INFLUENCE OF THE EYES, EARS, AND OTHER ALLIED SENSE ORGANS ON THE MOVEMENTS OF THE DOGFISH, MUSTELUS CANIS (MITCHILL)

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The common occurrence of the smooth dogfish, *Mustelus canis* (Mitchill), in the waters about Woods Hole, the success with which this fish can be kept in confinement, and the ease with which it resists the adverse effects of operations led me to undertake a study of its more important sensory reactions. This paper deals with the effects of the following sense organs on the movements of the dogfish: Eyes, ears, lateral-line organs, the ampullæ of Lorenzini, and the organs of touch. The work was carried out at the United States Fisheries Laboratory, Woods Hole, Mass.

CLASSES OF MOVEMENTS.

The more obvious external movements of the dogfish fall into four classes. The first class consists of the movements of the eyeballs, either backward and forward, as for instance when the fish is swimming, or rolling movements such as occur when the animal is rotated on its long axis. The second class of movements are those of the false eyelid or nictitating membrane, which can be made to rise from the ventral edge of the orbit and thus cover the surface of the eyeball ordinarily exposed. The third class of movements are the respiratory movements of the gill region. These vary much in rate dependent upon the momentary state of the animal. In a large resting fish they vary from about 35 to 45 movements per minute. The same fish when swimming slowly will respire 50 to 55 times per minute. In vigorous swimming the rate is doubtless still more rapid. The fourth class of movements are the locomotor movements which are carried out in the main by the fins. The specific gravity of the dogfish is slightly greater than that of sea water and when the fish ceases to swim it sinks to the bottom. As it has no swim bladder, it is incapable of floating in the water as many teleosts do, and whenever it is off the bottom it maintains its position necessarily by active swimming. In this operation all the fins are concerned, but of these none is so important as the caudal fin. If one dorsal fin or the anal fin is removed, the fish swims apparently as well as ever. If

all three fins, i. e., the two dorsal and the anal, are removed the efficiency in swimming is somewhat reduced though not as much so as when the caudal fin alone is removed. The removal of all the median fins leaves the fish still capable of forward locomotion but only with excessive effort, largely because of the small amount of surface that can be opposed to the water. The removal of the paired fins from one or both sides has very little effect on the swimming of the fish, though its ability to turn accurately is much reduced. The removal of all fins both median and lateral leaves the animal still capable of wriggling through the water, though with a somewhat rolling motion. It is probable that under normal conditions the lateral fins correct this roll. Of all the fins the caudal is the one chiefly concerned with locomotion; the others serve mainly as keellike guides and rudders, though the median fins other than the caudal certainly supplement this fin in the movements of swimming.

THE EYES.

When a normal dogfish is first put into even a large aquarium, it swims about with much awkwardness, colliding with such objects as the dark walls and glass sides of the aquarium and avoiding only the more conspicuous bodies, such as light-colored rocks, The impression given to the observer is that the dogfish has very poor vision, and etc. this opinion is current among many fishermen. After a few hours, however, such a dogfish will adjust itself to its new quarters and will swim about with only an occasional collision. That this condition is not dependent upon its acquaintance with the currents, etc., in the aquarium is shown from the fact that if the dogfish is etherized and its optic nerves are cut, it will swim slowly about bumping its nose continually against solid objects precisely as a blinded animal might be expected to do. Nor does it ever recover in any very marked degree from this state. It therefore seems clear that a normal dogfish possesses fair vision and that it is capable of adjusting its responses to the stimuli in its retinal fields with such precision that its locomotion is in large part guided by these stimuli. The relation of the two eyes in these responses is clearly seen when only one optic nerve is cut, Under this condition the dogfish will still swim much as a normal one does, though collisions will occasionally occur on its blinded side. Such a fish never moves in circles, as many of the lower animals do, showing that the directive discrimination in one retinal field is of more importance in its locomotion than the mutual relation of the two retinas.

