14.

Arris and Gale Lecture

ON

THE PHYSIOLOGY OF THE HUMAN LABYRINTH

Delivered before the Royal College of Surgeons of England on March 18th, 1910

BY

SYDNEY SCOTT, M.S., M.B. Lond., F.R.C.S. Eng.

ASSISTANT AURAL SURGEON TO ST. BARTHOLOMEW'S HOSPITAL; SURGEON FOR DISEASES OF THE EAR AND THROAT TO THE NATIONAL HOSPITAL FOR THE PARALYSED AND EPILEPTIC.

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THE PHYSIOLOGY OF THE HUMAN LABYRINTH.

General Anatomy and Topography of the Labyrinth.

Mr. President, Ladies, and Gentlemen,—The labyrinth or internal ear in which the eighth nerve ends is a membranous structure situated in the petrous portion of the temporal bone. The cavity in which the membranous labyrinth lies is called the osseous labyrinth. It is lined by a delicate periosteum. The membranous labyrinth contains a fluid known as endolymph, and is partly surrounded by a fluid called perilymph. The bony labyrinth consists of three main parts—the three semicircular canals, the vestibule, and the cochlea. In the vestibule are the saccule anteriorly and the utricle posteriorly; the latter receives the opening of the three semicircular canals. The saccule communicates with the membranous duct, which is lodged in the bony cochlea. Each semicircular canal is set in a plane at right angles to the others. The external canal is horizontal; the other two are vertical—viz., the anterior or superior, and the posterior or inferior, which is also internal. Contrasting the two labyrinths, the horizontal canals occupy approximately the same plane. In relation to the topography of the head, the superior canal lies in a plane which, according to my measurements, is inclined at an angle of 37° to the coronal plane; the posterior canal is inclined at an angle of 37° to the sagittal plane. The superior canal on one side, therefore, forms an angle of 15° with the posterior canal on the opposite side.

Morphologically—A Dual Organ.

Evidence shows that the eighth cerebral nerve is composed of two portions; although blended in their course, they differ in their peripheral terminations, central connexions (compare

Gordon Holmes), period of medullation, and functions. In some animals, according to Biehl,[1] e.g., the horse, and, more distinctly, the sheep—the two portions, the vestibular and the cochlear, are independent, and can be divided separately.

Vestibular Ganglion.

The vestibular ganglion, first described by Scarpa about 1760, is situated in the internal auditory meatus, and is connected by an upper branch with the utricle and ampulla of the superior and external semi circular canals, and by a lower branch with the saccule and the posterior semi-circular canal. Centrally, the fibres from the vestibular ganglion enter the medulla oblongata between the resti-form body and the bulbo-spinal root of the fifth cerebral nerve, and are indirectly connected with the cerebellum.

Cochlear Ganglion.

The cochlear ganglion is situated in a spirally arranged space in the modiolus or central axis of the cochlea. Its peripheral fibres are distributed in the organ of Corti, and its central fibres run dorsal to the vestibular nerve towards the restiform body, over which most of them pass, toward the mid-brain, and not the cerebellum. (Cf. Gordon Holmes, Comparative Anatomy of the Nervus Acusticus, Transactions Royal Irish Academy, 1903, p. 140.)

Development.

W. His, jun., is responsible for the view that the inferior branch of the vestibular nerve belongs to the cochlear nerve, which was physiologically doubtful, and which G. L. Streeter[2] has shown to be incorrect. Dr. John Cameron and Dr. William Milligan[3] have come to similar conclusions, after an embryological study of the otic vesicles and nerve histo-genesis in vertebrates.

Vestibular System.

The intimate connexion of the vestibular nerve with the cerebellum has been spoken of recently by Dr. Risien Russell in his Lettsomian lectures. "The most important peripheral

[1] Beitrag zur Lehre von der Bezielung Zwischen Labyrinth und Auge, Arb. a.d. Neurol. Inst. a.d. Wien Univ., Band. xv., Teil 1, 1907.

[2] American Journal of Anatomy, vol. iv.

[3] Development of the Auditory Nerve in Vertebrates, Journal of Anatomy and Physiology, January, 1910.

sense-organ from which the cerebellum receives afferent impressions is the labyrinth, and the path by which they are conducted is the vestibular nerve."[4]

Early Experimental Researches on Cerebellum and Labyrinth.

It is not, therefore, irrelevant to very briefly allude to the experimental study of the cerebellum which eventually led to the discovery of certain previously unknown functions of the labyrinth. The earliest experiments on the cerebellum, according to Sherington, appear to have been by du Verney in 1697.[5] Du Verney's name is of particular interest to otologists, for I find he was an aural surgeon as well as an anatomist. His book, translated and published in London after his death, 1727, was the first special treatise on aural diseases in our language.[6] In 1822 came Flourens, whose life forms an era in the history of the labyrinth. It will be remembered that Flourens found that injury to the deep structures of the cerebellum produced marked disturbance of equilibrium. But he went further than others had done, for in 1828 he observed what was certainly at that time an astonishing fact, that precisely similar results were evoked by injury to the semicircular canals alone. It was years before the significance of this epoch-making revelation was properly appreciated. The notion that the internal ear served no other functions than that of audition was so deeply rooted that no one seems to have attempted to repeat these observations until long afterwards. For nearly 20 years Flourens continued his researches in experimental neurology. He found that division of one canal caused rotatory movements of the body, and that the axis of rotation was at right angles to the severed canal. He was led to observe that these motor disturbances, like those produced by injury to the cerebellum, were of the nature of coördination—one set of muscles contracting, while another set relaxed.[7]

Flourens's Data Confirmed.

I can only mention the names of a few of the earlier observers to investigate Flourens's data. In 1869 Löwenberg showed that the phenomena produced by dividing the semicircular canals of pigeons were not due to injury to the cerebellum as some had averred, for he found that the

[4] Brit. Med. Jour., Feb. 19th, 1910, and Transactions of the Medical Society of London, 1910.

