EXPERIMENTS UPON THE EARS OF FISHES WITH REFERENCE TO THE FUNCTION OF EQUILIBRIUM.

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THE preservation of the equilibrium of the body and the power of performing coordinated movements are of such vital importance to the well-being of the animal that we should expect on *a priori* grounds that the utmost precautions would be observed in the physiological structure of the body to preserve in normal condition the sensations which give rise to a knowledge of position and thus supply the coordinating motor centres with the information necessary for their action. We find, accordingly, that ideas of position, or what may be called sensations of equilibrium, may be excited by impulses reaching the brain along very diverse channels. Indeed it might reasonably be urged that every sensation pays its tithe to the general sense of equilibrium. But for the present purpose it is only necessary to call attention to the well-known fact that our ideas concerning the position of our bodies are affected quite distinctly through the visual, tactile and muscular mechanisms; and when the combination of the various sensations excited through these different instruments does not accord with experience, the sense of equilibrium is disturbed and manifests its trouble in movements falsely designed to steady the body. But the fact that a knowledge of changes of position may be acquired without the activity of any of these sources of information, has suggested the hypothesis that there is in the body a special peripheral sense organ of equilibrium capable of being excited by movement; and the great number of physiological experiments which have confirmed the original discovery of Flourens have indicated as this peripheral organ the system of membranous semi-circular canals of the aural labyrinth. It need hardly be repeated here that the most elaborate and complete explanation of the physiological action of this supposed apparatus of equilibrium is that contained in the essentially similar theories of Goltz, Crum-Brown and Mach. According to these authors, the endolymph within the membranous labyrinth presses, with every new movement of the head, with greater or less force upon the endings of the auditory nerves within definite ampullæ of the canals and thus mechanically stimulates those nerve filaments. When a canal is severed there is supposed to be an escape of endolymph and this, by diminishing the pressure upon the ampullary apparatus, gives rise to false sensations of motion. According to this view the relation of the semi-circular canals to the sense of equilibrium is nearly as intimate as that of the eye to vision. Cyon, while assenting to the general hypothesis as to the function of the canals, believes that the disturbances of equilibrium provoked in an animal whose labyrinth has been injured are due, not to the failure of normal sensations, but to the direct irritation of the auditory nerve caused by the operation.

Baginsky[1], in renouncing all previous theories, calls attention to the fact that, in mammals, the perilymph spaces of the labyrinth are in communication, by way of the *aqueductus cochleæ,* with the sub-dural space of the brain; and that in the pigeon the interior of the labyrinth is continuous with the arachnoidal cavity through the *aqueductus vestibuli.* This author believes that all disturbances of equilibrium which arise from operations on the ear are the effect of direct irritation of certain areas of the medulla or cerebellum, and he divides the results into two groups of primary or transitory and secondary or permanent disturbances. The first effect of an operation upon the labyrinth is to place the arachnoidal space of the brain in open communication with the exterior. The alternate swelling and subsidence of the brain due to the respiratory variations of the blood flow, give all the pumping action that is necessary to force out and in the cerebro-spinal fluid and thus cause mechanical irritation of the brain by variation of pressure upon its surface at the point of the internal opening of the channel connecting the cavity of the labyrinth with that of the brain. It may be remarked that Högyes[2] describes more recent experiments in which he passed a fine tube into the brain space of a rabbit and by this means drew cerebro-spinal fluid from the region in question, without the least evidence of equilibrium disturbance. Baginsky denies, what has been so often affirmed, that lesions of individual canals are followed by specially definite peculiarities of motion or position; but some days after the apparent recovery of an animal from the effects of an operation,

[1] Baginsky, *Arch. f. Anat. u. Phys.* 1881, § 201.
[2] Högyes, *Pflüger's Archiv.* Bd. 26, § 558.

there may come on a secondary or permanent affection of equilibrium which is due to local inflammation of the brain near the labyrinthine opening, set up, no doubt, by the friction of the brain surface against the wall of the cranium, in the absence of a sufficient quantity of the cerebro-spinal fluid. Baginsky was able to functionally destroy in a dog the system of semi-circular canals on both sides and the animal, though under observation for months, showed no abnormality in its coordinating functions.

