

LABYRINTH AND EQUILIBRIUM.

II. THE MECHANISM OF THE DYNAMIC FUNCTIONS OF THE LABYRINTH.

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In a previous paper,¹ I have shown that the ampullæ alone, without the otoliths, suffice for all the dynamic functions of equilibrium of the ear, and that the otoliths alone, without the ampullæ, also suffice for all the dynamic functions except that of response to rotation in a horizontal plane. I wish now to point out what I believe to be the mechanisms by which these reactions are brought about.

The Dynamic Functions of the Ampullæ.

Mach, Brown, and Breuer at first attached paramount importance to the space relations of the semicircular canals. It was assumed that rotation of the head in the plane of a canal caused, by the inertia of the endolymph, a current within the canal contrary to the direction of rotation. It was supposed that the hair cells of the crista were deflected by the current and stimulation of the nerve endings resulted. Mach,² however, very soon saw that under the conditions existing in the labyrinth such a current could not be produced, and Breuer later admitted that the hair cells do not project into the endolymph but are covered by a gelatinous mass.

On the experimental side, Loeb³ found that in the dogfish the canals could be cut through and even large portions could be excised without

¹ Maxwell, S. S., Labyrinth and equilibrium. I. A comparison of the effect of removal of the otolith organs and of the semicircular canals, *J. Gen. Physiol.*, 1919-20, ii, 123.

² Mach, E., Grundlinien der Lehre von den Bewegungsempfindungen, Leipsic, 1875.

³ Loeb, J., Ueber Geotropismus bei Thieren, *Arch. ges. Physiol.*, 1891, xlix, 175.

affecting the compensatory movements or the functions of equilibration, and Ewald⁴ stated that in the pigeon, after the canals had been ligatured, plugged, and cut, compensatory movements of the eyeballs and eye nystagmus were produced by rotation.

These experiments show that the canals are not necessary to the dynamic functions. Certain objections, however, might be raised. Loeb does not state specifically that all the canals were cut. Since I have shown that all the dynamic functions except that of response to rotation in a horizontal plane may be performed by an ear from which all the ampullæ have been removed, it would be necessary to know that the horizontal canals had been cut before the proof could be considered complete. Furthermore, in the dogfish each horizontal ampulla reacts to rotations in one direction only; this according to Ewald is not the case in the pigeon but his proof also is incomplete.

Since in the dogfish the response to horizontal rotation is brought about by the horizontal ampulla only, it would be a crucial experiment artificially to change the plane of this canal with reference to the skull of the animal and see whether this change does or does not alter the response to rotation. I have succeeded in doing this by the following method.

The right horizontal canal was laid bare for nearly the whole distance from its ampulla to the point where its posterior end reenters the vestibule. It was then ligatured and cut as far posterior as possible and the cut end was gently lifted into a vertical position, laid over against the skull, and supported there by a pledget of cotton. Its new plane was at right angles to its original plane and also at right angles to the long axis of the body. It is needless to say that in this operation extreme care must be taken not to exert the least traction on the ampulla. It is clear that with the canal in the new position rotation of the animal in a horizontal plane, that is around a dorsoventral axis, could not even theoretically give rise to a current in the canal. On rotation to the right, however, the eyes turn to the left and on rotation to the left the eyes turn to the right; that is, the ampulla whose canal is now at right angles to its normal position acts just like the

⁴ Ewald, J. R., *Physiologische Untersuchungen über das Endorgan des Nervus octavus*, Wiesbaden, 1892.

other ampulla whose canal is still horizontal. On the other hand, rotation of the animal around its longitudinal axis (in the new plane of the canal) never produces a deviation of the eyes to the left as it might be supposed to do if the rotation causes a current in the canal and the current excites the ampulla. This experiment, then, shows conclusively that the excitation of the sensory structures in the ampulla is due to some other cause than the production of a current in the canal.

Since no further consideration need be given to the possibility of currents in the semicircular canals as the cause of the excitation which on rotation gives rise to the reflex compensatory movements we may consider other possible causes. These might be (1) effects dependent on the inertia of the mass of liquid or other material in the vestibule, or (2) due to the inertia of the contents of the individual ampullæ, or (3) to inertia effects within the sensory cells themselves. It would be impossible to decide between these *a priori*.