[5] Philosophical Transactions, London, vol. xix., p. 226.

[6] Cf. William Wilde, Aural Surgery, 1853, p. 15.

[7] Cf. also Sherington, Horsley and Löwenthal, Proceedings of the Royal Society, 1896 and 1897

incoördinate movements could be set up by stimulating the ampullary nerve endings in the divided canals.

The Influence of these Observations on Medical Opinion.

It is interesting to try to ascertain how these discoveries first began to affect medical opinion. During the first 30 or 40 years which followed the announcement of Flourens's discovery, we find no reference to his work on the labyrinth in general medical or otological literature, until 1861, when Ménière first introduced the subject. Ménière, therefore, stands out prominently, because he was the first to realise the value of these results in experimental physiology when applied to clinical medicine. Before this time the symptoms, which are often spoken of as Ménière's, were believed to be due to a threatened cerebral apoplexy ; and patients manifesting these symptoms were so treated, and treated rather desperately.

Chief Period of Physiological Investigation on the Labyrinth.

There seems no doubt that the relationship which Ménière established between physiology and practical medicine led to and encouraged the more thorough investigations which were carried on after 1870. This period witnessed the master work of Mach and Breuer in Austria, and Cyon, who came from Russia to Paris. In this country important work was done by Crum-Brown in Edinburgh in 1872, and confirmatory observations were made a little later by Dr. Peter McBride[8] in Edinburgh, 1880, and by William James[9] of Harvard in America, 1882. Exhaustive researches of Mach, Breuer, and Cyon extended over several years, and have since been supplemented by many others, including especially J. C. Ewald in Germany, Stanislaus von Stein in Russia, and van Rossem in Holland. To these we must add the names of Lee, who investigated the labyrinth of cartilaginous fish, and of Karl Biehl, who has studied it in the horse and sheep.

Clinical Physiology.

Our knowledge of the functions of the labyrinth was advanced by experimental physiologists, and during the 40 years which followed Ménière's prediction hardly any pro-

[8] Journal of Anatomy and Physiology, vol. xvii., p. 211.

[9] The Sense of Dizziness in Deaf Mutes, the American Journal of Otology, vol. iv.

gress can be claimed by clinical physiologists, except for Dr. Hughlings Jackson and one or two other contributors, including Schwabach, who described cases of vertigo and nystagmus associated with ear disease. In 1874 von Tröelstsch said: "The internal ear is completely removed from the direct operations of the physicians and surgeons," and so spoke of it in as few words as possible.

Real advance on the clinical side may be said to date from the stimulus produced by Jansen's paper giving an account of ten cases of operation upon the labyrinth in the human subject. This was in 1898 at the Otological Congress in Moscow. The possibilities awakened by Jansen's pioneer surgery of the labyrinth formed the great incentive to otologists to perfect the methods for diagnosing its diseases. The arduous work of those few who were engaged independently in clinical researches became recognised as of great practical importance and interest. In this country attention to the subject was first directed by Dr. Milligan, Mr. Whitehead, and by Mr. Lake. The way was prepared by Sir William Macewen and Mr. C. A. Ballance, to whom otology owes so much for the application to it of the principles of modern surgery. It was only natural that otologists should refer back to the important researches in experimental physiology carried out between 30 and 40 years ago, and amongst the first to appreciate the practical importance of this combined study of the physiological and clinical problems appear to have been Alexander and Bárány in Vienna. The latter's work especially has become well known to us owing to the papers by Guthrie,[10] Tweedie,[11] Pike,[12] McKenzie,[13] and others. Panse of Dresden (1902) also drew up a detailed guide for investigating the internal ear, which has received less attention in this country than it deserves.

Microscopic Anatomy.[14]

In order to understand the mechanism of the labyrinth of which we shall now speak, it is necessary to examine the peripheral distribution of the vestibular nerve. We shall first direct attention to the ampullæ of the semicircular canals, which are the parts peculiarly sensitive to stimulation. As we know, each canal is supplied with a branch of the vestibular nerve. In each ampulla is a transverse crescentic septum, the free margin and surfaces of which are covered with ciliated epithelial cells. In suitable sections cut in paraffin we find one cilium for each cell. The cilium is partly intra- and partly extra-cellular. The extracellular

[10] Brain, 1906. [11] Brit. Med. Jour., 1907. [12] Ibid.
[13] Journal of Laryngology, &c., 1909.
[14] See Journal of Anatomy and Physiology, July, 1909 (illustrated with microphotographs).

portion of the cilium is a fine, tapering filament, which in man measures nearly 0·04 millimetre in length (Schäfer gives the length 0·03 millimetre). The two portions of the cilium are in perfect continuity with each other. The intracellular portion is characterised by an ovoid expansion, which makes the total length of the cilium 0·064 millimetre. (I cannot find a similar appearance figured in the works of Gustav Retzius or of other anatomists.) The filaments of the ampullary nerve are traceable to this highly differentiated epithelium, where they end in beaded fibrillary network among the cells. The extracellular portions of the cilia project into the endolymph of the ampulla and are so slender that we can readily conceive how they sway to and fro in the slightest current set up in this fluid. We do not say such currents are normally produced, but it simplifies our discussion if at this stage we are permitted to assume this possibility.

Experimental Physiology—Animals.

By opening the external horizontal canal in a pigeon or rabbit, and blowing through a capillary glass tube which was introduced into the canal, Cyon found nystagmus was evoked; moreover, he observed the character and rate of rhythm of the oscillation of the eyeball were the same as those which Purkinje had described in connexion with post-rotatory nystagmus half a century previously. Ewald repeated these experiments, using a compression and rarefaction syringe and taking the precaution to seal the canal behind the artificial opening. He was thus able to bring pressure to bear on the fluid in the ampullary end of the canal. He found that compression caused the eyeballs to deviate towards the contralateral side, and the nystagmus occurred when the eyes looked toward the ipso-lateral side. Rarefaction produced opposite movements—viz., deviation towards the ipsolateral side and nystagmus when the eyes turned toward the contralateral side. In other words, *the eyes deviated in the same direction as the current, if we may still assume that the current is produced.*

Observations in the Human Subject.

