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THE FUNCTION OF THE LABYRINTH

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IN the prevailing conception of the function of the labyrinth it is assumed that there are the following varieties of movement of the semicircular canals and of the contained fluid. It is assumed that in the generality of movements of the head they move together as part of the temporal region, whereas, in movements of the head in the plane in which one of the canals lies there is a disparity between the movement of the canal and the contained fluid. In a movement in this plane there is no surface at right angles to the direction of movement to exercise the necessary pressure, and the movement of the fluid depends on its viscosity, and on the extent of surface in contact with the wall relative to the volume of fluid. The movement is, therefore, to some extent delayed, and it is to the delay, causing a relative movement of fluid along the canal, that the function of the canal is attributed.

In the following description it is demonstrated that any sudden movement of the head, in any direction, gives rise to an associated movement along one or more of the canals; that important, results are similarly obtained by the presence of the saccus endolymphaticus and saccule; and, consequently, rotation of the head in the plane of one of the canals is only one variety of movement for the detection of which provision has been made.

In order to enable an animal to travel, or any animal to be driven along a circular path, provision must be present to obviate the effects of centrifugal force. Its application to both horse and rider galloping round a circus ring is obvious to all observers. Its effect is obvious to the occupant of a car travelling round a corner, or round a racing track,

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at high speed. In the semicircular canals of an individual circling in this way, the fluid rapidly acquires the velocity of the bone, and the relative movement of the fluid, associated with the unaltering movement of the head, is inversely proportionate to the time it has continued and, after a brief interval, ceases, whereas the mechanism for the correction of the effects of centrifugal force remains perfectly in operation.

A mechanism which produced a movement of fluid in the head of a cyclist travelling round a corner at a speed which necessitated riding at an angle scarcely compatible with safety, and in which the movement of the fluid produced the reflex adoption of an attitude which was safe only so long as the movement continued, and also produced an identical movement in the slowly turning head of a man watching the performance would, of itself, be valueless for the maintenance of equilibrium. Yet the head of the riding master at the centre of the ring, of the spectator at the corner, and of the judge inside the racing track, would be rotating at precisely the same rate as that of the rider or driver.

The stimulus which calls into play the reflexly co-ordinated muscular action which maintains equilibrium in the presence of centrifugal force must come into being almost simultaneously with, and increase and decrease directly in proportion to, that force itself. The stimulus, and its response, must remain, and as a fact does remain, constant, or vary with the degree of the force irrespective of time.

Balance is usually lost through an excessive displacement, in a particular direction, of the centre of gravity, relative to the supporting structures and is not associated with any corresponding rotation of the head.

Two associated, yet independent, mechanisms are, therefore, necessary; one to maintain equilibrium throughout a movement, however prolonged, which would otherwise destroy balance, and a second to detect at its commencement, and obviate the effects of, a sudden independent movement which would also destroy it.

The saccus and ductus endolymphaticus in combination with the saccule and utricle provide all the requirements of a mechanism such as the first, and the vestibule with the semicircular canals those of the second.

The contents of the cranium and vestibule are subject to any centrifugal force which affects the body as a whole. Those of the cranium create over the saccus endolymphaticus an increase or decrease in pressure which is conveyed by the duct to the interior of the saccule and utricle, while a reverse change is simultaneously created on their outer aspects by movements of the perilymph in the vestibule. The movement of the endolymph within them contributes to the effect, and the function attributed to the mechanism depends on the position of the sacci within the cranium.

Position of the sacci. These are placed mid-way between the centre of rotation at the foramen magnum (fig. 1, C) and the periphery of the

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cranium (L, R). During rotation round the central axis, C, the pressure at the periphery increases, while that at the centre of rotation undergoes a corresponding reduction, but mid-way between, in the position of the sacci, it remains constant. During a forward movement, owing to the inertia of the contents, there is an increase at the posterior end P, B, P, while the pressure is lowered at the anterior end A, F, A, but it, again, remains constant mid-way between, in the position of the sacci.

On the contrary, during rotation round an extraneous centre such as L′ one saccus, in this instance (S), is subject to diminished pressure while

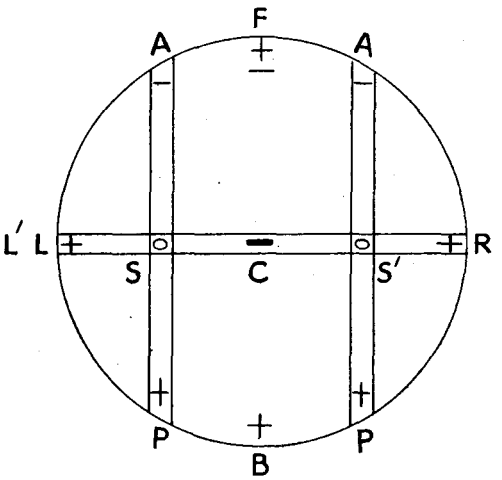


FIG. 1.