In my earlier experiments I found that after destruction of the structures in the vestibule I could never obtain compensatory movements on rotating the dogfish around its dorsoventral axis. For a long time I was inclined to think that the absence of the reflex was due to some sort of injury to the ampullæ, although these appeared to be as sensitive as before to direct mechanical stimulation; the slightest pressure caused decided eye movements. When, however, I was finally able to remove the otolith from the recessus utriculi by slitting open the utriculus lengthwise without tearing it across I found that the compensatory movements to rotation in the horizontal plane were not abolished.¹ Since the destruction or the transection of the utriculus abolished the reflex with no apparent reduction in the direct sensitivity of the ampulla it became clear that the utricular (and possibly the saccular) structures are essential parts of the mechanism.

In attempting to analyze more closely the arrangements of the parts concerned it is to be noticed that the movement of rotation which acts as a stimulus to any given ampulla carries foremost the side of the ampulla which bears the crista. Thus the cristæ of the anterior canals are on the lower side of their ampullæ and a rotation of the head downwards excites them; the cristæ of the posterior canals are also on their lower sides and a rotation of the head upward (back part

of the head downward) excites them. So also the crista of the right horizontal canal is on its right or outer side and the stimulus for it is rotation to the right. Of course a similar relation exists for the left ampulla. Examination of the extensive series of drawings by Retzius⁵ shows that the dogfish is not a special case but that the arrangement is general.

A second fact which is significant is that the mouths of the ampullæ are continuous with the utriculus, an elongated, thin walled sac, stretched across the cavity of the vestibule and occupying only a portion, in the dogfish a not relatively large portion, of the vestibular space. Furthermore the utriculus is so attached by means of the sinus superior and other structures that a movement of the liquid contents of the vestibule might readily press it upwards towards the dorsal side of the cavity, but could have little effect to move it downwards. The relations as far as the ampulla of the anterior vertical canal is concerned are shown diagrammatically in Fig. 1. Rotation of the head downwards, that is, in the direction of the outer arrow, would tend by inertia to produce the same effect as if, with the head stationary, the perilymph was rotated in the opposite direction, as indicated by the small arrow within. This would put pressure and tension on the under side of the anterior end of the utriculus; this tension would be communicated to the ampulla and especially to its lower side which bears the crista.

In order to convince myself of the correctness or incorrectness of the above reasoning, I constructed a model by carving cavities and channels corresponding to the relations shown in Fig. 1. In these I placed a thin rubber model of the two canals shown in the figure. The canals and utriculus as well as the perilymphatic space were filled with mercury. On rotating the apparatus it could be seen that movement in one direction gave a very perceptible pull on the ampulla; movement in the opposite direction was almost without effect. It is possible that the rotation which puts the ampulla under mechanical strain would also tend to produce an increased liquid pressure within it, but this I could not determine in my present model.

⁵ Retzius, G., *Das Gehörorgan der Wirbelthiere. I. Das Gehörorgan der Fische und Amphibien*, Stockholm, 1882.

Careful dissection shows that mechanical relations analogous to those just described hold also for the posterior ampulla and the horizontal ampulla.

I wish to point out the advantage which the vestibular mechanism possesses on account of the mass of liquid. A relatively large free mass of liquid with a relatively small surface would show more inertia effect than a small mass with a relatively large surface area.

This principle was shown in a model made by Mr. W. F. Hoyt. Rossi⁶ had constructed a model of the size of a human semicircular

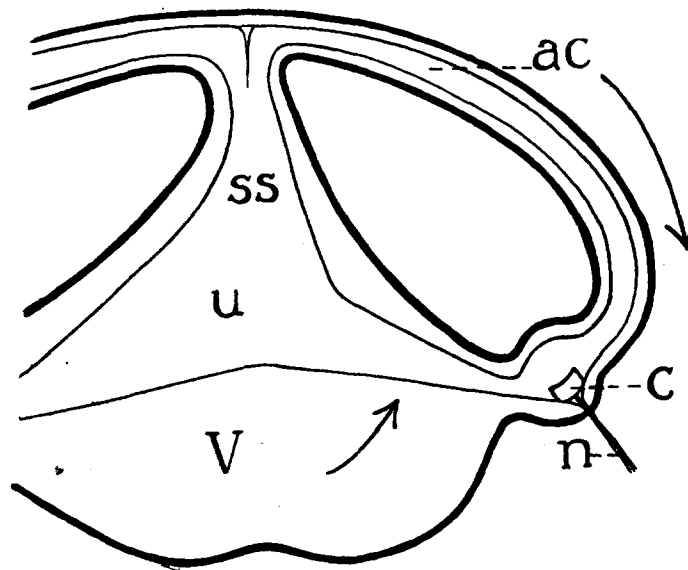


FIG. 1. Diagram to show relation of vestibular structures to ampulla; *v*, vestibule; *u*, utricle; *ss*, sinus superior; *ac*, anterior vertical canal; *c*, crista; *n*, nerve.