In human subjects affected with middle-ear suppuration we not infrequently meet with fistulous openings of the external semicircular canals similar to those artificially produced by Cyon and Ewald in animals. Hinsberg collected 198 examples of such fistulæ from literature, including 22 cases from his own practice, in 1902.[15] Two years ago Mr.

[15] Zeitschrift für Ohrenheilkunde, vol. xl.

West and I described 15 examples which we had met with. As a rule, such fistulæ are more often found only after the membranous labyrinth has become defunct owing to the fact that the symptoms produced by the process of disorganisation of the labyrinth are generally mistaken for some other affection. Occasionally we meet with the fistula while the functions of the membranous labyrinth are capable of direct excitation. During the last three years I have met with nine examples of this latter class of fistula.

Labyrinthine Fistulæ—Compression Phenomena

(9 Cases).

Case 1.—A man with a vestibular fistula reeled and nearly fell when the tragus was pressed inwards so as to compress the air in the external auditory meatus. No nystagmus was sought for in this case.

Cases 2 and 3.—Two women with vestibular fistulæ also reeled with vertigo and nearly fell when the meatus was compressed in a similar way. Violent nystagmus was observed, but its type was not analysed.

Case 4.—A young man with an external canalicular fistula responded to meatal compression in a similar way. The nystagmus was too violent to allow of analysis being made.

Case 5.—A boy with a canalicular fistula rotated circus-wise 90° to the contralateral side when pressure was applied to the fistula by means of a jet of water from a syringe. The movement was immediate, involuntary, and occurred when the head was erect.

Case 6.—A young woman with an external canalicular fistula had giddiness and spontaneous nystagmus to the ipsolateral side. Compression intensified the nystagmus and the existing vertigo.

Case 7.—An elderly woman had a cholesteatoma and fistula of one external canal which, owing to extensive bone destruction, was visible through the meatus. The slightest contact with a probe upon the fistula produced deviation of the eyes and rotation of the head towards the contralateral side, and horizontal nystagmus when the eyes were attentively turned towards the ipsolateral side. Very gentle meatal compression produced precisely the same results. When the pressure was increased the nystagmus became mixed in type, rotatory as well as horizontal, and it was then impossible to analyse, nor was it possible after repeated trials to aver that rarefaction of the meatus caused the contrary effect to ensue.

Cases 8 and 9.—The patients were boys with traumatic fistulæ, but no additional datum was obtained.

Thus, perhaps in an imperfect way, we are able to show that what Cyon and Ewald found in lower animals is true also in the human subject.

Hughlings Jackson's Case.

Dr. Hughlings Jackson gives an admirable description of what seems to have been a similar condition in a woman, aged 49 years, with mastoid disease due to middle-ear suppuration. Compression upon the meatus caused deviation of the eyes to the contralateral side. Nystagmus with the rapid movement towards the ipsolateral side, and also some rotatory nystagmus.[16]

In another contribution Dr. Jackson described two other cases of ocular movement during a paroxysm of auditory vertigo.[17] He quotes a somewhat similar case of Schwabach,[18] and also of Clarence Blake.[19]

Some years later Charles Kipp described cases of transient bilateral horizontal nystagmus which occurred with purulent inflammation of the middle ear.[20] But in none of these cases, so far as I can gather, was a fistula of the labyrinth actually identified, although Dr. Jackson naturally supposed that the phenomena were the result of direct mechanical stimulation of one or other of the semicircular canals.

Rud. Panse (1902)[21] however, mentions two cases in which meatal compression evoked deviation of the eyes and rotation of the head to the contralateral side, followed by horizontal nystagmus to the ipsolateral side. These observations tally with my own and with Ewald's experiments.

Caloric Reflexes.

In the "seventies" Breuer showed that similar phenomena were evoked by the effect of changes of temperature of the outer wall of the labyrinth. Breuer's observations formed the basis of the caloric test introduced to otology by Bárány.

Experiment.—If the ear of a normal person with intact labyrinth and, for preference, with a perforated drum is gently irrigated with tepid water the sensation of vertigo can be produced after a short latent period. The objective phenomena which accompany the state of vertigo depend upon the position of the head. When the head is turned face downwards and the left ear alone is irrigated, directly the vertiginous state begins irrigation is discontinued, the patient is directed to try to stand steady, keeping the face down. This he will not be able to do on account of strong, forced movements which in a typical case cause the head, and generally the trunk and limbs, to rotate circus-wise towards the contralateral side. An examination of the eyes while the head is bowed down reveals the presence of horizontal nystagmus, most evident when the eyes are directed towards the ipso-

16 For a full description see Transactions of the Ophthalmological Society of the United Kingdom, vol. iii., p. 201 (1883).

17 Brain, vol. ii., 1879–80.

18 Zeitschrift für Prakt. Med., No. 11, 1878.

19 Archives of Ophthalmology and Otology, vol. vii., No. 1, p. 113

20 Transactions of the American Otological Society, 1888.

21 Archives of Otology (Tr.), vol. xxxi., p. 480.

lateral side. In other words, we recognise the same set of phenomena which has been induced by mechanical compression of a fistula of the horizontal canal. The legitimate explanation is that in accordance with the laws of heat by cooling the outer wall of the internal ear, convection currents are set up in the endolymph, which pass from the horizontal canal downwards (because the face is turned downwards) towards the utricle. As before mentioned, Ewald succeeded in producing the contrary reflex movements by rarefaction—i.e., presumably—by inducing currents to flow from the utricle into the external semicircular canal. We can simulate these reversed currents by using hot water instead of cold. As we should expect, when the head is in the face-downwards position, the forced rotation of the head and eyes produced by hot water irrigation is towards the ipsolateral side, nystagmus on fixation being horizontal towards the contralateral side. Thus, as regards the horizontal canal, the hypotheses concerning compression and convection currents are in harmony.