Diagram representing the action of the saccus endolymphaticus. C the centre of rotation in the foramen magnum; F, R, B, L the periphery of the cranium; F the anterior and B its posterior end; S, S′ the left and right saccus respectively.

that over the other (S′) is increased. When the head and body are inclined towards the centre of rotation the effect of gravity over the saccus (S) is increased, and in a certain position the increase compensates for the decrease in centrifugal force. Over the saccus (S′) the decrease in the pressure due to gravity is compensated for by the increase due to rotation. In both instances the pressure is maintained at a constant level by a suitable inclination of the head. The plane in which the sacci lie is gradually inclined, in a manner similar to the end of a racing track and, when the right angle has been attained, the forces of gravity and rotation counter-balance, and equilibrium is established. Even if the sacci were not actually central, provided that they occupied symmetrical positions, any rotation round a central axis, or any movement of the head forwards or backwards, would produce identical results in and over the sacci; whereas movement round an external axis, or from

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side to side, would have a reverse effect on each, and the reasoning would be valid, though the mechanism not so ideal.

The excitation of impulses. These cannot be excited by direct action of pressure on the hairs or neuro-epithelium, nor by a similar action of fluid. There is conclusive experimental evidence that there is no relation between the magnitude of the stimulus and that of the nerve impulse which it excites. The weakest stimulus which will excite an impulse will excite one which is indistinguishable, either instrumentally or by the physiological response which it evokes, from that excited by the strongest. It is the increase in frequency of impulses, having the same strength, which is responsible for the increase in sensory effect, and the minimum which will excite an impulse is termed a threshold stimulus.

Any increase in pressure is substantially uniform over the entire macula and, if it were the means of stimulation, threshold degree would be reached simultaneously in every part, suddenly giving rise to a maximum number of nerve impulses. There would, no doubt, be accidental, nominal differences ; but, broadly speaking, there would be one sensory effect, the presence or absence of which would indicate the presence or absence of centrifugal force, giving no indication of its degree, increase or decrease, upon the recognition of which the maintenance of equilibrium entirely depends.

If a finger or hand is placed in mercury it is found that the sensation of pressure is experienced only where the surface meets the skin. That and other experiments demonstrate that, normally, it is distortion, and not uniform pressure, which excites nervous impulses and gives rise to the sensation of touch.

The saccule is somewhat flattened and as the fluid entered it would become more spherical. The walls of the saccule at the margin of the macula would be drawn away from the periosteum and the separation would progressively increase from the periphery towards the centre, subjecting an increasing number of hairs and cells to distortion. This may not be the actual method present, but it exemplifies the nature of the mechanism by means of which stimulation is effected.

In my little book " Hearing and Equilibrium " I maintained that the prevalent theory, that the spiral shape of the cochlea was to neutralize the effects of gravity, would not stand criticism. The reasons given were as follows. The cardinal feature of a hydraulic system was that forces such as that of gravity and momentum affect it as a whole. The fluid in the vestibule had to be taken into consideration, and if it moved towards the scala vestibuli under the influence of gravity, or as the result of inertia or momentum, acquired through movements of the head, the movement would be transmitted along the scala towards its outer wall, in the same way, that I believed, sound waves were along the scala tympani.

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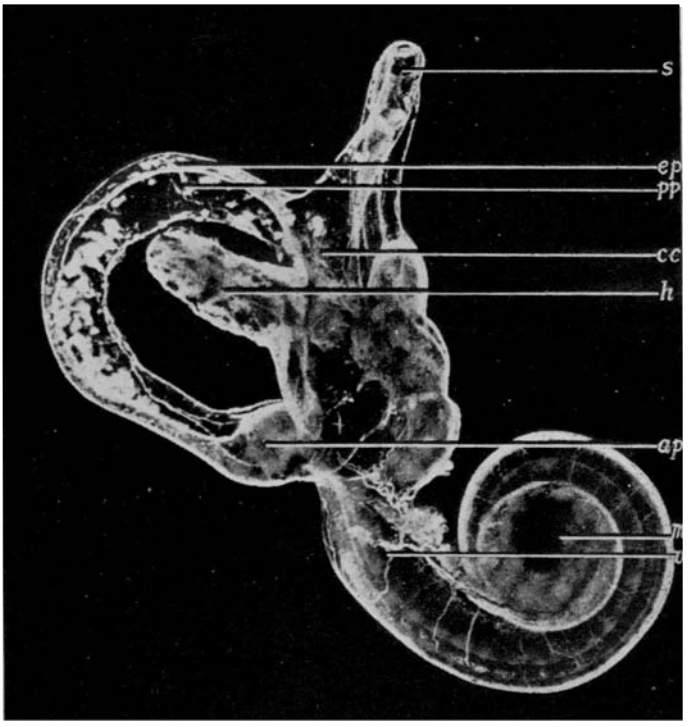


FIG. 2.

Membranous Labyrinth: Viewed from Behind. s, superior canal. e p, endolymph space, p p, perilymph space, and a p, ampulla of posterior canal. c c, common crus h, horizontal canal

(A. A. Gray—"Diseases of the Ear"—By permission of Baillière, Tindall and Cox.)