Not only does a blinded dogfish fail to recognize the detailed illumination of its surroundings, but its remaining sensory apparatus is apparently unstimulated by light. If a beam of concentrated sunlight is thrown on any part of the skin of a blinded dogfish, no response is obtained, showing that the integumentary nerves of these fishes, unlike those of the young lamprey (Parker, 1905 b) and many amphibians, are not stimulated by light.

Another feature to be observed in the blinded dogfish as compared with the normal one is the region of its swimming. A normal dogfish will swim indiscriminately through an aquarium, whereas a blinded one remains usually near the bottom and swims about in

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such a way as to be almost continually in contact with some solid surface, as though relying on its sense of touch for its location.

If the nictitating membranes of a dogfish are drawn across the eyes and stitched to the upper eyelids, the fish does not respond as a blinded fish does, but swims about in the most brightly illuminated part of the aquarium. This is usually the top, but it may be the bottom if light is admitted from low down on the sides. Such fishes are liable to collide with solid bodies in their paths of motion and are doubtless reduced to the condition of many lower animals in which the visual organs are not image-forming eyes but mere direction eyes, i. e., the fishes are reactive to the presence or absence of light and to the direction of a chief source, without, however, being able to respond to the details of illumination in their surroundings. This condition is doubtless dependent upon the fact that the intercepting nictitating membranes are at best only slightly translucent and thus prevent the formation of efficient retinal images.

When a bright light is brought to the glass side of an aquarium otherwise dark, normal dogfishes and those whose eyes are covered with the nictitating membranes will gather near it. Very likely a submerged light in clear water could thus be made a lure for dogfishes in the night. These reactions, however, cease in a generally illuminated field such as surrounds the dogfish during daytime. As might be expected from what has already been observed, blinded dogfishes show no response to a single light in an otherwise dark field.

From these observations it is clear that the only part of the dogfish sensitive to light is the eye and that the retinal image is an important factor in guiding the locomotion of these fishes. In an otherwise unilluminated field dogfishes will swim toward a single light, i. e., they are positively phototropic.

THE EARS.

The original function attributed to the vertebrate ear was of course that of hearing. In 1828 Flourens recorded observations that led to the belief that the ear was also concerned with equilibrium, and this opinion, though not without its opponents, has been supported by Goltz, Mach, Breuer, and others. In 1891 Ewald advanced the view that the ear likewise had to do with the maintenance of muscular tonus. These three functions are the chief ones ascribed to the vertebrate ear. To what extent they are characteristic of the ears of the dogfish will now be discussed.

In a previous paper (Parker, 1903), on hearing in fishes, I made the statement, recently confirmed by Lafite-Dupont (1907), that the ears, lateral-line organ, and skin of the dogfish were not open to stimulation by vibrations such as are produced by a bass-viol string and transmitted to this fish through the water. But I also noted that this fish was responsive to the same vibrations when it rested on a solid transmitting base. It would seem from these observations that the smooth dogfish is at best only slightly sensitive to material vibrations, and my subsequent work has shown the correctness of this opinion. To test the question of hearing in the dogfish, I followed the plan previously adopted for *Fundulus* (Parker, 1903), and experimented in the main with three classes of fishes: (1) Normal individuals; (2) those with the eighth nerve cut but

with the surface of the skin normally sensitive, and (3) those with the ears intact but with the surface of the skin rendered insensitive.

When a normal dogfish is placed in a large wooden aquarium, it at first swims about in a disturbed and irregular manner. After half an hour or so it becomes so far accustomed to its new quarters as to move about with apparent complacency. If, while the dogfish is swimming through the water and is not in contact with the sides or bottom of the aquarium, a fairly vigorous blow is struck with a mallet on the wooden wall of the aquarium, the dogfish will almost invariably respond with a sudden jump forward. This can be repeated many times provided that a few minutes intervene between the trials. If the blow is not very vigorous the response may be only a slight waving of the fins, best seen on the posterior edges of the pectorals.