On taking up this subject more than two years ago, it seemed to the writer that the fish was better fitted than any terrestrial animal for giving an experimental solution of the problem concerning the relation of the semi-circular canals to the equilibrium sense. For in the fish it would seem that the visual, tactile and muscular sensations can have comparatively little influence in giving rise to ideas of the position of the body. The visual field of that animal is not mapped out by very clearly distinguishable objects, so that sensations arising from it probably neither normally give so much assistance to the maintenance of equilibrium nor aggravate the disturbances which may be artificially set up, as is the case among land animals. The whole surface of the body is equally touched and buoyed by the water and therefore the tactile and muscular sensations, which in the animals best known have a very important relation to the equilibrium sense, here probably have comparatively feeble influence upon the ideas of position. Moreover, the frame of the fish is incapable of that distortion which in the injured pigeon, for example, perhaps complicates the results of experimentation. For reasons like these it seemed that the fish might be expected to depend to an unusual degree, for the maintenance of its equilibrium, upon sensations arising from the stimulation of some special sense organ; and that any results arising from operations upon its ear should be complicated to a minimum degree by the sensations arising from other organs. The cartilaginous fishes were chosen as the subject for experiment because the ear of animals of that group is unexampled in the size of its parts and the ease with which operations may be carried out on it.

The experiments to be described were carried on by means of the facilities offered at the Marine Laboratory of the Johns Hopkins University during the summer of 1881 at Beaufort N. C. and again in 1883 on the Chesapeake Bay. My hearty thanks are due to Dr W. K. Brooks, Director of the Laboratory, for aid rendered in the prosecution of the work. At Beaufort large numbers of very young specimens, 12 to 15 inches long, of the common man-eater shark (*Carcharodon* ?), were caught by fishermen in their drag-nets. The common skate (*Raia*), measuring some 12 inches across the fins, was also obtained in abundance. In the Chesapeake the sharks operated upon were apparently of the same species as those found at Beaufort but of much larger size, measuring from 3 to 4 feet in length.

The anatomy of the shark's ear.

It may not be out of place to give here a short description of the arrangement of some of the parts of the shark's ear. The membranous labyrinth lies in a very roomy space which preserves the general form of the membranous apparatus though not nearly filled by it. The labyrinth is mostly firm and thick walled; the bore of the canals is relatively minute. On cutting open the labyrinthine spaces a somewhat dense, tough framework of connective tissue, rather richly supplied with blood-vessels, is seen attached to the wall of cartilage and more or less completely filling the space around the membranous labyrinth and closely investing the latter. This connective tissue roofs in the vestibule, forming a sac filled with perilymph. Looked at from above, the three semi-circular canals form a triangle with the apex near the median line; at this point the anterior and posterior vertical canals unite separately with the utriculus. The anterior canal passes forward, outward and downward, and the posterior backward, outward and downward, and each, after more or less completing a circle in its respective plane, swells out into a globular, thick-walled ampulla. The median and anterior part of the horizontal canal lies in a horizontal plane; its ampulla is near and a little below and behind that of the anterior vertical canal. Within the space inclosed by the three canals is the vestibule which is incompletely divided, by a cartilaginous partition, into a large posterior and a smaller anterior chamber which contain respectively the utriculus and the sacculus each of which is filled with a white mass of microscopic, crystalline otoliths. The utriculus is triangular in shape and lies upon the floor and median wall of the vestibule; its under wall is thin and firmly adherent to the cartilage except at the upper inner apex of the sac where the three semi-circular canals unite with it separately. The ampullæ of the anterior vertical and horizontal canals send out each a tubular prolongation of greater calibre than, and opposite to, the corresponding canals; these prolongations unite and pass as a rather thick-walled tube to enter the upper and median part of the utriculus.