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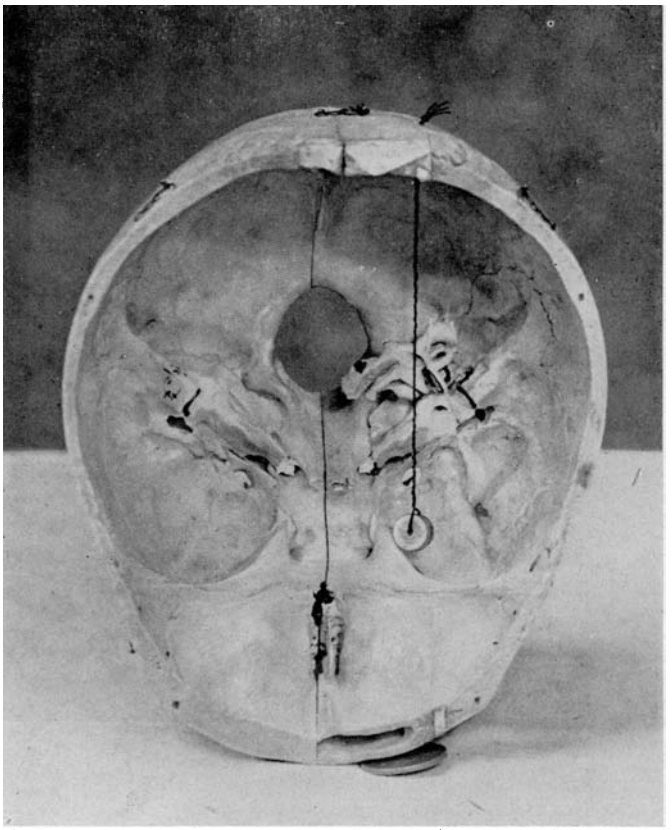


FIG. 3.

Photograph of a transverse section of the cranium, rotated through 90° round a transverse horizontal axis. In order to bring all the semicircular canals into view it was necessary to photograph the specimen from a slight angle to the normal line. This caused the slight, but immaterial, departure from the true relation between the plumb line and the structures which is referred to in the text.

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The result would be the reverse of the elimination of the effects of gravity or of momentum, which was the function attributed to the curve of the cochlea. On the contrary, I maintained that it was an ideal provision for the preservation or, alternatively, for the maximum utilization of the energy of any movement of the perilymph along the scalae. But while making these and cognate observations I failed to recognize the true method of their elimination.

Some authorities write as if waves entered the cochlea. The longer waves, in a watery medium such as the perilymph, are between one and two hundred feet in length, and if sound waves passed through the cochlea, in any sense, the fluid in both scalae would occupy practically the same phase in the wave, the difference in pressure on the reverse sides of the basilar membrane would be negligible, and correspondingly little movement of it would be possible.

The present suggestion is that the function attributed to the curved shape of the cochlea is perfectly fulfilled by the balanced columns of perilymph. The columns of perilymph in the scalae represent the two sides of a balance, the fulcrum of which is situated at the helicotrema and the scales at the entrance to the scalae. Perfect functioning of the balance is unaffected by gravity, centrifugal force, or by the movements of the head, since all these have an equal effect on both the scales and are counterbalanced at the helicotrema.

On the other hand any change in pressure limited to one entrance, such as an increase or decrease in pressure at the vestibular end of the scala vestibuli without a compensating change at the fenestra rotunda, or *vice versa*, produces an equivalent movement of the two columns of fluid which constitute the balance, and the movement is registered in the sensorium.

The principles applicable to movements of the fluid in the cranium which operate the saccus endolymphaticus are equally applicable to movements of fluid in the vestibule. The presence of the fenestrae permits the expansion and contraction of the saccule which has been described and, in addition, the movement of the fluid in the ear farther from the centre of rotation, under the influence of centrifugal force, reduces the pressure on the outer aspect of the capsule, supplementing the pressure within it ; while in the nearer ear centrifugal force carries the fluid against the inner wall of the vestibule increasing the pressure on the saccule.

At the commencement of a somersault movement in a forward or lateral direction, or during rotation of the head, there is a relative movement of fluid round one, or more, of the canals ; but a very much more delicate mechanism has to be sought. We know from experience that a mechanism is present which detects, and automatically, or reflexly, rectifies any involuntary displacement of the body before the head has

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moved one foot, or the centre of gravity six inches, away from a line passing vertically through one of the feet ; and that serious injury of the mechanism may mean deprivation of normal activity.

Evidence is now adduced that in the canals the movements of the perilymph rather than those of the endolymph require consideration ; that those in the vestibule are primarily responsible, and are the immediate result of a single movement in any direction and, consequently, that movement along the canals is not solely, or even mainly, due to relative movements of bone and fluid as the result of rotation of the bone round the centre of curvature of the canal.

The relative movements of endolymph and perilymph. " As a tube is increased in size the cross-sectional area increases more rapidly than the surface where friction losses develop. Consequently, at any constant pressure-head the velocity of flow in a tube (if there is streamline motion) varies as the square of its radius, and the *volume* flowing per minute varies as its fourth power ".*

" The semicircular ducts are elliptical on transverse section and about one quarter of the diameter of the bony canals which contain them."†

If the duct and the canal were circular in section and similar conditions prevailed in both, the *velocity* of the perilymph would be 16 times as great as that of the endolymph, and the transverse section of the bony canal being 16 times as great as that of the membranous canal, or duct, 16 times the volume of fluid would flow at 16 times the velocity past any given point in a given time, and there are other considerations which probably increase this estimate.