To get some measure of this response, I suspended on a stout cord from the ceiling of the room in which the experiments were conducted a large spherical iron weight so that it formed the bob of a pendulum which, when at rest, just touched the middle of one of the wooden sides of the aquarium. By drawing this iron bob away from its position of rest and letting it swing squarely against the wooden side of the aquarium, a noise was produced that would be louder or fainter depending upon the distance between the bob and the aquarium side when the bob was liberated. The momentum with which the blow given by the bob was struck was taken as a rough measure of the noise produced. As the whole apparatus was a simple pendulum, it was comparatively easy to make the necessary calculations for a scale to be placed next the cord of the pendulum to indicate the positions from which the bob must be liberated in order to generate given momenta. The length of the pendulum was 260 centimeters and the weight of its bob was 3,800 grams. The momenta used in the experiments and expressed in centimeter-gram-second units were (1) 83,600, (2) 125,400, (3) 167,200, (4) 250,800, and (5) 334,400, or, calling momentum (1) unity, they could be more conveniently designated as 1, 1.5, 2, 3, and 4.

Normal dogfishes when swimming freely in the water of the aquarium occasionally responded by pectoral fin movements to the sound generated by the bob of the pendulum striking the wall of the aquarium with a momentum of 1, and invariably responded when the momentum was 1.5. The range from 1 to 1.5 was therefore taken as the range of minimum stimulus for a normal fish.

Six dogfishes, which had previously been tested to ascertain that they were normally responsive, were now subjected to the operation for cutting the eighth nerve, and after recovery they were again tried for their responsiveness. None reacted to the sounds produced when the ball struck the side of the aquarium with a momentum of less than 3, and they responded invariably only when the momentum was 4.

At first sight this considerable reduction in the sensitiveness of the fish might be taken to be a final answer to the question of the significance of the ear as a receptive organ for sound, but it is possible that its real explanation lies in the reduced physiological state of the animal as a result of so severe an operation as that of cutting the eighth nerve. I therefore repeated these tests on several dogfish in which for other purposes the optic nerves had recently been cut, and I found that notwithstanding the severity of the operation these fishes were as sensitive to sounds as normal fishes are. I therefore believe that the loss of sensitiveness in dogfishes whose eighth nerve has been cut is not due to the severity of the operation, but to the actual loss of the ear as an effective sense organ.

As it has often been maintained that the responses of fishes to sounds depend upon stimulation of the skin and not of the ears, I prepared another set of dogfishes in which I endeavored to render the nerves of the whole integument insensitive to mechanical stimulation. As in the case of Fundulus, so in the dogfish, I cut the fifth and seventh nerves as well as the lateral-line nerves. I also pithed the animals by cutting off the tail, plugging the caudal artery and vein with a ball of absorbent cotton so as to prevent excessive bleeding, and inserting a wire into the spinal canal and twirling it as far forward as the neck region so as to destroy the spinal cord. After recovery from these operations the skin of the dogfish was found insensitive to mechanical stimuli except in the region of the gills and pectoral fins. In my experiments on Fundulus this region was also of necessity left sensitive to mechanical stimulation and might therefore serve as a receptive surface for sound vibrations. In reporting my results on Fundulus I noted this fact with regret, and it has been used as an argument against the validity of my results by a recent critic, Körner (1905). It seemed to me therefore highly important to ascertain whether this region of the skin played any important part in the reception of sound, and for this purpose I attempted to render it insensitive without, however, interfering with the nervous control of its underlying muscles.

To accomplish this end I endeavored to cut the dorsal roots of the spinal nerves of this region, but my efforts were unsuccessful. I finally found in cocaine a means of accomplishing my purpose. If a 2 per cent solution of cocaine is applied to a tactile area on a dogfish's skin, in from fifteen to twenty minutes the area becomes somewhat mottled and loses its sensitiveness. I therefore placed, on a frame in the open air, a dogfish in which the appropriate nerves had been cut, and after having started a current of sea water through its mouth and gills for respiration I covered the remaining sensitive part of its skin in absorbent cotton soaked in 2 per cent cocaine. Before the application of the cocaine the dogfish responded by movements of the pectoral fins to mechanical stimuli applied to these fins, but after a quarter of an hour these responses ceased. After half an hour's treatment the dogfish was taken from the frame and suspended by its anterior dorsal fin in the sea water of the wooden aquarium and subjected to sound stimuli. The animal occasionally responded by movements of the pectoral fins to the sound produced when the bob of the pendulum hit the side of the aquarium with a momentum of I and it invariably reacted when the momentum was 1.5 or more; in other words, the animal, so far as its responses to sound were concerned, differed in no essential respect from a normal dogfish. Three other dogfish were tested in like manner and gave similar results. I therefore conclude that the skin of a dogfish is not essential to its response to sound.

