SOCIETIES' PROCEEDINGS

ROYAL SOCIETY OF MEDICINE—SECTION OF OTOLOGY

SUMMER MEETING, CAMBRIDGE

June 29, 1923.

Chairman—Sir CHARLES BALLANCE, K.C.M.G.

The Work of Sherrington on the Physiology of Posture.—F. M. R. WALSHE, M.D.

Experimental Physiology of the Labyrinth.—Dr A. DE KLEIJN, Utrecht.

The papers are published in the *Journal of Laryngology and Otology*, December 1923, pp. 642 and 646.

DISCUSSION.

Sir JAMES DUNDAS-GRANT said that much of what we had heard was new to him, and Dr de Kleijn had raised so many points that it would have been most difficult to grasp them had it not been for the admirable way in which Mr Tweedie had already presented much of the matter to us. As practical people we looked for the application of these reflexes in our ordinary work. We had a good deal of knowledge of the dynamic reflex produced in the semicircular canals, but the complications arising from the other static reflexes were still unfamiliar to us. The question asked by many of us was, "Why was it that after the compensatory movement we had the return movement?" that is to say, why did we get the "jerk" of the nystagmus after the "slow drag"? He (the speaker) had read with interest the description of the experiments in which Dr de Kleijn cut through all the motor nerves of both eyes except the left sixth, and detached the left external rectus from the eyeball, connecting it with a lever so that a tracing of its movements could be obtained. He removed the cerebral hemisphere and the brain-stem down to the anterior corpora quadrigemina; when he applied cold to the opposite ear, he obtained the slow drag on the part of the left external rectus followed by the jerk. That was supposed to test whether the jerk of the return movement was of cerebral origin; he (Sir James) confessed that he could not see how the experiment exactly proved it.

There had been some further experiments made on the brain in which the bone had been removed from the frontal region and caloric stimuli applied there: the results had been very much the same as those obtained by stimulating the labyrinth. While he expressed his great admiration of Dr de Kleijn's description of his operation, he would point out that the latter had not referred to Ewald, whose labours were not forgotten, and from whom much illuminating information had been derived.

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press

Mr SYDNEY SCOTT asked if Dr Walshe, in connection with his observations, could say whether there was an alteration in Babinski's reaction in hemidecerebrates, when the positions of head and trunk were altered in space without flexing the neck?

In regard to the demonstration to-day, he felt that all must greatly admire Dr de Kleijn's brilliant piece of work and investigation. To be able to destroy the otolithic membrane by centrifugalisation, without damaging the semicircular canals, enabled the observers to isolate the functions of the saccule and utricle from those of the semicircular canals. He had shown that the changed reflexes after centrifugalisation were really due to injury to the particular parts of the labyrinth, and not, as some might possibly suppose, to injuries to brain tissue, or to the labyrinth as a whole. As Dr Gray had said "the human labyrinth is virtually a closed cavity," for we found that pressure-changes produced in the labyrinthine cavity as a whole could be estimated manometrically by inserting glass capillary tubes filled with coloured fluid. The manometric readings showed that the extreme mobility of the stapes caused a range of movement equal to quite 3 or 4 cm. (in a tube of the calibre of the superior semicircular bony canal). Unilateral obstruction in the Eustachian tube of an intact tympanum with a mobile stapes could lead to appreciable differences of the intra-labyrinthine pressure, comparing one side with the other. These facts had a bearing on the elucidation of certain forms of vertigo.

In the class of vertigo now under consideration, all the canals of the labyrinth reacted normally: the tympanum was intact: hearing for low tones was preserved: one Eustachian tube was inefficient. The vertigo coincided with this inefficiency. Dr de Kleijn would no doubt allow him to draw attention to a case that was under his observation some five years ago, that of a young man who had an extremely obstinate obstruction in the Eustachian tube of the left ear. He saw him every day in hospital in France, but it was about a week before he succeeded in inflating that very obstinate ear. At last when the air went in, the patient was seized with vertigo and nystagmus to the left. His head became inclined to the right, and the face was turned to the right. He (the speaker) kept the catheter in place and waited till the vertigo ceased, then gave one more blow, and, to his astonishment, the vertigo returned more violently, the head moved in the opposite direction, and the patient showed intense nystagmus to the right. However, the attack stopped in a moment, and everything untoward disappeared. That was not his only observation, because he had opportunities of carrying out these tests every day for about three weeks. When the drum membrane was invaginated from external atmospheric compression, and suddenly released, the head movement was always in one direction; when the tympanum was distended, the head moved in the opposite direction. F. S. Lee's investigations on elasmobranchs showed that he obtained eye-movements in one direction when he pressed *gently* on the ampullary nerve, and, when he pressed harder, the eye-movements were in the opposite direction. There seemed to be a parallel with Lee's observations and clinical findings in connection with the differences in pressure which are transmitted to the normal labyrinth from the tympanum.