The sacculus unites with the under part of the tube just described, appearing as a diverticulum from it, and the mass of otoliths within the utriculus is continuous with a similar heap in the sacculus. The branches of the auditory nerve attached to the ampullæ of the anterior vertical and horizontal canals and to the sacculus are readily seen when these parts are laid bare. Some time after death the endolymph filling the labyrinth is found as a gelatinous mass, but it appears that this is a coagulated condition and that in the living animal the endolymph is in a perfectly fluid state. The perilymph is watery in consistency and does not appear to coagulate after removal from the body.

In order to carry on the observations, a thread some ten to twenty feet in length was tied round the tail of a shark and made fast to the side of the small boat in which the operations were performed. The normal motion of the animal is unmistakable, the creature usually swimming straight away from the boat and obliquely downward. In the case of the skate the string was passed by means of a needle through the skin at the root of the tail spine and tied round the latter. By no means at my command was it possible to keep alive even uninjured sharks for many hours; but the skate appeared to be much hardier and specimens have been kept under observation in a "live-box" from one to seven days after having undergone an operation. In the experiment the fish was taken out of the water for a few seconds continuously and, while held on the side of the boat, a triangular flap, with the apex above, was cut out of the skin just over the position of the semi-circular canals and the muscular tissue covering the cartilage was cut or scraped away; the bleeding was insignificant in amount. The animals were observed during one to six hours after operating. Records were made of experiments performed upon more than ninety individuals.

Section of the semi-circular canals.

When, in a shark, either or all of the semi-circular canals on one side only are cut through the results are wholly negative; that is, the animal swims in the same manner as when uninjured; whatever peculiarity of position or motion may ensue is, without doubt, due to general muscular weakness. The same want of positive effect succeeds section of the two vertical canals on both sides, both in the shark and the skate. Each of the six canals of both shark and skate has been individually severed with uniformly negative result.

Most of the bony fishes at my command were ill adapted for experiment; but in the sea-mullet (*Umbrina*), the ear-bones are soft and spongy and the membranous canals of large size. In one such specimen all the canals on one side were cut through and in another the vertical canals on both sides were divided without producing any disturbance of equilibrium.

The methods of experiment were varied as widely as possible. In a shark, for example, the anterior vertical and horizontal canals were successively divided on both sides close to their corresponding ampullæ, and nearly completely excised, with quite negative results. In another shark, in addition to the foregoing operation, the canal of communication between utriculus and sacculus was carefully opened by a cut with the scissors on each side without effect. It will be noticed that by this procedure the saccules with the ampullæ of the anterior vertical and horizontal canals were completely sundered as channels from the rest of the labyrinth.

Effects of laceration of the vestibular sacs and of the removal of otoliths from them.

It is easy, especially in the shark, to cut away the cartilaginous roof of the vestibule without injury to the labyrinth. On removing the thin membranes contained in the perilymph space, the utriculus with its mass of otoliths is seen lying on the floor of the chamber, and the point of a glass pipette may be readily inserted through the wall of the sac and the otoliths drawn and washed out of it. Such an operation is rewarded by the most discordant results. Occasionally, both in the shark and skate, neither extensive cutting of the sac nor removal of otoliths from it produced the slightest apparent change in the behaviour of the animal. On the other hand, the same treatment was frequently followed by quite definite, undoubted signs of disturbance of equilibrium. Mere opening of the utriculus in the skate is without effect, but on removing the otoliths there is usually a tendency to swim downward in a circle toward the side operated on, and after the otoliths are removed from both sides the animal dives downward and occasionally turns somersaults in a vertical plane. The effects come out more strongly if the floor of the vestibule be smartly scraped with the point of a scalpel. Much more marked disturbances following similar treatment, have been observed in sharks. After a unilateral operation the fish dives downward, usually toward the injured side; when the otoliths are removed from both sides there follows a complex disturbance apparently resulting from a combined tendency to perform somersaults and to turn round the long axis of the body, the resultant being a spiral or corkscrew motion through the water. Similar effects sometimes follow simple laceration of the utriculus without removal of the otoliths. All disturbances of equilibrium come out most strongly when the animal is agitated, as by being suddenly thrown into the water.