To check these conditions in relation to the ear, two of the four dogfishes with insensitive skins were subjected to the further operation of having their eighth nerves

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cut. On testing these with sounds before the effects of the cocaine had disappeared they were found not to respond to any sounds produced by the pendulum apparatus. It therefore seems clear that the relatively slight response that the smooth dogfish shows to sounds is mainly dependent upon the ear and that this fish, like *Fundulus* (Parker, 1903), *Carassius* (Bigelow, 1904), and *Cynoscion* (Parker, 1910), may be said to hear.

Having ascertained that the smooth dogfish is capable of hearing, I next endeavored to determine what part of its ear is concerned with this function. The deep seat of this organ and its relatively small size made my task so difficult that I was at last obliged to abandon it, but one set of experiments in this direction are not without value. Following the directions given by Lyon (1900) for cutting cranial nerves, I found that the sacculus of the ear of the dogfish was accessible for operative purposes through the roof of the mouth and that this organ could be exposed in favorable cases without causing bleeding. I made this exposure in seven dogfishes with the intention of opening the sacculus and washing out its otolith with a fine current of sea water. In four cases the operation was successful on both sides. These four dogfishes were given time to recuperate and then were tested. All were strong and vigorous in their swimming and, contrary to what would be expected from the statement made by Kreidl (1892). they were absolutely indistinguishable from normal individuals in their equilibrium. In their reactions to sounds produced by the pendulum apparatus they resembled fishes in which the eighth nerves had been cut in that they were responsive only to sounds made by a blow of the bob with a momentum of 3 or more.

Objections might be raised to these results, at least so far as equilibrium is concerned, because the animals tested had had both otoliths removed, and in fact Loeb (1891 a) has already declared that when only one otolith is taken out the animals show disturbed equilibrium in that they swim with the operated side low. I removed a single otolith from each of three dogfishes, but though I kept them under observation several days I was never able to make out any characteristic irregularity in their equilibrium. These results show that the large friable otoliths of the dogfish's ears, like those of *Siredon* and the frog (Laudenbach, 1899) and *Cynoscion* (Parker, 1908), are not essential to equilibrium, but are, as in the case of *Cynoscion* at least, concerned with hearing.

That the ears of the dogfish have to do with equilibrium is so well attested by previous investigators that this aspect of the subject calls for no special reconsideration. After having had their eighth nerves cut, some smooth dogfishes will acquire the ability to swim slowly in normal equilibrium—a condition which, as experiments have shown, is certainly in part dependent upon the eye and perhaps in part upon the sense of touch; but these animals when made to swim with ordinary rapidity lose equilibrium and present a condition of irregular locomotion such as characterizes the majority of operated animals at all times.

Possibly exceptional cases of this kind influenced Sewell (1884) and Steiner (1886, 1888) in their opinion that the ear of the dogfish was not concerned with equilibrium—an opinion that has been set at naught by the more recent work of Loeb (1891 b), Kreidl (1892), Lee (1892, 1893, 1894, 1898), Bethe (1899), Gaglio (1902), and Quix (1903).

Although some of these investigators differ among themselves as to the details of their conclusions, they all agree in ascribing a function of equilibration to the ear, and this conclusion is abundantly borne out by my own observations. If both eighth nerves of a smooth dogfish are cut, the animal becomes profoundly disturbed in equilibrium. It usually swims in irregular spirals and will rest on the bottom in any position, dorsal or ventral side up. When only one nerve is cut, the disturbance is much less pronounced. After such an operation a dogfish will often swim and rest in the usual position and be almost indistinguishable from a normal individual. If such animals are made to swim rapidly, however, they usually show much unsteadiness and may even lose equilibrium. A comparison of dogfishes in which one nerve has been cut with those in which both have been severed makes it perfectly evident that the loss of one ear can be largely compensated for by the other and that it is only after the loss of both ears that profound disturbance of equilibrium can be looked for with certainty. These conditions are so uniform and clear that the conclusion is fully justified that the ear of the dogfish is a receptive organ from which emanate impulses that influence its locomotor mechanism so far as to retain the equilibrium of a body that is naturally in a somewhat unstable state.