The relative extent of surface and, therefore, of friction increases with any deviation from the circular in transverse section, and this is generally more pronounced in the ducts. Papilliform eminences are described by Schafer as projecting into the interior, and Gray describes " little conical ridges running along the inner surface ". The viscosity, which primarily determines the degree of retardation, is higher in the endolymph than in the perilymph. On the other hand there are trabeculae traversing the perilymph space, but they are indispensable and are designed to obstruct the flow to a minimum extent.

The evidence appears conclusive that, at a low estimate, the *volume* of perilymph entering the bony ampulla is 256 times as great as that of endolymph. Finally, the perilymph in the canal is in a direct line with the endolymph in the ampulla and the action would be analogous to that in the cochlea (fig. 2).

As the perilymph enters the bony ampulla it moves the free wall of the membranous ampulla, and the endolymph beyond it, towards the utricle, meeting with little resistance. Any movement in the reverse

* Macleod's *Physiology Barber.*
† Cunningham's *Anatomy.*

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direction draws endolymph into the ampulla, dilating the membranous wall so that it more completely fills the bony ampulla. Any further flow of perilymph is correspondingly reduced and, consequently, movement of threshold degree is possible in only one direction, and movement of the head in any direction produces effective movement in only one of any two associated canals.

In striking contrast to that arrangement is the negligible movement of endolymph along the duct, the equal facility with which it moves in both directions; and that if it were the origin of nerve impulses, equal movements in both directions would produce stimulation of the neuro-epithelium and give rise to the same response for the correction of body movements in diametrically opposite directions.

Experiments were conducted with a view of ascertaining the relative effects of centrifugal force and of rotation of the canal round its centre of curvature. While they were being conducted it became evident that neither played the most frequent or important part in the production of movement along the canals; that any movement of the head in a forward, lateral, or intermediate direction, produced a relative movement of the fluid which acted as a stimulus; and that being due to, and being present during, the lapse of time required for the fluid to acquire movement, its application was instantaneous. A glass tube having a bore of 4 mm. was rendered circular, leaving a gap just sufficient to introduce spirit which, as its use in spirit levels indicates, has a low viscosity and a little fine sawdust to indicate any movement. During rotation of the body, the tube was held on a bottle held in front and filled in a similar way. The movement in both bottle and tube could be observed in this way at the same time. The movements in the tube were negligible both in extent and duration in comparison with those in the bottle which were solely the result of the greater velocity at the distal end compared with that at the proximal.

A half circle and a straight length of the same tubing were then substituted, in turn, for the complete circle. When the half circle was held with the concavity towards the body so that the effects of centrifugal force in each quadrant nullified those in the other, the movement was greater than in the complete circle, but not comparable to that when one end was held towards and the other away from the body, and centrifugal force was substituted for rotary effect. When the curved and straight tubes were in comparable positions the movement was greater in the straight; and the difference was most pronounced when the tubes were in positions analogous to those of the semicircular canals. The movement was least in the complete circle when on the prevalent theory it should have been greatest.

It is recognized that sound waves produce movements along the scalae between the fenestra rotunda and fenestra ovalis; but not that

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considerably greater movements between the fenestrae would be produced by movements of the fluid in the vestibule, to or from the fenestra ovalis as the result of centrifugal force or movements of the head. As just indicated these movements are not affected by the action of gravity or momentum on the columns of fluid in the scalae, and are probably unaffected by their action on the structures in the middle ear, which are probably balanced by the upper ends of the malleus and incus.

MOVEMENTS OF THE VESTIBULAR FLUID.

To give a conception of the value of these movements a modification of an experiment described in the issue of this *Journal* for June 1941 will be given. A pellet of steel, weighing one grain, was dropped from a height of one inch on to a light, resonant box, and a friend at a distance of 83 feet could detect the sound.

If the entire energy of the impact were converted into sound, a fraction, not exceeding 1/12,000,000 would reach each square inch of the periphery of a sphere at a distance of 83 feet. The energy of waves travelling the same distance across a level surface would decrease less rapidly, but the entire energy contained in *the chain* of waves impinging on a square inch of surface would probably not exceed 1/8,000,000, of the total, and that entering the ear would be considerably less; and a general impression is all that it is required to give.

The fluid in the vestibule exceeds a grain in weight; frequently, in movements of the head, it has a velocity imparted to it exceeding that with which the pellet reached the box and, on the cessation of the movement of the head, the entire energy is in the momentum which, if the fluid were free to move, would carry it with corresponding force against the wall of the vestibule in the direction towards which it had been moving. The fenestra is at its anterior end, on its outer side, and on the arrest of any movement or rotation of the head to the opposite side, the fluid would be carried against the stapes which would be forced outwards. Such a movement would be rendered possible, as in the instance of sound waves, by the presence of a second opening, in this case that of the scala vestibuli, which would permit the entrance of additional fluid.

The substitution of the conception, that momentum carries the fluid in the labyrinth against the walls, for the conception that the walls move against a stationary, inert, fluid, is not so fantastic as it might appear. It is what frequently, actually, happens in what would be described as a sudden movement of the head.