This may be stated in the form of a law: *The deviation of the head and eyes is in the same direction as the current in the endolymph, and the nystagmus is in the opposite direction.*

The Superior Semicircular Canal.

Fistulæ of the superior semicircular canal leading into the accessory cavities of the tympanum are very rare, and no opportunities have occurred for watching the effect of mechanical compression or rarefaction in this canal in the human subject. Data for consideration can, however, be obtained by use of hot and cold water irrigation. We examine the superior canal with the head erect. Cool water irrigation now causes pleurothotonos, instead of circus rotation. The lateral inclination of the head and trunk is very evident as soon as the feeling of vertigo comes on if the patient attempts to stand with feet together and eyes closed. The direction of flexion is toward the ipsolateral side and the nystagmus, which is rotatory in type, is contra-rotatory.[22]

Hot water irrigation also produces pleurothotonos, but to the contralateral side, with ipso-lateral nystagmus. The direction of the nystagmus is reversed by inverting the head.

The law of deviation is thus confirmed: *The direction of the reflex forced movements of the head, eyes, and trunk is the same as the current in the endolymph.*

[22] The terms "ipso-rotatory" and "contra-rotatory" nystagmus apply to the direction of the rapid movement of the upper meridian of the globe of the eye rotating about the antero-posterior axis of the eyeball.

Posterior Canals.

When we come to investigate the posterior semicircular canals we are confronted with the disadvantage that mechanical methods of compression cannot be applied, as fistulæ of this canal have not been met with clinically in the human subject. Moreover, the deep-seated position of this canal precludes any effect from the use of convection currents.

Post-Rotatory Phenomena.

Our difficulties respecting the posterior canals can be overcome by the application of passive rotation, and we shall therefore first refer to a reinvestigation of Purkinje's post-rotatory phenomena. The results are dependent upon the position of the head. When an individual is rotated uniformly in a horizontal plane, with the head in an erect position, certain forced movements follow sudden change in the rate of movement. If the angle of velocity is not less than about 80° per second, sudden cessation produces a negative acceleration. The forced movements produced are best made evident when the patient, with normal labyrinth, attempts to stand up with feet together and eyes closed. In a typical instance it will be noticed that it is necessary to protect the patient from falling, but where space permits definite circus movements are performed. In other words, the patient continues to rotate actively circus-wise in the same direction as that in which he has been passively rotated. If the eyes are examined for nystagmus it will be found that horizontal nystagmus is present when the eyes are turned towards the direction opposite to that of the passive rotation.

These phenomena are in harmony with those observed as the result of compression, rarefaction, and caloric tests, and they are explicable by the inertia laws on fluid currents.

To test the value of post-rotatory phenomena by applying the method described to the superior canals the head must be bowed with face downwards, or may be extended so that the face is directed upwards. In either position the two superior canals are symmetrically placed as regards the plane of rotation. (If we know from other data that there is only one intact labyrinth the head should be rotated with the chin 30° toward the ipso-lateral shoulder, in addition to the face-down or face-up position when we wish to demonstrate the activity of the remaining labyrinth.)

When the rotation is suddenly stopped, as in the previous experiment, and the patient attempts to stand, pleurothotonos is produced instead of circus movements. Rotatory nystagmus is also evident and its direction is opposite to that of lateral flexion.

The results of comparative experimental physiology would lead us to expect that the posterior canals are concerned with rotation movements in a vertical plane.

Experiment.—A normal individual is uniformly rotated as before about a vertical axis, but with the head placed on one side so that the sagittal plane of the head coincides with the plane of rotation. This really represents turning head over heels. On coming to sudden rest the patient is directed to stand with feet together. Assistance will be required owing to the production of powerful opisthotonos, or emprosthotonos, according to the relative direction of passive movement. When the direction of the passive rotation of the head about its transverse axis is towards the occiput, opisthotonos and upward deviation of the eyes are produced. Conversely, emprosthotonos and deviation of the eyes downwards result from passive rotation in the opposite direction—i.e., when the crown of the head moves forwards instead of backwards around the transverse cranial axis. These powerful motor reflexes, opisthotonos and emprosthotonos, are explicable on the assumption that currents are produced in the ampullæ of the posterior canals similar to those described in the external and superior canals. The view that posterior canals are mainly, at all events, concerned with movements of the eyeball in the sagittal plane is also supported by observations made upon a patient some years ago during an operation on the labyrinth. Direct pressure with a seeker upon the ampulla of the posterior canal caused the eyeballs to move, first, slightly upwards and then slowly downwards. All these reflexes are absent if both labyrinths have been removed previously.[23] In the present state of our knowledge, therefore, it seems justifiable to suppose that we can investigate the posterior canal by passive rotation, the superior canals by passive rotation and by calorific methods, and the external canals by rotation, calorific methods, and sometimes also by mechanical compression too.[24]

Mach,[25] with great authority, showed that it was a mathematical error to suppose that the radius of the arc of rotation influenced the inertia in the semicircular canal. I confess to be one of those who were prepared to allow for some influence due to variations in the radius of the arc of rotation, and it seemed in a measure surprising to find clinically that the

[23] Cf. Mr. Lake's case, which he courteously allowed me to examine, Proceedings of the Royal Society of Medicine, Otological Section, 1908; Dr. Gibson and Mr. Lake, Ablation of Both Vestibules.