Mr Scott wished to raise the question of the influence of retinal reflexes

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press

on the tonic reflexes, which he believed had been erroneously attributed to labyrinthine stimuli, though we were acquainted with the forced movements of individuals who had a prism placed in front of the eye. During investigations on flying, he had observed that slow rotation, as in a slow spin of an aeroplane, could set up forced movements of the limbs. Many experienced airmen had to close their eyes or avoid looking at the ground, if in a spin, in order to avoid these forced movements. It was a most important matter in connection with flying, but one to which little attention seemed to have been paid.

Dr ALBERT A. GRAY thought that the reason for reserve in making definite statements as to the relationship of the different structures in the vestibule was due to the difficulty in being sure of one's facts. For the most part the membranous structures were floating in a fluid which bathed them on both sides. Consequently, when the preparations were put into alcohol, distortion was almost certain to occur, with the result that incorrect judgments were formed in regard to the anatomy of the organ. Such an error was made by Frau Anna Kraus in stating that the canalis reuniens was a closed tube in the adult human subject. As a matter of actual fact, the ductus cochlearis in the adult human subject could be injected from the saccus endolymphaticus, if the injection were made before the preparation had been subjected to the influence of hardening and dehydrating agents.

He wished to pay the highest tribute of admiration to the work which had been carried out by Dr de Kleijn and his colleagues at Utrecht. The work opened up a new field not only for the otologist, but for the physiologist and the physician. It explained many of the curious symptoms which occurred in diseases of the labyrinth and also in those which affected the cerebellum. In addition, it would enable clinicians to make more accurately the diagnosis of diseases affecting these parts.

Mr ALEXANDER R. TWEEDIE said it was most gratifying to him to find his friend, Dr de Kleijn, before the Section, giving a first-hand demonstration of the work being conducted by Professor Magnus and himself in Utrecht on the otolithic and allied reflexes, an account of which he (Mr Tweedie) had endeavoured to give, very imperfectly, on his return from Utrecht in the autumn of 1921.*

Dr de Kleijn had taken infinite trouble in showing him all that he possibly could in his laboratory.

In referring to Dr Walshe's communication, Mr Tweedie pointed out that the particular aspect of the specialty, which was being discussed to-day, was inseparably associated with the nervous system, that it was not only important to receive occasionally the views of neurologists on these matters, but also that it was only by very close and constant collaboration with them that we should be able to progress in our knowledge of this subject. There was already established in France the "Société d'Oto-Neuro-Oculistique de Strasbourg," which was only concerned with phenomena of interest to these particular specialties. He thought that the example of the French should be followed, and every opportunity taken for obtaining assistance by collaboration with the oculist and neurologist.

* Proceedings, 1921-22, xv. (Sect. Otol.), pp. 15, 19.

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press

The labyrinth appeared to be essentially an organ for presiding over balance and progression, and further, according to one theory, it was primarily stimulated in fishes by sensations received by way of the "lateral line." He believed that, in the future, we should find the missing links between the association of the "lateral line" with the labyrinth and the development of the cochlea.

The main point at issue, as had been mentioned, was the clinical significance of this work. Accounts of several cases, in which these phenomena could be demonstrated, had already been published by Professor Magnus and Dr de Kleijn, and to these he had referred in his original report to the Society.* He (the speaker) was pleased to think he had already had cases of intracranial lesions, in which certain of these phenomena could be demonstrated, and he had had other patients with vertigo and with raised blood pressure, probably hypersensitive cases, in whom nystagmus could be induced by an altered position of the head in space; but whose responses to the routine tests of the semicircular canals were normal.