We are, as a fact, travelling through space with an absolute motion the direction and velocity of which are unknown. Heads are moving in all directions; many are, therefore, moving in the reverse direction to the absolute motion. In these instances the apparent sudden movement is, in reality, an infinitesimal reduction in the speed at which the

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walls of the labyrinth are travelling, and the fluid continues to move with the original velocity until arrested, and in the original direction as far as the curves of the canal will permit. Similar reasoning would apply to movements in the labyrinth when on a ship, during uniform movement, or in a vehicle the movement of which was regular.

Before detailing the functions of the vestibule, and suggesting modifications of the prevalent views regarding movements along the semicircular canals, it is necessary to digress in order to question statements in current literature and to direct attention to anatomical features with which function has not been associated.

It is stated in textbooks that if the head is rotated forwards or backwards through an angle of 90° the superior canal is brought into a horizontal plane, and a description is given of the effects of rotation on patients whose heads are in this position, and the movements of the fluid in the semicircular canals are described.

The photograph (fig. 3) was taken with the skull in the position which it would occupy during life if rotated as described. The superior canals are *in situ,* the roofs having been removed and the interiors blackened. A second specimen can be seen fixed in position, care having been taken that the orientation of the internal auditory canal was, as far as possible, identical with that of the canal in the skull. The semicircular canals have been dissected and the walls of the superior and posterior can be clearly discerned.

It is immaterial whether the photograph be regarded as taken with the skull in vertical position or, from above, with the skull horizontal. It is evident that the superior canals do not become horizontal and that the ends of the canals which normally occupy approximate horizontal planes, and are the chief consideration, have been rotated into planes which are correspondingly vertical. The posterior canals have moved towards a horizontal position; but the specimen was rotated a little in order to bring the canals into view, and the superior appears more vertical and the posterior more horizontal than they actually are.

To illustrate the principle upon which the proposition rests, the movement primarily selected is that backwards and to the right, following the line of the left superior canal, indicated by the white arrow (fig. 4).

Since in all the movements momentum and inertia are indistinguishable, and may be present in any proportions, a sudden movement backwards and to the right may be regarded as the arrest of movement forward and to the left. The superior and external canals occupy planes meeting along this line which, therefore, lies in both and, if such a movement were present the fluid in both canals might be regarded as sharing it, but if the movement of the head suddenly ceased that of the fluid would not continue in the form of a relative movement, unless another agency intervened; a column of fluid in the vestibule, of equal length,

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would possess equal momentum and would counter-balance the column in the canal and the position would be analogous to that in the scalæ.

The solution of the problem depends on the application of two well recognized principles. Firstly in any closed system filled with water, owing to its incompressibility, there must be an opening in, or in connection with, any situation in order to permit movement towards it and, owing to atmospheric pressure, there must be an opening in connection with any situation to permit of the movement of water away from it. In the vestibule there are only two suitable openings, namely, the fenestra ovalis and the termination of the scala vestibuli, and all the movements under discussion, whether in a straight line, round by the semicircular canals, or along the scalae of the cochlea are directly, or indirectly, from one of these openings to the other. Secondly, the movements to and from either of these openings are essentially different. The difference is illustrated by an experiment previously described in the *Journal* in June 1941. If the nozzle of a syringe with a fairly fine bore be held about an inch from the flame of a candle and the piston be forcibly withdrawn the flame remains unaffected, because the air travels equally from all directions towards the nozzle. If, however, the air is expelled, using very gentle pressure, a small dark patch appears in the flame, because the air being expelled has acquired momentum which carries it in a direct line to a distance from the orifice.

Fig. 5 represents a section through the left superior canal S and the vestibule V. In order to render the posterior canal P visible it is represented to one side of, instead of immediately behind, the superior, and the orientation of the scala vestibuli has been modified for the same reason. The true relations are seen in the photographs (figs. 4 and 6), and the proportionate measurements are, as nearly as possible, those of the specimen photographed.

The central arrow indicates the assumed direction of the movement of the head. If the perilymph were free, it would move throughout the depth of the vestibule towards the fenestra and the wall beneath ; under the conditions present only the upper layer can move in that direction, carrying the stapes before it and increasing the capacity of the vestibule. Perilymph would, therefore, enter from the scala vestibuli SV and would be carried in the direction of its termination towards the postero-internal wall and the adjacent openings of the crus commune and external canal, and the outward movement of the upper layer necessitates the replacement of its inner end by perilymph from below.

Owing to the immobility of the walls of the vestibule movements immediately to and from them may be regarded as virtually absent, and movements from the apertures pass along, rather than towards the walls in the immediate vicinity. The movements of perilymph traversing the

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vestibule are thus, substantially, confined to streams. In the movements of the vestibule which have been selected for illustration, namely, those in a postero-internal (anti-fenestral) direction, there are two; one transverse stream near the roof, in an antero-external (fenestral) direction; and a second, which is a continuation of the perilymph in the termination of the scala vestibuli, is inclined upwards and postero-internally (anti-fenestrally); but the anti-fenestral movement of the

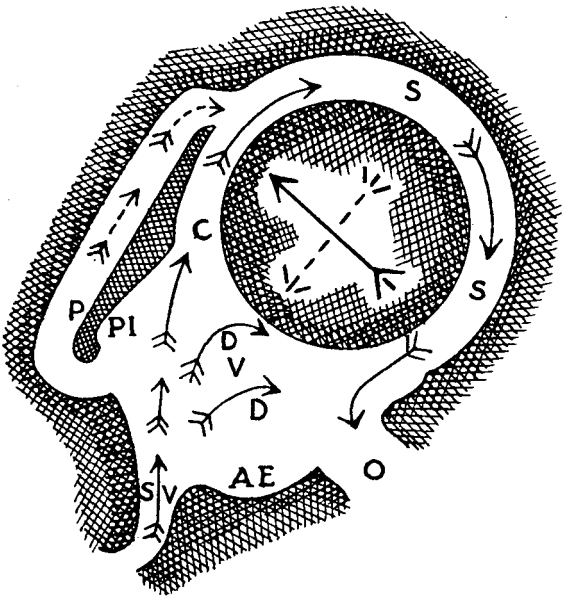


FIG. 5.