[24] We have noted that E. P. Lyon failed to produce forced movements in the planes of the posterior and superior canals in dog-fish by direct stimulation of these canals with the same certainty as could be obtained in the case of the horizontal canal. Cf. Loeb, Comparative Physiology of the Brain, and Lyon, A Contribution to the Comparative Physiology of Compensatory Motions, American Journal of Physiology, vol. iii., 1900.

[25] Grundlinien der Lehre von den Bewegungsempfindungen, 1875.

intensity of the physiological reaction varied only with angular acceleration, but not with tangential speed.[26]

Currents in Endolymph.

The conclusions to be drawn from the foregoing data are in no way vitiated by difficulties in the conception of currents through such small canals. Some variation in diameter of the canals is allowed among different species in the animal kingdom, as a study of Dr. Gray's beautiful photographs of the labyrinths of animals reveals. The production of currents must be dependent upon positive and negative pressures in successive portions of the endolymph. If the gradation of pressure involves the endolymph throughout the semicircular canal one of two things must happen: the shape of the wall of the canal must be altered or there is a flow of fluid until uniformity of pressure occurs; whether there is a flow throughout the canal or not does not affect the possibility of movement of endolymph in the ampulla alone. If normal stimulation of the ampullary nerves is due to temporary change of pressure it must be because this change of pressure has produced a movement in the endolymph. It is only a stage further to suppose that this is accompanied by a movement of the extremely delicate fibrillæ of the epithelial cells of the ampulla.

Normal and Excessive Stimuli.

The controversies on this part of our subject do not appear to me to allow for the distinction between normal stimuli, which regulate normal deviation, and excessive stimuli, which produce forced movements and nystagmus. I wish to side myself, therefore, with those who believe the evidence in favour of the production of currents, and the only explanatory qualification which seems called for is that the actual movement of endolymph may be relatively very slight without negation of the hypothesis. In no case is it necessary to imagine the current flowing rapidly through the semicircular canals, although it is necessary to admit movement of endolymph in the ampulla itself. There is one other point of importance to which reference must be made.

Principal and Subordinate Function.

The physiological reactions differ quantitatively according to the direction of flexion of the cilia in a given ampulla. In the case of the external ampulla currents from the canal

26 Proceedings of the Royal Society of Medicine, Otological Section, p. 41, 1909.

towards the utricle produce stronger reflex movements than currents in the contrary direction. On a previous occasion when I went fully into this subject I ventured to think that this undoubted difference was dependent upon a physical difference of the relationship of the canal to the ampulla according to the direction of flow.[27] But such physical argument was based upon consideration of the external canal only, and a further study of the problem last year confirmed me that the conclusion is refuted by considering the superior canal. For in cases in which one labyrinth has been extirpated the duration of the post-rotatory nystagmus is longer after rotation in one direction than after rotation in the opposite direction. Currents from the extenal canal to the utricle and from the utricle to the superior canal produce nystagmus of longer duration than can be produced by currents reverse in direction (under otherwise equal conditions).

Galvanism.

Stimulation of the labyrinth by means of galvanism has been carried out in the lower animals by innumerable experimenters, and it has been shown that the application of the current direct to the labyrinth or to the ampullary nerves, or the eighth nerve as a whole, may cause forced movements and nystagmus. In the human subject similar phenomena, varying in degree according to idiosyncrasy, can be induced by placing one electrode against the tragus and the other in a neutral position. If the patient with normal labyrinth is examined in a standing position, with feet together, or with one foot in front of the other, and eyes closed an imperceptible current is sometimes sufficient to invoke strong involuntary movement. I have found 2 milliampères in normal subjects sometimes sufficient. Usually a current of 3 to 5 milliampères continued for a minute or two will cause lateral swaying of the head and trunk, and in a typical case pleurothotonos is produced. *Stronger currents are necessary to evoke nystagmus* and in this case the patient must be seated, for unpleasant sensations may be produced. The deflexion of the head is towards the anode and from the cathode. The reaction with the anode is stronger than the reaction with the cathode. *The anode pulls harder than the cathode pushes.*

Conclusions from a Study of Galvanic Stimulation.

I have found that the method forms a useful supplementary test in some cases, but cannot be employed to take the place of caloric and rotatory tests in all cases. Before any infer-

[27] Ibid.

ences can be drawn it is absolutely necessary to test the effect of anode and cathode separately on each side. As a rule, weak and quite painless currents of less than 5 or 6 milliampères, if continued for a few minutes, evoked forced movements when the labyrinth and its central connexions are normal. It is often impossible to display nystagmus without a strong and painful current of more than 10 or even 15 milliampères in normal subjects.

According to Bárány, galvanic nystagmus is evoked first, while deviation of the body is produced later. (Presumably his patients were always seated.) It will be seen from my experience that the reverse was noticed, if we gradually increase the current and watch the effect of the current on an individual who stands with feet together, as described above. This is also in agreement with Lemaitre and Halphen,[28] and also with Buys and Henebert.[29]

Ablation of One Labyrinth.

The extirpation of one labyrinth in an animal produces an immediate effect upon (1) the attitude of the resting state, and (2) the character of the animal's movements in space. These effects in the course of time become less noticeable, and an animal that survives long enough may acquire such compensation that it may pass muster with its fellows without any noticeable defect. The same is true in man. The immediate effect of removing one labyrinth in frogs was studied by Hasse, 1873, who noticed inclination of the head to one side. Schiff, 1891, noticed that when the frog jumped the contralateral limb was partly abducted, and Ewald, 1892, noticed that when the frog was swimming, the body on the side operated upon was lower in the water. He also noticed that the contralateral forelimb was extended —i.e., unilateral ablation of the labyrinth in the frog causes ipsolateral flexion and contralateral extension of the head and limbs. Van Rossem [30] has found the same in tortoises. Ewald, 1892, and Girard, 1892, investigated the muscular tone and found weakness in the limbs on the ipsolateral side. Emmanuel described changes in the muscle curves which are in accord with Ewald's views.