He believed that we should regard the otolithic apparatus in man as essentially a degenerative organ, normally of extremely little importance, and only becoming evident, so to speak, when involved in pathological disturbances. This view he thought had already been suggested by the description Dr Gray had given of the labyrinth of various fishes, birds, and animals, indicating its gradual decadence as we ascended the animal scale, and it was also supported by the fact that the otolithic reflexes were said to disappear in normal children after the age of three months, and that they thereafter, as yet, could only be elicited in cases with intracranial lesions and other pathological conditions. One reason for this gradual degeneration of the otolithic apparatus was, he submitted, the higher development of other senses—alluded to by Dr Hartridge—as the sense of touch, sight, and above all volition became elaborated, we learned to depend perhaps more on the greater efficiency of these senses, rather than be governed by an organ which automatically controlled the movements of the lower animals. It was most interesting, in this connection, to note the results of certain very practical experiments that had already been undertaken. He reminded his audience of the account by Mr Sydney Scott of his personal investigations in an aeroplane (*Journal of Laryngology*, 1920, No. 8), where he found that observers, if blindfolded, lost their sense of position in dense clouds. Similar experiments were also conducted in Holland by van Wulfften Palthe, who came to the conclusion that the vestibular organ was of no special significance to the aviator, and did not enable him to steer an aeroplane in clouds or mist (*Acta-Oto-Laryngologica*, vol. iv.). This attitude of "disregard" towards the perceptions received by way of the eighth nerve was not confined to its vestibular branch: audition was largely a matter of "disregarding" the many sounds which we had gradually learned to ignore. Indeed it was only by these means that we were able to regulate what we heard in contradistinction to the methods we could adopt in respect of our other senses, where we had the opportunity, for example, of contracting our pupils, or even closing

* Proceedings, 1921-22, xv. (Sect. Otol.), p. 24.

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press

our eyes altogether against excessive light or objectionable sights, and in the case of our sense of smell, holding the nose to avoid offensive odours.

Dr Gray had alluded to the old experiments of "hypnotising" hens by laying them down, and drawing a chalk line from the beak. These experiments had been made as early as the seventeenth century, and amongst the various animals on which they were carried out, it was stated that fish, if turned on their back, and undisturbed, could be induced to lie still in that position. Although rather incredulous, he (the speaker) found to his surprise that with very little manipulation he could keep a goldfish in a bowl of water turned on its back. It seemed quite reasonable, therefore, that these so-called instances of "hypnotising" animals must really be otolithic reflexes as suggested by Dr Gray.

The Ear as Morphologically an Apparatus for Perceiving Depth below Sea-level: An Explanation of the close Anatomical Association of Cochlea and Vestibule — H. HARTRIDGE, M.D., Fellow of King's College, Cambridge.—The reason for the close anatomical association of structures so different in their physiological purposes as, on the one hand, the semicircular canals and otolith organs, and on the other, the cochlea, has long been a matter for conjecture. The explanation here advanced is that the mammalian organ of hearing subserved in the ancestors of mammals the function of perceiving depth below the water surface, and was, therefore, associated with the semicircular canals and otolith organs in the identification of position and direction of travel.

This hypothesis is supported:—

(*a*) By the close mechanical analogy between the auditory apparatus of mammalia and the depth controlling gear in the naval torpedo, and

(*b*) By the fact that in certain fish (Siluridæ) a mechanism is found consisting of ossicles, which connects the internal ear and the swim bladder. There is strong evidence that this is used for the perception of depth and not for audition.

Analogy with Naval Torpedo.—In the naval torpedo there are two mechanisms which operate together to control the depth at which the projectile shall travel beneath the surface of the water (1) a pendulum, (2) a hydrostatic membrane.

The former mechanism under the influence of gravity records any deflection that the long axis of the torpedo may make with the horizontal, and if such a deflection exists it turns the horizontal rudders in such a direction that the deflection tends to be corrected.

The hydrostatic membrane is a sheet rubber diaphragm situated in the side of the torpedo, being in contact with the water on the outside and on the inside with the air-filled interior. If the torpedo is at a depth below the surface the hydrostatic pressure tends to press

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press

the diaphragm inwards, but this motion is resisted by a spring. If the torpedo is at the correct depth at which it is required to travel, the hydrostatic pressure produces a force on the diaphragm that is just balanced by the force exerted in the opposite direction by the spring; but if the torpedo gets too deep or too shallow, the forces no longer balance and the diaphragm is pressed inwards or allowed to move outwards respectively, and this causes appropriate deflection of the rudders. Experiment shows that either mechanism by itself causes an alternate deflection of the torpedo from the straight line, because of back-lash and friction. But it is found that if both pendulum and hydrostatic membrane operate together, that the one eliminates the tendency to deflection introduced by the other, and the torpedo is thus caused to travel along a straight path at a given distance below the surface.

Applying these conclusions to the fish, it would seem clear that for the proper direction of path in three dimensions of space, at least two mechanisms would be required, namely, one to give information concerning depth below surface, and one to be influenced by gravity, and therefore to show deflection from the horizontal axis. Now the latter mechanism has long been identified as the otolith organ; the hypothesis advanced is that the tympanum, middle ear, and cochlea are to be identified as the depth-recording mechanism.