By far the most positive results follow experiments upon the sacculus. When this sac in the skate is opened on one side with the scissors there is an immediate tendency to dive more abruptly than usual and to turn round the long axis toward the injured side. On pursuing the same treatment on both sides, the lateral motion commonly becomes converted into a series of somersaults. When, in addition, the otoliths are drawn from each sacculus, the skate becomes much agitated, swimming round and round in a vertical plane in a circle two or three feet in diameter. One skate treated in this way shewed the same motions with undiminished force on the seventh day after the operation. In another specimen, kept alive for two days, the definite disturbance passed finally into a more general agitation and uncertainty of movement.

It frequently happens in effective operations of all kinds that unilateral injury is followed by hardly perceptible disturbance which, however, becomes marked when both sides have suffered. In the shark, laceration of the saccules and removal of the otoliths are, as a rule, attended with the same general results which have been described in the case of the skate; but sometimes similar injuries were attended by no special disturbance.

In all instances the results of experiment were more nearly negative the more neatly the operative manipulation was performed.

Effects of operations upon the ampullæ of the anterior vertical and horizontal canals.

These ampullæ in the shark are laid bare with little difficulty; but in the skate they lie much deeper and are not readily isolated without injury to other parts.

In the preliminary operations the ampullæ were cut into or excised bodily with a somewhat constant result of equilibrium disturbance. The character of the movements after such an experiment is not simple but apparently determined by an effort to swim in more than one plane at the same time. It could not be made certain that definite differences existed between the unnatural movements arising from operations upon the various ampullæ, though after injury of those belonging to the anterior vertical canals there seemed to be a more general tendency to turn round the long axis of the body, while like treatment of the ampullæ of the horizontal canals was followed by diving movements with a disposition to perform somersaults. As before, unilateral operations caused the animal to swim toward the injured side.

For a considerable time it was thought that a peripheral organ of equilibrium had thus been proved to have its seat in the ampullæ of the semi-circular canals; but some trustworthy operations having failed to produce in a decided manner the disturbances which have been referred to, the subject was taken up at greater length and the experiments were conducted with much care.

The bundle of nerve fibres which passes from the auditory nerve to the ampulla of the horizontal canal may be readily cut across without interfering with the membranous labyrinth. When such an operation is skilfully performed on either or both sides, the result is wholly negative. I have frequently succeeded also in completely dividing and even in excising the ampullæ with like negative results.

It was thought that perhaps this want of positive effect might be due to simple removal of part of the apparatus of equilibrium whose function might be so well vicariously supplied by other organs that no marked disturbance could be detected. Accordingly it was sought to irritate the ampullary nerve endings and watch for positive effects. In a shark, four ampullæ were exposed and one by one were crushed between the blades of a pair of forceps; the fish shewed not the least disturbance of equilibrium either in the course of or after the manipulation.

It has been attempted to give with full force all positive results occasioned by operations upon the labyrinth. But the chief object of this paper is to call attention to those experiments in which the most complete destruction of the various parts of the ear were attended with no apparent failure of equilibrium.

The experiments upon sharks, as described above, were all performed upon the very young specimens found at Beaufort. But the larger animals obtained in the Chesapeake appeared to have more resistant vitality and to suffer but very slight disturbance of equilibrium after the most extensive lesions of the labyrinth. The record of a single experiment on an active shark about three feet in length may more forcibly illustrate the point. Cut through the ampullary nerve of right horizontal canal; no result. Broke, by pulling, the same nerve on the left; no result. On the right side excised the ampulla of the anterior vertical canal and divided the horizontal canal near its ampulla; no result. With forceps removed the sacculus and the ampulla of the horizontal canal on the left; the shark is much weakened but swims naturally and shows no disturbance of equilibrium. Removed the sacculus on the right side; no result. Destroyed the retina of each eye with the point of a scalpel; there is no active disturbance, but the shark swims upon the back when so placed, probably because of general weakness. Roughly scraped the utriculus on each side; the animal still swims with natural motion, though it does not turn over when placed upon the back, a result explained by its general weakness. The whole series of observations lasted about one hour.