Certain apparently special functions of the vestibular labyrinth have been particularly studied by Ewald [31] and von Stein. Sir Victor Horsley drew attention to an altered

[28] Nystagmus et Oreille Interne, Annales des Maladies de l'Oreille et du Larynx, tome xxxiv., p. 700, 1908.

[29] Archives Internationales de Laryngologie, d'Otologie, et de Rhinologie, 1909.

[30] Onderzockingen gedaan in het Physiologisch Laboratorium der Utrechtshe Hoogeschool, p. 151.

[31] Phys. Untersuchungen über das Endorgan des Nervus octavus, p. 185.

attitude during a recent discussion on the subject of vertigo, which led me to watch for the effect in human subjects. Last year Dr. Gordon Wilson, late professor of anatomy, University of Chicago, kindly gave me a photograph of a dog whose right labyrinth he had removed. The photograph showed not only lateral flexion and rotation of the head, but also what might pass unnoticed, abduction of the contralateral limbs.

Schiff investigated the effect of passive rotation on frogs before and after unilateral and bilateral ablation of the labyrinth. His method was to rotate the animal on a disc at a uniform velocity, starting from rest, which, acting as a positive acceleration, produced a reactionary movement of the frog and caused it to turn its head in the contrary direction. During the rotation the frog would remain motionless in its new position, but when the disc was suddenly stopped a reactionary movement was set up by the negative acceleration, which resulted in post-rotatory movement in the direction of the previously rotating disc. To the initial movement or reaction I propose to apply the term "alpha reaction," and to the post-rotatory reaction the term "omega reaction." In the normal frog the alpha reaction is equal to the omega reaction, estimated by the number of degrees to which the animal moves on the disc.[32] These movements do not occur when both labyrinths have been removed, therefore they cannot be due to inertia of the whole body.

Unilateral Ablation.

When the rotation is made to the ipsolateral side the alpha reaction is much weaker than the omega reaction, which is exaggerated. When the frog is rotated to the contralateral side the alpha reaction is much greater than the omega reaction. Ewald found that in normal pigeons the alpha reaction was equal to the omega reaction, but after one labyrinth had been removed the reactions were unequal, like those of the one-labyrinth frog.

Coming to our own experiments, measurement of the alpha and omega reactions under like conditions in the human subject is impossible to carry out satisfactorily with hand-rotation chairs, which though useful for general clinical purposes after some experience, do not possess the mathematical accuracy required for records of permanent value.

As far as it is possible to estimate with hand-rotated apparatus, I am disposed to think that the alpha and omega reactions before and after ablation are similar to those described in animals, differing in degree.

In a normal child on hands and knees on the rotating table the alpha reaction was about 20° and the omega reaction 20°

[32] Schiff and Ewald.

(angular acceleration 90° per second). In two others similar results were obtained. It is the usual experience to find that after unilateral ablation the omega reaction produced by rotation towards the ipsolateral side with the head erect is greater than the omega reaction produced by rotation in the opposite direction.

Attitude.

Since Sir Victor Horsley drew attention to the subject[33] I have noticed the head to be very slightly deviated towards the side of the lesion (I can recall seeing cases some years ago); the angle of deviation from the perpendicular plane was in one recent case 15°. It was also noticed that there was some lateral deflection of the head and trunk towards the same side—*in other words, slight pleurothotonos towards the side of the lesion.*

Besides an altered attitude of the head, there is a change in the posture of the limbs: the patient may stand with feet wider apart. Dr. Risien Russell has mentioned this to be generally observable in cerebellar lesions. This wider base is probably secured not by equal abduction of the limbs, but by *forced abduction of the contralateral limbs* (cf. Dr. Wilson's dog).

Von Stein's Tests.

After disorganisation of one labyrinth patients sometimes have a sense of weakness in the muscles on the ipsolateral side. This is not always noticed and may soon pass off, but the patient may not be able to maintain the upright position when standing on the ipsolateral leg, although he may be steady on the contralateral leg alone. For the clinical value of this observation, which we have practised in varying ways for some five years, we are indebted to von Stein, who has also shown (and the observation can be easily confirmed) that hopping on the ipsolateral limb is generally impossible in recent infection or disorganisation of the labyrinth, although it may still be possible on the contralateral limb.[34]

Hypotonus, Dysdiadokokinesia (Babinski), &c.

I have never been able to detect weakness in the flexor to the forearm by the finger-grip test, nor have I been able to obtain the brachial bicipital reaction in labyrinthine infections, described by Stewart and Holmes in cerebellar lesions.[35]

[33] Proceedings of the Royal Society of Medicine, 1909.

[34] Von Stein: Die Lehren von den Funktionen der einzelnen Theile des Ohrlabyrinths, German translation by von Krzywicki, Jena, 1894, quoted by Panse, Archives of Otology, 1902; also Eagleton, Archives of Otology, 1907, and Schafer, 1900.

[35] Quoted by Risien Russell, loc. cit.

I have not found any interference with rapid alternating pronation and supination of the wrist in disorders of the labyrinth. In contrast with cerebellar tumours[36] it is interesting to observe that two cases in which suppuration extended from the labyrinth into the cerebellum showed no such dysdiadokokinesia, nor was this sign present in a third case of cerebellar abscess in which the labyrinth was normal.

Before leaving the vestibular system I should like to draw attention to the further researches of van Rossem, which have led him to calculate the mean reaction time of rotation consciousness. This he estimates to be 0·8 second. If compared with the mean reaction time of other sensations we shall find it rather slow: visual, 0·195; tactile, 0·145; muscular contraction, 0·151; thermal, 0·162; taste, 0·502; and sound, 0·150.[37]

Van Rossem also worked out the minimal perceptible acceleration it was possible to detect. The mean minimal perceptible angular acceleration was 1·36° per second. As far as seemed reasonable, I have attempted in this discourse to restrict the matter to the results of actual experiment and to clinical observations, believing that by adhering to these methods more reliable data may in time accrue. I have also omitted considerations of the action of the utricle and saccule which are probably concerned with acceleration in straight lines, forwards and backwards, upwards and downwards, and possibly sideways.