Vertical section through the left superior canal, viewed from the inner side and in front. AE, the antero-external wall: C, canalis commune: D, arrows representing deviation of the perilymph, due to the movement of the vestibule in the direction of the central horizontal arrow: O, fenestra ovalis: P, posterior canal: PI, postero-internal wall: S, superior canal.

The arrows in interrupted outline represent incidental movements, which might result from inertia during the downward movement described in the text.

vestibule, of which the tranverse stream is an expression, equally affects the upward stream and causes it to follow an increasingly fenestral direction. Its upper end would reach and join the anti-fenestral end of any transversely moving stream, extending it, thus permitting its movement away from the anti-fenestral wall and contributing to the movement.

The resulting configuration would be such as that suggested by the arrows marked D. There are other paths, namely those round the superior and external canals, and the perilymph might move along either.

The same drawing (fig. 5) illustrates the movements which would be

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present if the head were to move directly downwards, not bent forwards, in the direction indicated by the central arrow in interrupted outline. Again, owing to the relative positions of the scala vestibuli and the fenestra, there would clearly be a movement between them ; but it would be essentially from the floor to the roof of the vestibule.

In the absence of the anti-fenestral movement of the vestibule, the gradual conversion of the upward stream from an anti-fenestral to a fenestral direction does not take place. It continues its original direction towards and up the anti-fenestral wall, the upward movement being accentuated by the downward movement of the head. There would be no movement in the direction indicated by the arrows D, and the single natural path, even if the superior canal were absent, would be one along the site which it occupies.

The same result would be obtained if the head were inclined to one side during horizontal rotation of the body.

The horizontal canal is horizontal only at the fenestral end. The other end dips downwards to an extent which permits a stylette to be passed into the opening through the end of the scala vestibuli. Fig. 6 is a photograph of a specimen in which a strand of flexible wire was passed through the end of the scala, and crossed the lower part of the vestibule into the opening sufficiently to permit the end to be seized and pulled up through it. The end of the wire is bent over the posterior canal so that the external should be more fully exposed.

It will be observed that while the opening of the superior canal is at the upper end of the anti-fenestral wall, and is so directed that the maximum quantum of movement sweeping up it will enter the canal, the opening of the external canal is situated in the middle region of the vestibule where an upward movement would produce a minimal change in pressure, that it is at a distance from the anti-fenestral wall, and that its margin is in a vertical plane so that any vertical movement would carry the perilymph across, and not into it. (Figs. 4 & 6.)

If the movement were in a horizontal plane in the direction indicated by the black arrow in fig. 4, the fenestra ovalis would move towards and vertically over the position which the scala vestibuli had occupied. This movement would produce a relative movement of the perilymph in the reverse direction ; but not along a straight path. The fluid in the scala is counter-balanced and its momentum does not contribute to the degree of movement, but it substantially modifies its direction. It imparts an initial upward and anti-fenestral direction to the stream issuing from the scala. The movement of the vestibule leaves the upward component in the movement unchanged, but it alters the movement towards the anti-fenestral wall into one towards the fenestra. The stream follows a path resembling that indicated by the arrows marked D (fig. 5) with an exaggeration towards the external canal. In brief,

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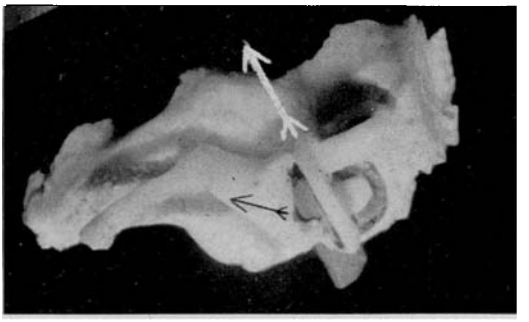


FIG. 4.

Left Internal ear, seen from the inner side and in front. The white arrow, therefore, points backwards and to the right of the head.

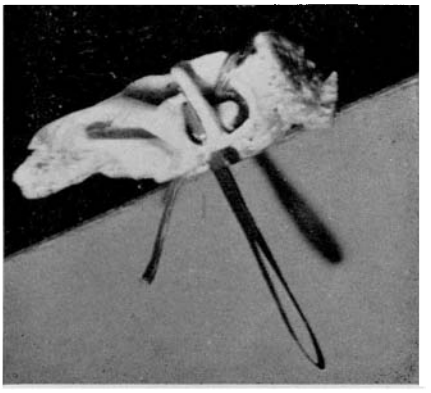


FIG. 6.