A dogfish in which one of the eighth nerves has been cut is slightly weaker after the operation than before it, and one in which both eighth nerves have been cut is invariably very much weaker than it was previously. These differences are very noticeable in handling the fishes, and they are characteristic of operations involving the eighth nerves. Where, for instance, the second nerves have been cut, this diminution in muscle tonus does not occur. It is, as Ewald (1892) has pointed out, a distinguishing feature of the eighth nerve.

From these various observations and experiments on the ears of the smooth dogfish, I conclude that these organs, like the ears of the higher vertebrates, are concerned with hearing, equilibrium (Flourens), and muscular tonus (Ewald), and that the otoliths are not essential to equilibrium, but are in some way concerned with hearing.

THE ORGANS OF THE LATERAL LINE.

As I have elsewhere shown (Parker, 1905 a), the lateral-line organs of the smooth dogfish can be stimulated by material vibrations of low frequency. This stimulation gives rise to movement of the fins, especially of the caudal fin, and to actual locomotion in which the fish swims, where possible, downward into deeper water. Lee (1898) has maintained on the basis of the movements of the fins as a result of the direct stimulation of the lateral-line nerves that the lateral-line organs are concerned with equilibrium and that in this respect they are closely related to the ear. I have repeated Lee's experiments so far as possible, but with rather different conclusions.

Lee states that if the lateral-line nerve is cut near its anterior end and stimulated centrally, perfectly coordinated, definite movements of the fins occur. Thus if the left lateral-line nerve is stimulated, the dorsal fins and caudal fin move to the right, the right pectoral and pelvic fins move downward and the left upward. It is true that if

the lateral nerve is exposed and directly stimulated electrically precisely these move-They also occur if the lateral line on the surface of the body is stimulated ments occur. electrically. But none of these movements take place if previous to the stimulation of the regions mentioned the spinal cord is destroyed. If the spinal cord of the dogfish is destroyed from the tail to the neck region and the animal allowed to recover, no amount of stimulation of the lateral line or its nerve in the region in which the cord has been destroyed will, in my experience, call forth the fin movements described by Lee: but if the lateral-line nerve is cut anteriorly these movements may be induced by stimulating any spot along the appropriate side of the body, provided the stimulus is applied anterior to the pelvic fins. Thus the responses described by Lee depend on a stimulation of spinal nerves, not of lateral-line nerves. As Lee nowhere states that he took steps in his experiments to eliminate the spinal nerves, I suspect that he mistook reactions dependent upon these nerves for true lateral-line reactions. Thus the evidence that he has brought forward for the equilibrium function of the lateral-line organs falls to the ground.

Although the lateral-line organs, in my opinion, do not influence the fin movements in the way that Lee believed, they are capable of effecting important responses. If the skin of a dogfish whose spinal cord has been destroyed is pressed upon above or below the lateral line, no reaction occurs; if, however, the pressure is brought to bear on the lateral line itself, there is a considerable slowing in the respiratory rate or even a temporary cessation of movement. This respiratory response can also be obtained when a current of water is played on the lateral line, but it disappears permanently on cutting the lateral-line nerve. With the lateral-line system intact it is, however, so invariable in its occurrence that I believe that pressure may be regarded as one of the normal means of stimulating this system. This view has already been advanced by Fuchs (1894) as a result of his experiments on Raja.

The influence which the lateral-line organs of the dogfish have on its respiratory rate is not limited to the side stimulated. A stimulus applied either to the right lateral line or to the left one will effect a change in the whole respiratory mechanism.