Cochlear System.

Ever since the eighteenth century it has been recognised that a fully developed spiral cochlea exists only in mammals; its homologue, the lagena of birds, is comparatively a simple tube and only slightly curved. In reptiles it is quite rudimentary, absent in some amphibians and fishes.

The tympanum with a columella and fenestra rotunda and Eustachian tube are simple in birds and in those reptiles in which they exist; there is *no* tympanum in snakes—e.g., yellow cobra and hoary snake of South Africa. As regards the organ of Corti, there are no rods in the organ in birds, so that they cannot be indispensable structures.[38] The membrana basilaris on which the organ of Corti rests is said to vary considerably in different animals.

In the past it has been assumed—e.g., 1867, John Marshall, "Human and Comparative Physiology"—that practically all animals possess the power of hearing. This is a preconceived premiss which has no scientific foundation and represents a prejudice which dies hard. An amusing

[36] Cf. Stewart and Holmes and Risien Russell.

[37] Cf. Schäfer: Physiology, 1900.

[38] Cf. Dr. Urban Pritchard and others.

account of the supposed hearing power of the garden snail is quoted because it is so extraordinary in the "Cambridge Natural History" (see article on Molluscs). After reading this I kept a number of garden snails under close observation, and when they emerged from their shells they were exposed to the influence of Bezold's continuous tone series of instruments, to which they invariably displayed supreme indifference. Not one of the 16 snails at any time during the two months they were kept ever showed any attraction for, or repulsion from, or stationary attention to, the loudest sounds the instruments were capable of emitting. They were tested with every tone in the series, from 16 to 50,000 double vibrations per second. The instrument was applied to the shell, to the board on which they were crawling, and as close to the body or antennæ as was possible without actual contact. These molluscs are excessively sensitive to touch. Contact with a fine hair will cause instant retraction.

The presence of weak formalin on wool within an inch or so of the body causes the snail to instantly withdraw. Sounds of pure and mixed tones had no such effect. The so-called otocyst in molluscs is much better regarded as a stato-cyst and should be so named. The value of hearing in most fishes, amphibians, and many reptiles is extremely doubtful.[39] It has been assumed rather than proved to exist, except in a few species. Moreover, the tactile sense is so acute in some of these animals that they are possibly, indeed probably, affected by tactual vibrations in the water which surrounds them, or of the ground on which they lie at full length. Such tactual sensations may be set up by vibrations which accompany loud sounds of relatively long wave-lengths.

Some animals, for instance the common fowl, are peculiarly sensitive to tones of a certain pitch, as one can readily prove with a Galton whistle. On the authority of Dr. Plimmer, pathologist to the Zoological Society, a bull-frog was indifferent to the noise of a pistol fired close to it, even its respiratory rhythm being unchanged, yet it is conceivable that it is capable of hearing a monotone of a certain pitch or the croaking of its mates.

Attempts to make investigations into the *modus operandi* of the cochlea must be founded upon an accurate anatomical basis, both normal and pathological, and should be considered side by side with physiological experiments in lower animals, clinical phenomena, and physical laws. It is merely so much guess work to deal with other than ascertained data. Our present knowledge, however, is insufficient to substantiate any full and satisfactory explanation of the function

[39] I have found that rattlesnakes, Indian pythons, South African cobra take no notice of the loudest tones of the three Edelmann whistles (which encompass the upper half of the scale of sound). Green lizards respond to certain tones, frogs do not.

of the cochlea, and we must seek the most acceptable working hypothesis as a basis for further investigations. The problem is reduced to the stage when we wish to ascertain whether sound waves produce a movement of the hairs in the organ of Corti, and if so what is the character of the movement of these hairs and by what direct means is such movement accomplished.

It is thought possible that the motion produced by sound waves on the labyrinth reaches the cells through the fluid of the labyrinth, either through motions in the basilar membrane, or by motion of the membrana tectoria, which impinges upon the free ends of the cilia of the hair-cells. By means of the mechanism of the stapedial foot-plate and the formation of the membrana secundaria which closes the fenestra rotunda, it will be understood that any to-and-fro movement of the stapes, due to compression and rarefaction waves of sound, will cause synchronous movements of the membrana secundaria through the intervention of the perilymph.

Those who have studied the cochlea from the physical aspect conclude that the motion in the perilymph can be no other than mass motion.[40] Such mass movement of perilymph must affect the pressure in the endolymph, possibly in the form of compression and rarefaction waves; otherwise we cannot possibly explain the mechanism of the sound stimulus. We cannot imagine an effectual resistance to changes in pressure in the perilymph from the membrane of Reissner, and although it is by no means clear in what form sound waves traverse the cochlea we must admit a mechanical motion of some kind is produced. But we cannot ignore the fact that sound-waves fall upon the membrana secundaria synchronously with those which reach the stapes—e.g., after removal of the tympanic membrane.

It is assumed that either the basilar or tectorial membrane vibrates; which should be regarded as the essential vibrator is a matter of controversy. If these membranes vibrate, do they do so in part, or throughout their whole length, and to all sounds, or only to some? Or do they only vibrate in a particular part for a particular sound? Von Helmholtz propounded and elaborated the theory that each portion of the basilar membrane was set into reciprocal vibration by tones of one and only one pitch. Normally, the human subject is capable of hearing about 11½ octaves—i.e., tones of from 16 double vibrations per second up to tones of nearly 50,000 vibrations per second.