The tympanum is on this view the counterpart of the rubber hydrostatic membrane of the torpedo. The ossicles are the counterpart of the levers which convey the motion of the diaphragm under varying hydrostatic pressure to the rudder control mechanism, the stapedius muscle acting as the spring which in the torpedo balances the force produced on the diaphragm by the hydrostatic pressure. In fish, the homologue of the cochlea, with its basilar membrane, hair cells, and rods of Corti, is on the above view the mechanism by which the changes in position of the hydrostatic membrane (caused by changes in depth) are perceived by the sending of corresponding stimuli up the cochlear branch of the eighth nerve.

Mechanism of the Ear in Fish.—It is an essential feature of any mechanism for recording changes in hydrostatic pressure, that one side of the diaphragm should be exposed to the fluid pressure (in this case water), while on the other there should be a readily compressible fluid such as a gas or air. And, further, since the gas or air is liable to be absorbed, there must be means provided of renewing the supply. In the case of shallow water fish and most reptilia, the supply of air in the middle ear may be readily renewed by the fish coming to the surface of the water and causing air to enter by way of the mouth and Eustachian tubes. (In some fish the air in the swim bladder is renewed in a similar way.) In the case of fish living below the surface,

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press

a different method of renewing the air has to be provided, namely, by forming a special connection with the gas-secreting gland (the swim bladder). This may be effected by either connecting the swim bladder with the middle ear by a tube or duct (Owen says this is the case in many osseous species of fish), or by making the swim bladder itself form the chamber, the change in volume of which (with change of depth below surface) brings about movements of the mechanism which connects with the internal ear. This is the arrangement found in carp, loach, and sleat-fish. About these fish Weber wrote (quoting the abstract given by Owen):

> A canal is sent from the sac of each vestibule to a common sinus impar . . . which communicates on each side by a small orifice with two subspherical atria . . . which atria are supplied externally by the ossicles *l* and *m*, and by means of the large ossicle *o* are brought into communication with the forepart of the air-bladder *p*. Both the atria and common sinus are filled with endolymph. . . .

Weber actually named these three ossicles the malleus, incus, and stapes, and held that they existed chiefly in subserviency to the organ of hearing.

Muller concluded that the air-bladder in fishes, in addition to other uses, serves the purpose of increasing by resonance the intensity of the sonorous undulations communicated from water to the body of the fish. This conclusion is not accepted by Bridge and Haddon, who examined the anatomy of the swim bladder in many groups of fish. They state that the ossicles connecting the labyrinth with the swim bladder are less adapted to the conduction of fine sound vibrations than they are to the indications of gross changes in the capacity of the air-bladder, such as would be brought about, either rapidly by external changes in the hydrostatic pressure, or slowly by alteration in the volume of gas in that organ by secretion or readsorption. They advance the following points against Weber's theory that the mechanism has an auditory function: (1) Sound vibrations would be passed from water to the air in the swim bladder with great loss of intensity. (2) In many Siluridæ, the walls of the air-bladder are very thick, and are therefore ill-adapted for conducting sound. (3) The ossicles have considerable inertia, have no useful lever action, and are not firmly connected (as they are in the ears of mammalia), so that they can vibrate rapidly under the action of sound waves as one concrete mechanism. (4) There is no evidence that the Siluridæ, which possess this mechanism, have exceptional powers of hearing.

None of the above objections apply to the alternative view that the mechanism is used for measuring air-bladder volume under changes of hydrostatic pressure. It would seem clear, therefore, at all events so far as this type of mechanism is concerned, that the perception of

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press

depth and corresponding control of direction is the function performed, and not that of audition.

The intermediate type of mechanism described early in this paper, in which the water exerts its pressure directly on an externally placed tympanum (as it does in the naval torpedo), now comes up for examination. It is at once found that so far as the anatomy and mechanical features of the apparatus are concerned, the function performed could be either that of audition or that of depth perception. And it would seem that both functions could be efficiently performed without modification. If any differentiation were possible, one would say that those fish in which the mechanism appears to be well designed (so far as freedom from friction, inertia losses, and back-lash are concerned) are more likely to employ the organ for audition than for depth perception, but this is probably a purely artificial criterion. It is probable, then, that in this type we see the direct connecting link between the depth-perceiving mechanism used by fish, and the apparatus for audition found in mammalia.

SUMMARY.

The view is advanced that the auditory apparatus of mammalia which is represented by the cochlea, fenestræ, ossicles and tympanum, once formed in their ancestors an apparatus for perceiving not sound vibrations, but the depth below sea-level. If this view be correct it would explain why the cochlea, the semicircular canals and the otolith organs are associated together anatomically and have a common nerve, since if the cochlea perceives depth below surface, all three would be directly concerned with the perception of position and the control of direction.

https://doi.org/10.1017/S002221510002541X Published online by Cambridge University Press