canal and ampulla and reported that movement of the liquid in the canal could be seen when the model was rotated. Hoyt made his model of glass for the greater transparency, and filled it with a liquid containing flakes of aluminium powder in suspension. When the model was rotated very rapidly and then suddenly stopped he could indeed see some movement in the canal, but the striking fact was that a marked movement of rotation took place in the ampulla.

⁶ Rossi, G., Di un modello per studiare gli spostamenti della endolinfa nei canali semicirculari, *Arch. Fisiol.*, 1914, xii, 349.

This movement was very much more readily produced and lasted much longer than that in the canal.

It has not been a part of the problem I have set myself to find explanations for the existence of structures in the labyrinth, but, on the contrary, to find out where and how definite functions are performed. Nevertheless nearly every person to whom I have communicated these results has asked, "What then are the functions of the semicircular canals?" It may be suggested that possibly a movement of liquid does take place through the canals, not as a stimulus to the nerve endings in the cristæ, but as a means of equalization of pressure. Indeed if the ampullæ were merely diverticula from the vestibule it is conceivable that pressure conditions could arise in them which might seriously affect their functioning. It is not unreasonable to suppose that the canals provide a means for the equalization of liquid pressure quite analogous to the use of the Eustachian tubes in equalizing air pressure.

The fact that in man and many mammals a nystagmus may be caused by irrigating the auditory canal with hot or cold water and that the character of this nystagmus differs for different positions of the head can be explained perfectly without assuming an unbelievable flow of liquid in the semicircular canals. If the temperature difference can cause convection currents in the inner ear at all under the conditions existing in such an experiment, it is certainly more reasonable to suppose that such movements of convection would arise in the mass of liquid contained in the vestibule than in the much smaller space of the canals where the friction would more readily overcome the tendency to movement. These considerations would not in the least invalidate the diagnostic use which Bárány has made of the phenomenon, but they do supply a rational explanation of its causation.

The Dynamic Functions of the Otolith Organ.

Breuer and others had suggested that the otoliths are concerned only with the static functions of the ear. Importance was attached to the space relations of the different otolith masses. But Parker⁷

⁷ Parker, G. H., Influence of the eyes, ears, and other allied sense organs on the movements of the dogfish, *Mustelis canis* (Mitchill), *Bull. Bureau of Fisheries*, 1909, xxix, 43.

and I each found that in the dogfish the large otolith of the sacculus has nothing to do with equilibrium; and I have shown that an ear from which the otolith of the sacculus as well as of all the ampullæ has been removed retains both static and dynamic functions. In this case the only part remaining which can mediate these functions is the small otolith organ in the recessus utriculi.

The otolith of the recessus utriculi is, in the dogfish, an oval or nearly circular mass, 3 or 4 mm. in diameter, shaped like a planoconvex lens. Its convex surface rests upon the corresponding concave surface of the macula in the bottom of the recessus. I have described it as resting on the macula, but the relation of its edges to the membranous walls suggests the idea that it is in reality partially suspended. To one who is actually performing these experiments it is a remarkably striking fact that all the functions performed by the ampullæ of the vertical canals can also be performed by this one organ. In the case of the ampullæ each one has a highly specialized function, responding to rotation in a single plane. The otolith organ on the contrary responds to rotations in all planes except the horizontal.

The approximation of the surfaces of the otolith and the macula, each almost perfectly spherical, suggests a mechanical arrangement by which any alteration of the position of the head would cause a corresponding change of pressure relations between the two structures. A pressure change of this sort could act as a stimulus to excite the compensatory movement appropriate to any particular rotation. Whether there is within the area of the macula a local differentiation of function comparable to that of the different ampullæ I have been unable to determine. The small size of the area to be explored and the difficulty of exact localization of an artificial stimulus have so far prevented an answer to this question.