the water superficially, but such would form only a very slight exception to the general law that in nature water, unlike air, is devoid of sound.

But experimentation can best answer the question as to the power of audition in Fishes.

In the summer of 1894 I tested a number of species as to their power of hearing, employing ordinary sounds, such as the human voice, clapping the hands, and striking stones together in the air and under water.\footnote{See footnote p. 132.} I obtained no evidence whatever of the existence of a sense of hearing as the term is customarily employed, although I learned that fishes are exceedingly sensitive to gross shocks, such as the jarring of their tank or concussions upon its walls, \textit{i.e.}, such vibrations as human beings recognize through other sensory mechanisms than the ear as distinct mechanical vibrations. The accompaniment of such apparently gross vibrations was the indispensable condition upon which the fishes in my experiments reacted to sounds. I have learned recently of Bateson's similar experiments\footnote{BATESON, W.: The sense-organs and perceptions of fishes. Journal of the marine biological association, 1890, i, p. 225.} which were
interpreted in much the same way. In 1895 Kreidl\(^1\) published the results of a considerable series of experiments carefully conducted upon goldfish. He used as sources of sound in the air various whistles, electric and other bells, clapping of the hands, and the firing of a revolver, and in the water vibrating rods; and he studied their effects upon normal fishes, those whose excitability was greatly increased by strychnine, and those that had been deprived of their ears. Neither normal nor strychnized fishes showed any reaction whatever to musical sounds of any pitch or intensity, produced in the air or water. Concussions, such as striking the walls of the aquarium in the case of normal animals, or clapping the hands or firing a revolver in the case of strychnized animals, produced marked reactions, especially in the latter; but such reactions were equally well-marked after both ears were removed, and still remained after the removal of the whole cerebrum and a portion of the mid-brain. His experiments leave no doubt of the correctness of his conclusions, which were: "(1) That hearing through the 'auditory organ' cannot be demonstrated in the goldfish; (2) nevertheless, they react to sound waves, which they perceive through a specially developed skin-sense."

In a subsequent paper Kreidl\(^2\) explodes the oft-repeated tale of hearing by fishes that come for their food at the sound of a bell, by investigating carefully the actions of trout at the famous old Benedictine monastery in Krems, Austria. He proved that the fishes come because they see the man who brings the food, and appreciate the vibrations of the water caused by his step and communicated through the stone basin; and that, when these are excluded, the sounds of the bell have no effect.

The conclusion seems justified beyond doubt that fishes do not possess the power of hearing, in the sense in which the term is ordinarily used.

We must believe that in vertebrates this sense was evolved along with a change of the mode of life from a water to a land existence, and was contemporaneous with the appearance of a papilla acustica basilaris.

It appears plain that the sole function of the ear in Fishes is equilibration.


Functions of the Ear and Lateral Line in Fishes.

The mechanism by which Fishes appreciate certain mechanical vibrations and which Kreidl proved not to reside in the ear, is no more understood in them than it is in other animals and in human beings. This power is widespread in animals, even in many Invertebrates in which there is an absence of the power of hearing, e.g., in earthworms, and it is astonishingly developed in some human beings. My friend, Professor Hallock, tells me that Helen Keller, who, it is well known, is totally deaf and devoid of other special senses except that of touch, is able, by keeping her fingers in contact with the larynx of a person who is singing, to appreciate accurately the changes in pitch; she can thus accurately reproduce with her own voice the notes sung by her companion. There is no question here of the absence of the sense of hearing, yet the vibrations are appreciated. As regards these two sense-activities, the case of the normal fish is without doubt analogous to the case of such defective human beings.

II. The Lateral Line.

The original view of the function of the lateral line was that its canal produced mucus for moistening the surface of the body of the fish. When in 1850 Leydig discovered the numerous sense-organs in it and later ascribed to them the mediation of a sixth sense, the original view was laid aside for others of a sensory function. Upon little experimental evidence it has been suggested that the organs are true touch-organs, are auditory organs, that they appreciate currents in the surrounding water, the chemical nature of the water, and so on. There has been no consensus of opinion as to their exact function or mode of action.

During the summers of 1892, 1893, and 1894, I carried on at different times experiments of various kinds upon the lateral-line system (not including the ampullae of Lorenzini or Savi's vesicles). I studied several species of fishes, especially the dog-fish (Galeus canis, Mitchill), the toad-fish (Batrachus tau, L.), and the butter-fish (Stromateus triacanthus, Peck), and obtained certain suggestive results. The main points will be communicated here.