The specimen shown in fig. 4, rotated in the plane of the superior canal sufficiently to bring the fenestra ovalis into view. The strand of wire which is seen was passed up the termination of the scala vestibuli. It crossed the floor of the vestibulum and entered the lower (inner) end of the external canal. The end of the wire was drawn upwards along the canal and its end bent backwards over the posterior.

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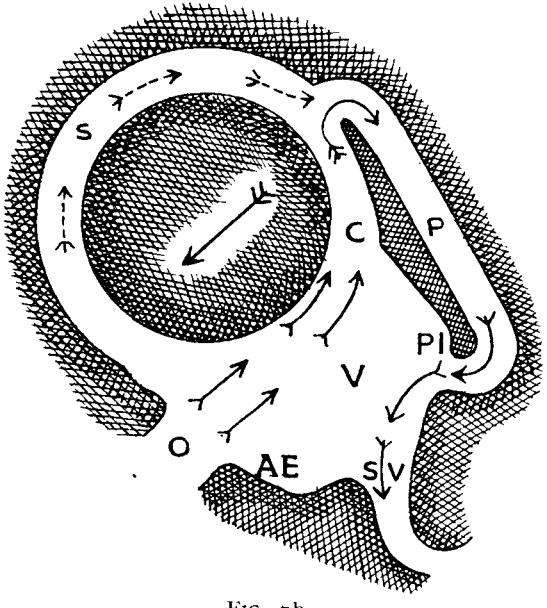


FIG. 7b.

Vertical section through the right superior canal, viewed from the inner side and in front: lettering as in Fig. 5.

In the photograph a strip of black paper has been shaped so as to fill the fenestra ovalis and demonstrate the correct orientation of its inner margin, which is at an angle to the outer,

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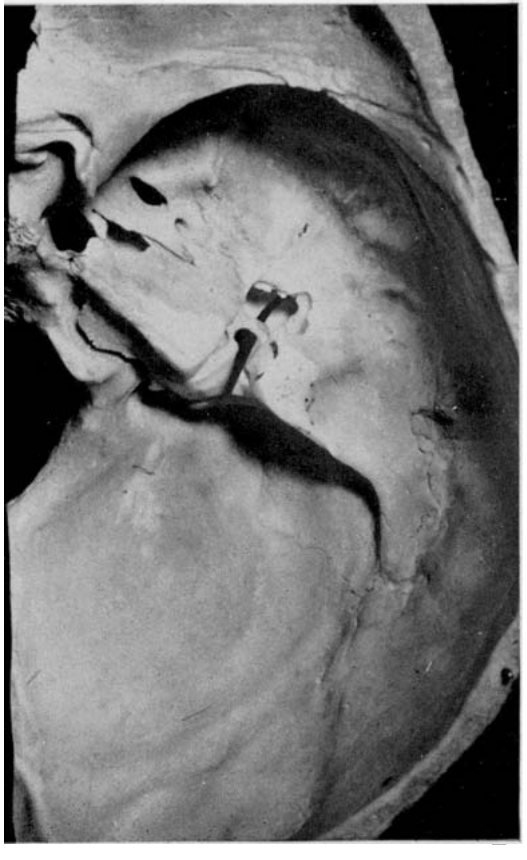


FIG. 7a.

the external canal lies along the path which the movement would naturally follow.

Virtually all movements contain a vertical and horizontal component and the construction secures that a corresponding proportion of the relative movement representing each reaches the appropriate canal.

Fig. 7 illustrates the effect of movement of the vestibule in the reverse direction to that indicated by the white arrow in fig. 4. In this instance the movement of the fluid would be from the fenestra to the scala vestibuli. The entire fluid in the vestibule, if free, would

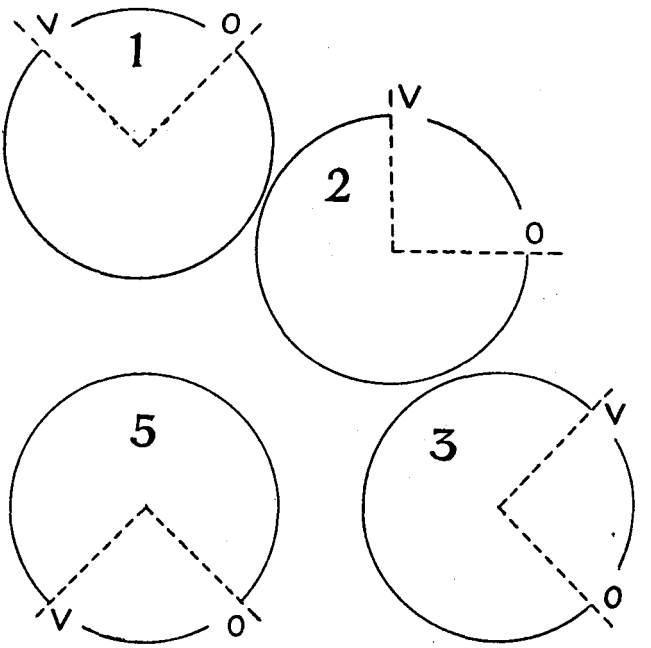


FIG. 8.

have a relative movement towards the anti-fenestral wall: but the only layer free to move would be that in contact with the stapes. This upper layer would be carried against the wall, where it would be deflected downwards and drawn outwards to the exit at the scala vestibuli. Its natural path would be along the position occupied by the posterior canal.