The experiments thus far carried out show that the lateral-line organs of the dogfish are stimulated by vibrations of low frequency and by simple pressure, both mechanical forms of stimuli, and that these organs can influence the respiratory rate and the locomotion of the animal, but not in a way especially concerned with equilibrium.

THE AMPULLÆ OF LORENZINI.

The head of the dogfish is marked with symmetrically placed clusters of minute pores which are often mistaken for lateral-line pores. Each of these pores opens into a long, narrow tube which makes its way below the skin and ends in a bulb-like enlargement. These are the ampullæ of Lorenzini. They have long been suspected of being related to the lateral-line organs, an opinion that is supported by their innervation. So far as I am aware, no experimental evidence has thus far been obtained concerning their function. As the region in which they occur is covered with a skin filled with

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tactile organs and penetrated by certain parts of the lateral-line system, it was necessary first of all to eliminate these sense organs before conclusive experiments could be made on the underlying ampullæ. To effect this elimination, I painted the skin over a given patch of ampullæ with a 2 per cent solution of cocaine, hoping thereby to destroy the receptiveness of the superficial tactile and lateral-line organs and leave that of the deepseated ampullæ. After half an hour I tried various stimuli on this surface and I found that pressure upon this spot was accompanied by a momentary slowing or cessation of the respiratory movements. As I had also obtained this reaction from the lateralline organs and as these organs were possibly involved here, I abandoned this method of procedure for another. This consisted in dissecting off the skin over a patch of ampullæ and thus removing the tactile and lateral-line endings completely. If, now, into the mass of ampullæ thus exposed, a blunt glass rod is gently pressed, the same partial or complete respiratory inhibition takes place as was seen in the earlier experiment. As this ceased on cutting the bundle of fine nerves that supplied the cluster of ampullæ, I conclude that pressure is a normal stimulus for the ampullæ of Lorenzini, and that these organs are in truth closely related to lateral-line organs.

THE ORGANS OF TOUCH.

The whole outer surface of a smooth dogfish, like that of many higher vertebrates, is open to stimulation from a deforming pressure, i. e., it is sensitive to touch. As a result of this stimulation no alteration in the respiratory rate has been observed, but movements of the nictitating membrane and fins have been called forth. The fin movements often appear in coordinated groups such as would result in normal locomotion. Wherever tactile stimulation occurs, electrical stimulation is also usually effective, with this difference, however, that the electrical stimulation may call forth a much more vigorous response than the purely tactile does.

The surface of the dogfish's body may be divided into some five tactile regions characterized mainly by the responses that result from their stimulation. The first of these regions is the part of the head anterior to the hindermost limits of the orbit. So far as the fins are concerned tactile stimulation of this region results in only slight irregular movements. When the stimulus is applied to a considerable stretch in front of the eyes. or above or below them, or to a very restricted area behind them, quick closing movements of the nictitating membrane occur. These movements, which are the really characteristic ones of this region, are strictly homolateral in that mechanical stimulation of the appropriate region on one side of the head never calls forth movements in the nictitating membrane of the opposite side, but only in that of its own side. Since they originate from a stimulus that in most cases is anterior to the eye and result in a closure of the nictitating membrane, they may be regarded as primarily concerned with the protection of the corneal surface of the eye-ball. Strange to say, they do not occur with anything like the certainty when the cornea is touched as when the adjacent skin is stimulated. This protective winking movement can be called out so far as I am aware only by mechanical stimulation; the nictitating membrane is not moved when intense sunlight is thrown into the eye or the surface of the cornea is bathed with even so stimulating a solution as normal sulphuric acid. The protection apparently is only against mechanical injury.

The second general tactile region includes the whole surface of the fish from the posterior edge of the orbits to the pelvic fins except the ventral surfaces of the pectoral fins and the skin on the breast between these fins. The second region is bilaterally divided and a stimulus applied to any part of one side may call forth a movement of the two dorsal fins, the caudal fin, and the anal fin away from that side, an upward movement of the pectoral and pelvic fins of the stimulated side, and a downward movement of those of the opposite side, a group of coordinated movements already described by Lee (1898). These movements are undoubtedly concerned with guiding the fish in swimming.