In the dog-fish the lateral-line organs of the head are supplied by the superficial ophthalmic, the buccal, and the hyomandibular branches of the seventh nerve; those of the body by the so-called lateral branch of the vagus. In this species I have cut all of these

branches, and, moreover, have stimulated the central end of the lateral branch. In the toad-fish, where the organs are normally exposed and not enclosed in canals, I have destroyed by thermo-cautery all of the organs upon one and upon both sides of the body. In general, it may be stated that the results indicate that the organs of the lateral line have a sensory function, closely connected with the motor organs and analogous to the functions of the ear, and hence may be regarded as organs of equilibrium.

Simple cutting of the lateral nerve on one side or even both sides, cutting of all the nerves supplying the lateral-line organs of both head and body, or destruction of all the organs themselves, does not seem to interfere much, if any, with the animal's equilibrium. I have observed at times an abnormally slow return to the normal position after an animal so operated upon has been turned upon his back, but whether this was due to dulling of a sense of equilibrium or to general weakness, I am unable to say. All these experiments were performed more than five years ago, however, and before experience had taught me to observe and interpret interferences with equilibrium, hence I would not now be willing to make a categorical statement regarding the effects of operations of this kind. The animals so operated upon are always much less active than before; they swim little, lie quiet, and rarely survive more than a day or two at most.

An extension of such operations has given more decided results. It occurred to me that a reduction of the motor mechanism employed in maintaining equilibrium might be an indirect aid in demonstrating a possible equilibrium function in the lateral-line organs. In the toad-fish, which spends much of its time lying upon the bottom of the sea, especially in holes under stones, the pectoral fins are enormously developed and seem to act as mechanical supports. Removal of these fins does not, however, of itself cause marked inconvenience in the maintenance of statical equilibrium or the performance of movements; the subsequent removal of the two smaller ventral fins is followed by no apparent genuine lack of the power to appreciate equilibrium and only a comparatively slight handicapping of the power of movement. It is remarkable how closely the actions of a fish deprived of these four fins resemble those of a normal fish; he is lively, vicious, quick in responding to mechanical stimuli, and certain in his movements; he guides himself accurately, turns about suddenly, and moves forward without lateral swaying of his body. But removal of the four fins combined with destruction of all the
organs of the lateral line (except the supraorbital ones, which are few in number and lie too deep for ready operation), produces a marked effect. This has been performed in several individuals. No genuine forced movements seem to follow, but there are decided evidences of a lack of the sense of equilibrium. This is manifested in various ways. There is decided uncertainty in movement, the animal swaying from side to side in forward progression. Such a fish is easily turned upon his side or back and lies quiet in this position. In one case, some two hours after the operation, the toad fish was turned upon his back upon the bottom of his aquarium and remained thus for fifteen minutes, apparently without discomfort, and without attempting to return to the customary position. He was then returned to the latter by the hand. Such a fish swims irregularly upon his back or his side, with a general preference for the normal attitude. In one case in which the lateral organs of one side only were destroyed, and the pectoral and pelvic fins were removed, the power of maintaining equilibrium was found to be markedly weakened. When tested five hours after the operation, and presumably after the direct shock of it had passed away, the fish lay on his back when placed there; in swimming upward he thrust his head far out of water in much the same way as a fish deprived of his otolithic organs; and he showed the lateral swaying movements and uncertainty in forward progression, mentioned above. On the next day he exhibited the same phenomena. All the actions of a fish so operated upon remind one much of a lobster that has lost his otolithic sacs and chelae. The phenomena indicate strongly that the organs of the lateral line have something to do with equilibrium. In this connection it is of interest to know that Bonnier has recently found that fishes whose lateral organs have been destroyed by galvano cauterity have largely lost the capacity of correct orientation in presence of disturbances in water.

It might be objected that the severity of the operation of cauterizing so many spots in the skin and removing the four fins might of itself be the cause of the disturbances of equilibrium above described. I have anticipated and nullified the possible force of such an objection by cauterizing an equal number of spots upon the skin of a nor-


normal fish, carefully avoiding the lateral line, and then removing the four fins. Such an animal does not behave differently from one lacking the fins and not otherwise injured; he is active and certain in his movements, shows no lack of equilibrium, and in general closely resembles a normal fish.