The efficacy of the construction is more evident if it is visualized in connection with the action of gravity with which we are so much more familiar. In fig. 8 a receptacle, resembling the vestibule in construction, is shown in four positions. It has two orifices O and V representing those of the fenestra ovalis and scala vestibuli, respectively, which are to be regarded as closed with a delicate elastic membrane. If it were full of water and were rotated round the fluid from the first to the second

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position the pressure at the lower end of O would rise from zero to 50 per cent of that at the bottom of the receptacle, and in the third position would rise to 70 per cent. of it. Rotated in the reverse direction, corresponding pressures would be present at the lower end of V. If two similar receptacles were, respectively, in the first and third positions and were rotated simultaneously in the same direction, while the pressure at a given point in one rose that at a corresponding position in the other would fall, but at any period of the rotation there would be a minimum pressure of 50 per cent. at one of the orifices, and if the various pressures were registered the mutual positions of the receptacles would be indicated.

The principle difference between the operation of gravity, and momentum is that in the former pressure would be already present in the positions into which a membrane was moving and the resulting movement would take time to develop, whereas in the ear its development is instantaneous. In ordinary mechanical stimulation it is the terminal blow which constitutes the stimulus ; in the ear it is the movement, the actual acceleration, which provides it.

The principles involved in the foregoing description have been so repeatedly verified by experiment that though the final intuitive deductions may be questioned, this cannot be said of the premises on which they are based.

It has been ascertained, and corroborated by different methods, that the volume of a solution passing along a tube depends on the ingredients, on their concentration and on the temperature ; but owing to the complexity of the factors entering into the computation, and their constantly changing nature, it would be necessary to employ tests in each individual case to estimate the effects. It has been ascertained, however, that the viscosity of the endolymph is greater than that of the perilymph and would retard its transit to a greater extent.

On the other hand it has been demonstrated that the volume transmitted along a tube is proportional to the pressure, is proportional to the fourth power of the radius, and inversely proportional to the length of the tube. Consequently it can be definitely asserted that the volume of endolymph moving along the endolymph channel is only a fraction of 1 per cent of that of the perilymph moving along its channel, in the same time, under an equal pressure.

The fluid in the vestibule moves solely as the result of direct pressure on it by its walls with a corresponding counter-pressure by the fluid. Owing to the position and direction of the openings into the vestibule of the fenestra and scala vestibuli, pressure and counter-pressure resulting from every movement of the head are situated at the non-ampullated end of a specific canal, or ends of specific canal, in either the right or left ear.

Where the ampullated ends are in a similar position with reference

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to a movement, or in a position in which a rise in pressure would otherwise occur and have a counter-balancing effect, an increase does not take place owing to the presence and special position of the fenestra or the scala vestibuli. There is one exception, namely, a movement directly upwards.

Owing to the disposition of the walls and orifices and the direction of the end of the scala vestibuli, movements traversing the vestibule are concentrated along definite paths ; and, owing to the limitations imposed on their extent by those of the stapes and secondary membrane, it would be more accurate to visualize the fluid participating in a movement as a flexible column being carried by its momentum, or in virtue of its inertia, against a particular region of the wall.

Every drop of endolymph or perilymph, and every fragment of membrane situated along the path of the movement contributes to the effect, and every movement modifies, in accordance with its direction, the shape and position of the saccule and utricle and their attachments to the wall in various situations.

It is a matter of conjecture whether the impulses generated at the maculae are delicate indicators of the degrees of movement, the direction of which is revealed by the semicircular canals, or whether they also indicate direction.

There is one important indication for which they alone can be responsible. In an upward movement of the head the relative movement of the fluid is directly from the fenestra to the scala vestibuli. It is the result of a downward movement of the fluid in the vestibule in virtue of its inertia, with a relative fall in pressure in the upper stratum, and the induction into it of fluid from the direction of the fenestra. The nature of the movement may be represented by a reversal of the arrows marked D (fig. 5). There would be a displacement of the utricle, and possibly of the saccule, in a specific direction with an absence of any associated movement along the semicircular canals. It is the only movement in which this can occur, and would clearly indicate its direction. In other movements with an upward component there would be a disproportionate and specific displacement of the sac, or sacs, which would indicate its presence and its degree, the vestibule supplying the place of a semicircular canal.

Conclusion. By attributing to the fluids in the cranium and the vestibule the movements which would result from the operation of recognized laws these fluids appear to become part of, and to operate, a mechanism, which provides for the reflex adjustment of the body to varying degrees of centrifugal force, and provides for the most rapid possible transmission of impulses to the sensorium indicating, the effects of a movement in any direction, the procedure requisite for the maintenance of equilibrium, and securing its instant, reflex, adoption.

Rotation of the head round its own central axis would also produce

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relative movements; but a synthesis of the impulses transmitted from both ears would eliminate confusion, and these movements are not within the scope of this communication.

It could also be demonstrated that, owing to the relatively slow rise in pressure and the presence of the helicotrema, the movements described would not produce material displacement of, or injury to, the basilar membrane.

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