The third general tactile region extends from the pelvic fins to the end of the tail. This region, like the preceding one, is bilaterally divided. The same fins that respond to the stimulation of the second region also respond to stimuli applied to this region, but the response is in the reverse direction. A stimulus applied to one side of this region calls forth a movement of the median fins toward that side, a downward movement of the paired fins of the same side, and an upward movement of those on the opposite side. Comparing this condition with that of the second region, it is clear that the fin responses produced by stimulating a given side in the second region agree with those called forth by stimulating the opposite side of the third region. This diagonal relation is probably significant in the swimming movements of the dogfish.

The fourth tactile region is the ventral surfaces of the pectoral fins and the breast region. Mechanical stimuli applied to almost any part of these surfaces call forth a fairly symmetrical ventral approximation of the pectoral fins. At times there is almost an overlapping of the posterior median edges of the two fins, but never a scissors-like movement, such as Sheldon (1909) has demonstrated by chemically stimulating the breast region.

The fifth region is the ventral surfaces of the pelvic fins. When these surfaces are stimulated a symmetrical movement of the pelvic fins toward the median plane takes place, thus closing the cloaca. There is some correlation between the response of this region and that of the fourth, though in the main the two regions are independent.

The movements of the fins produced from the fourth and fifth region partake of the nature of protective movements in that they wipe surfaces or close apertures. They probably have little to do with locomotion. The reactions initiated in the second and third regions are chiefly locomotor and probably have little significance otherwise. In this connection the movements of the posterior dorsal fin are significant. This fin moves with extreme freedom and in such a way that its posterior finger-like tip is wiped over the back of the animal on the side stimulated as though it were intended to remove some offending body. If, however, a weak stimulus is applied to a point low down on one side of the body, the fin thus made to move slightly to one side, and then a strong stimulus is applied between the dorsal line and the fin, the fin instead of wiping back over the newly stimulated part turns still further away from the dorsal line and vigorously wipes a part of the skin to which no stimulus whatever has been applied. It is

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therefore evident that the direction of the movement of this fin is dependent upon the stimulation of any part of a given side and is not related to particular spots on that side. Hence the movement probably subserves a general function like swimming rather than a special one like the protection of the surface.

Not only are these fin movements called forth by the obvious tactile stimulation of given areas of skin, but, as Lyon (1900) first pointed out, they can be induced by moving certain parts of the body. If the end of the tail of a dogfish is seized symmetrically and turned to a given side, the dorsal and anal fins bend toward that side as though a tactile stimulus had been applied to that side in what has been called the third tactile region. That this reaction is really dependent upon a mechanical stimulation of the skin and not upon the activity of more deeply seated sense organs, is seen from the fact that the reaction disappears when the skin of the tail is rendered insensitive by about twenty minutes' treatment with a 2 per cent solution of cocaine. Not only can these correlated fin movements be called forth by turning the tail, but they can also be induced by moving the head. If the head of a dogfish is taken hold of symmetrically and turned toward a given side the median fins, particularly the anterior dorsal, turn toward that side. Thus the tactile surfaces of the dogfish are most intimately concerned with the correlated movements of this animal's fins and in such a way that they are undoubtedly significant factors in the animal's locomotion.

CONCLUSIONS.

The eyes of the smooth dogfish are the only receptive organs for light possessed by this animal. The dogfish reacts with sufficient accuracy to the details of its retinal images to show that it has moderately sharp vision. When the sharpness of its vision is greatly reduced, it becomes simply positively phototropic.

The ears of the dogfish are organs of hearing and are concerned with equilibrium and muscular tonus. The removal of their otoliths interferes with hearing but not with their two other functions.

The lateral-line organs are stimulated by vibrations of low frequency and by pressure. They are relatively insignificant as organs for the control of equilibrium.

The ampullæ of Lorenzini are stimulated by pressure and are doubtless closely related in origin and function to the lateral-line organs.

The whole integument of the dogfish is a receptive organ for mechanical stimuli. From it arise impulses for the movement of the nictitating membrane, and for a complicated system of correlated fin movements most of which are concerned with locomotion and equilibrium.

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