But perhaps more significant than the above experiments on elimination is the result of stimulating the central end of the lateral nerve. In the dog-fish I have cut the nerve upon one side and stimulated it by an induced current just behind the head, thus including the nervous supply of all the organs of that side of the trunk. The result is perfectly coördinated, definite movements of the fins of both sides of the body. These fin-movements are the same as those called out by stimulating centrally the cut acoustic of the opposite side, and the same as those resulting from section of the acoustic of the same side. Thus, stimulating the left lateral nerve centrally caused: the two dorsal fins to move to the right; the caudal fin to move to the right; the left pectoral fin to move upward; the right pectoral fin to move downward; the two pelvic fins to move like the corresponding pectorals. This is exactly the result of stimulating the central stump of the right acoustic, and also the exact result of cutting the left acoustic. In the case of the acoustic I have shown that the result of stimulation is only what would be expected from a simultaneous and equal stimulation of the three ampullar branches of the acoustic. Since these branches are plainly equilibrative in function, it would seem to suggest strongly that the lateral nerve is also equilibrative. Occasionally, movements of the fins in directions opposite to those specified above take place, but they are by no means so constant or persistent, and, thus far, I have not attempted to determine the conditions of their appearance. In this connection it may be recalled that moderate or strong stimulation of the ampullae of the semicircular canals causes movements of the eyes in a certain direction (principal function), and slight stimulation causes movements in exactly the opposite direction (subordinate function). Movements of the trunk also result from stimulation of the lateral nerve, but thus far I have not endeavored to analyze them.

This is the extent of the experimenting that I have performed upon the lateral line, but, so far as it goes, it seems very suggestive. It would be interesting to test the lateral nerve at different parts of its course, and observe whether movements of the fins of different

1 Lee: Journ. of physiol., 1894, xvii, p. 192.  2 Ibid, 1893, xv, p. 311.
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segments result. Further, I have observed no eye-movements from lateral stimulation. It is conceivable that eye-movements may be mediated by the lateral-line organs of the head only, but so far I have not tested this possibility by stimulating the branches of the seventh nerve.

Without further work, which is already projected, it is impossible to specify in detail the nature of this possible equilibrative function of the sense-organs of the lateral line. The phenomena suggest Schulze's 1 idea of the possibility of appreciation of mass-movements of the water or of movements of the body through the water, just as the movements of the hairs of the crista through the inert endolymph mediate the appreciation of rotary movements of the body. Such a function seems more easily understood in the case of those fishes, such as the toad-fish, in which the sense-organs project freely to the outside, than in those in which the organs are enclosed within canals that open to the outside only at intervals. Yet in all species such a function seems to me a priori the most probable of all that have been suggested. The appreciation of rotary movements and that of progressive movements can hardly be separated here. It is not inconceivable nor improbable that, in addition to this function, contact with solid objects, such as the sand and stones at the bottom of the sea, may stimulate the organs and assist crudely in giving the fish a notion of his position in space. The structure of the organs suggests, as in the sense-organs of the ear, that they are pressure-organs of some kind. In this connection the work of Fuchs 2 is interesting. This investigator has shown by experiments upon Raja clavata and Raja asterias that touching the skin over the ventral canals of the head causes in most cases a negative variation of the current of rest in the cut nerves supplying these canals. He infers, not wholly with justification it seems to me, that the canals mediate the appreciation of changes of hydrostatic pressure.

In whatever specific way future experiments may prove the sense-organs in question to act, it is at least clear that those of the trunk are connected through the central nervous system with the muscles of the fins, and that a reflex arc is thus present, analogous in nature to that formed by the same motor mechanism with the acoustic nerve.

We must believe, moreover, that the impulses of whatever kind that come to the central nervous system from the organs in question assist in enabling the animal to maintain the equilibrium of his body: in other words, the organs of the lateral line are equilibrating organs.

Hence, a consideration of the physiology of the ear and the system of the lateral line, by showing that the two systems of organs are functionally analogous, would seem to offer indirect support to the morphological deduction that the former organ is a derivative of the latter. The primitive function, not improbably, was the appreciation of movements of the water against the body and movements of the body in the water, combined with appreciation of contact, and, hence, indirectly and crudely, of position in space; by the exercise of this function, through functional connection with the locomotor mechanism, the equilibrium of the body was maintained. In some unknown way a bit of this sensory system became cut off from the rest and enclosed within the skull; it still retained its power of appreciating bodily movements and contact, and this power became refined and differentiated; the capacity of appreciating rotary movements was separated from that dealing with progressive movements and position in space, and the two were associated with distinct organs, the semicircular canals on the one hand, and the otolithic organs on the other, which were appropriately constructed to subserv their respective functions. Thus a well-marked sensory organ for equilibrium was evolved in fishes. When aquatic animals began to leave the water and live for a shorter or longer time upon the land, and the possible advantage of a sense of hearing was presented, a portion of this sensory organ of movement became still further differentiated; a new patch of sensory nerve-terminations appeared, the papilla acustica basilaris; apparatus for conveying the waves in the air directly to the membranous ear was developed; and thus the power of appreciating the movements that we call sound was acquired. By natural selection this was still more refined and specialized, the range of appreciation was extended, and the result is the mammalian cochlea with its great functional powers.

It seems to me that this explains naturally and in a manner not improbable the mysterious association in one organ of two functions at first sight so widely separated as equilibration and audition.