Von Helmholtz showed how it might be possible for high tones to cause sympathetic vibration of the basilar membrane at its basal extremity, where the membrane is narrowest

[40] Weber. Von Helmholtz, p. 106. Cf. Sir Thomas Wrightson: On the Impulses of Compound Sound Waves and their Mechanical Transmission through the Ear, 1907.

radially, and that low tones could produce vibration of the basilar membrane in the apex of the cochlea where it is widest and most lax. Helmholtz distinguished musical notes from noises, and supposed the former were appreciated by the cochlear and the latter by the vestibular apparatus; we have, however, clearer views of the functions of the vestibular nerve than had been admitted in Helmholtz's time; moreover, Albert Gray [41] has successfully shown that noise is not fundamentally different from musical tones, but that the cochlea may appreciate noise just as it does pure tones. Albert Gray's modification of Helmholtz's theory to include the appreciation of noises by the cochlea has been so ably expounded that we must refer to it as the Gray-Helmholtz theory. Essentially it is the application of the principle of sympathetic vibration. If the Gray-Helmholtz theory had maintained that the whole of the basilar membrane vibrates for each kind of sound wave it would not have been possible to explain by it how certain deaf individuals have partial defects in the range of hearing. We know that notes of low pitch are obstructed more easily than notes of high pitch, but how is it that certain deaf persons can hear notes low in the bass and perhaps high in the treble, but are unable to hear even the loudest notes in the middle of the normal auditory field? I have met with a number of such cases in tabes dorsalis and other diseases. An explanation is provided by Helmholtz's theory.

One of the objections raised to the hypothesis as it stands is embryological. As Shambaugh has pointed out,[42] we should suppose that in a special sense organ derived from epiblastic structures the important rôle of stimulating the "hair-cells" would be by a structure of epithelial origin—e.g., the tectorial membrane—and not by one of mesoblastic origin, like the basilar membrane.

An important anatomical objection to the basilar membrane theory is also lodged by Shambaugh, and is also noticed independently by Ter Kuile and Hardesty [43]—viz., that at the lower end of the basal coil of the cochlea in the pig the basilar membrane frequently cannot be found where the organ of Corti is perfectly developed, and also that the organ of Corti, here seen rests upon a solid bony plate which bridges between the lamina spiralis ossea and the outer wall of the cochlea.

Ter Kuile and Hardesty describe the inner pillar of Corti as resting upon the labium tympanicum in the basal coil. The significance of these observations cannot be disregarded; on the other hand, it would be necessary to ascertain whether

[41] Proceedings of the British Association for the Advancement of Science, 1899.

[42] The Membrana Tectoria and Tone Perception, Archives of Otology, vol. xxxvii., No. 6, p. 458.

[43] American Journal of Anatomy, vol. viii., 1908.

the animal in which this condition was found showed signs of appreciating as high tones as other animals of the same species in which a basilar membrane for the basal extremity of the organ of Corti was present.

Tectorial Membrane.

The possibility of the tectorial membrane vibrating in response to sound waves seems to have been first suggested by Rinne in 1865. It also occurred to Rutherford and to Voltolini, who built up an important hypothesis explaining its action (1885–86). Ewald and Max Meyer suggested modifications in the hypothesis. It was supposed that the basal end of the membrana tectoria would be capable of responding to the impulses produced by high-pitched tones, while succeeding tones, lower in the scale, might respond to larger and larger areas in descending the scale, until the deepest tones would cause vibration of the membrane from one end to the other. Such an explanation fails to account for the ability to perceive separately all different sounds which act upon the ear simultaneously; nor does it account for the presence of defects in hearing known as tone islands and tone gaps in the auditory field. Shambaugh maintains that the principle of sympathetic resonance is applicable to the membrana tectoria, which gradually increases in breadth from base to apex, after the manner of the basilar membrane.

Comparison of the Breadths of the Basilar and Tectorial Membranes.

Basilar membrane.		Observer.	Tectorial membrane.		Observer.
Base.	Apex.		Base.	Apex.	
mm.	mm.		mm.	mm.	
0·21 (man).	0·36	Retzius.	0·12 (man).	0·24	Von Ebner.
0·2 ,,	0·3	Kolmer.	0·08 ,,	0·240	Kishi.
0·041	0·495	Hensen.	0·038 (pig).	0·432	Shambaugh.
			0·046 ,,	0·220	Hardesty.

That there is a difference in the breadth of these membranes passing from base to apex is not difficult to show in histological sections, but it is a matter of extreme difficulty to be sure that measurements made are perfectly radial at the base and at the apex too. Unless special methods are adopted to prevent distortion and contraction of the membrana tectoria, measurements of this structure are of no value, and for this reason I have not added my own figures from specimens passed, e.g., through alcohol, which causes shrinkage of the membrana tectoria.

Hardesty's work on the tectorial membrane is the most praiseworthy. This observer succeeded in isolating the membrane from the cochlea in pigs. Dissections under saline fluid were carried out with the aid of the microscope. He thinks the tectorial membrane is much more qualified to act as a vibrator than the basilar membrane on account of its evident elasticity, transverse flexibility, sensitive to agitation in fluids in which it is examined, and lastly because it is attached along one instead of along both sides.

As a working hypothesis, Shambaugh's application of the Gray-Helmholtz principle of sympathetic resonance to the tectorial membrane is, in the present state of our knowledge, the most satisfactory explanation: possibly we may combine these theories.

Many useless controversies seem to be occasioned by retention of the term "telephone theory," which is surely a misnomer. Every sound, simple or complex, will produce a distinctive effect on the cochlea. All modern theories, call them by what names we choose, are based upon the assumption that the analysis occurs in the "periphery" before it can be appreciated centrally. Those who claim that the membrane vibrates as a whole agree that it must vibrate differently for different sounds—"sound patterns."[44] This is peripheral analysis, as Shambaugh rightly, I think, maintains.

[The lecture was illustrated by lantern slides of micro-photographs, charts, and diagrams.]

[44] Waller, "Human Physiology," 1891.