Reflex effects upon the eyes and other organs which follow irritation of the labyrinth.

Peculiar jerking motions of the eyeballs have long been recognized as occurring during experiments upon the semi-circular canals, and have been ascribed to vertiginous sensations aroused by the stimulation of nerves subserving the sense of equilibrium. Högyes[1] has recently observed nystagmus in a mammal upon mechanically irritating the ampullary nerves. I can confirm these results to the fullest extent. Touching with an instrument the nerve attached to an ampulla in the fish produces active jerking motions of both eyes. Slight mechanical irritation of the ampulla itself has the same effect, provided its nerve be intact. Stimulation of the vestibular sacs, especially the act of removing the otoliths from them, produces violent nystagmus. Section of the canals alone was without any such result. The nystagmus lasted only during the application of the mechanical stimulus and was not necessarily followed by any disturbance of equilibrium. It is interesting to notice that operations upon the ampullæ and their nerves were very frequently followed by vomiting, often without equilibrium becoming affected.

There is an interesting reflex eye motion which has frequently presented itself to my attention, and which may be profitably considered here. If the head be quickly severed from the body of a living fish and laid upon some horizontal surface, the eyes will assume a certain position which is the result of active muscular effort. If now the head of the fish be rotated through 100 degrees or so to the right and then brought

[1] Högyes, *loc. cit.*

to rest, the eyeball can be seen, after the rotation is stopped, to slowly turn through a small angle to the right. The converse after-motion of the eye follows a rotation of the head to the left. This after-motion of the eyeball is a reflex action, involving the excitement of a nervous centre, as is proved by the fact of its failure after the destruction of the brain. The reflex may no doubt be properly regarded as the evidence of a sense of position of the eyeball, the afferent stimuli which affect the centre originating in a strain upon the muscles of the globe as it lags after the mass of the head when the latter is turned round. Special pains were taken in a number of experiments to determine whether the sense of position, as indicated by this after-motion of the eye, was affected by operations upon the labyrinth. The matter was tested by simply holding the fish upon its side and turning it through an angle in a horizontal plane; in the uninjured animal the after-motion of the eyeball was invariable. As a general result of experiments in this direction, it was found that the reflex was only interfered with by those lesions of the labyrinth which were attended with very decided and permanent disturbances of equilibrium; in such cases the eyes became fixed and staring; any manipulation of the labyrinth, however extensive, which did not result in distinctly unnatural locomotion was without influence upon the ocular reflex, and even in some cases in which equilibrium disturbance was quite apparent the reflex was tolerably well preserved, though gradually failing after more extensive injury and disturbance.

The experiments which have been described were performed under unusually favorable anatomical conditions, but it must be confessed that the results obtained are far from forming a solution of the problem investigated. Perhaps Baginsky would explain the many negative sequences of operations as due to the probable lack of respiratory oscillations in the volume of the brain which, in the bird and mammal, he supposes to be effective in forcing the cerebro-spinal fluid through the divided semi-circular canals. In this connection it is noteworthy that lesions produced less positive effect in the larger sharks, in which it may be presumed the anatomical structure of the ear has reached a more perfect development.

The positive disturbances of equilibrium so often witnessed, the reflex nystagmus following mechanical stimulation of the ampullary nerves and the vestibular sacs, and the vomiting sometimes succeeding injury of the labyrinth, all point decidedly toward some sort of functional relation between the ear and the sense of equilibrium.

But as it appears that the most extensive lesions of the labyrinth and its nerves *may* be completely devoid of any effects upon the equilibrium of the fish, it would be a bold assumption to consider that apparatus a special sense organ, in the usual acceptation of the term, for the preservation of the equilibrium of the body.

As the most decided disturbances of all kinds succeeded injuries of the vestibular sacs, particularly the saccules, rather than of the ampullæ, considering at the same time the lack of definite disturbance accompanying special lesions, and the uniform failure of positive result after section of the canals alone, it seems impossible to consent to the ingenious endolymph-pressure as propounded by Goltz, Mach and others.