

LABYRINTH AND EQUILIBRIUM.

III. THE MECHANISM OF THE STATIC FUNCTIONS OF THE LABYRINTH.

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The Static Functions of the Ampullæ.

In a preceding paper¹ I have shown that removal of the otolith organs from the labyrinth of the dogfish does not destroy the static functions; that, on the contrary, the compensatory changes of position of the eyes and fins occur when the animal so operated is tilted out of the normal or primary position; and that if the animal is held in the abnormal position permanently the compensatory positions of the eyes and fins are also retained permanently. I have also pointed out that the stimuli for the maintenance of these compensatory positions do arise from the labyrinth; that they are not affected by the exclusion of other sensory stimuli; but that they disappear at once when the remaining parts of the labyrinth are destroyed. I also proved that rotations around the body axes excite the dynamic responses through changes of tension on the ampullæ due to the inertia of the vestibular contents, and not through the production of currents in the semicircular canals. I wish now to show that the same mechanism which excites the ampullæ to the exercise of their dynamic functions serves also to produce their static effects.

While an animal is undergoing rotation around a body axis there is brought about through inertia a displacement of the contents of the vestibule, and this displacement and the consequent change of tension acts as a stimulus. If on cessation of the movement of rotation the

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.

contents of the vestibule returned at once to their original position the stimulus would cease and the eyes would return to the primary position. If, however, the new position of the vestibular structures continued to exist after cessation of the movement the tension differences would also continue and the resulting stimuli would give rise to sustained forced position of the eyes; *i.e.*, to the static effect. The latter condition could exist in case the specific gravity of the utricular tissues is greater than that of the lymph. This I have found to be the case.

In most selachians the lymph of the vestibule is in free communication with the exterior sea water through the ductus endolymphaticus. It is reasonable therefore to expect that the density of the lymph would be practically equal to that of sea water. On this assumption I determined the relative weights of the membranous labyrinth and sea water by dropping small bits of utricle, ampullæ, and semicircular canals into a tall jar of sea water and saw that they all sank to the bottom. In order to be more certain, however, I succeeded in getting a sufficient amount of lymph from the ears of several fish killed at one time and dropped bits of the membranous labyrinth into it, with the result that they sank just as in sea water.

Since the membranous labyrinth and the lymph differ in specific gravity it is evident that when the membrane is displaced to a relatively lower position its weight will have the tendency to prevent its return to the original position in the cavity as long as the new body position is retained. I believe that this difference in weight, then, is the cause of the continued forced position in the absence of the otolith.

It has been frequently stated that the stimulation of an ampulla gives rise only to a momentary movement, not to a sustained forced position, and that therefore its function can be only dynamic and not static. I have found the contrary to be very definitely true. Sustained mechanical stimulation of an ampulla, even the ampulla of a horizontal canal, causes a sustained forced position of the two eyes; namely, a conjugate deviation to the side opposite to the stimulated ampulla. It is self-evident that in the ordinary functioning of the horizontal ampulla, when the rotation to which it responds is in a horizontal plane, no changed relation to gravity can occur and hence the reaction to rotation cannot continue after the rotation has ceased.

That the horizontal ampulla reacts to its normal stimulus by a response then is due only to its space relations, and not to a different kind of physiological function. Of course my experiments have demonstrated the ability of the other ampullæ to produce sustained static effects.

The Static Functions of the Otolith Organ.

In the dogfish and related forms it is comparatively easy to remove all the ampullæ and to see that in their absence both static and dynamic functions are retained by the remaining parts of the labyrinth; that is, compensatory movements and compensatory positions of the eyes and fins still occur in response to rotations in all planes except the horizontal. The removal of the large otolith of the sacculus has no effect whatever on these reactions; but if now, in addition, the small otolith of the recessus utriculi is removed the compensatory movements are at once abolished.

The original suggestion of Breuer that the otolith organs constitute the apparatus for the static functions of the labyrinth has been widely accepted. It has also been generally believed that the pressure of the otolith due to its weight is the stimulus which gives rise to the static function. If, for example, the animal is rotated to the right around its longitudinal axis and held in this new position, the pressure of the otoliths is shifted to the right and presumably the epithelium on the right side of the macula is now subjected to a relatively greater pressure, or even a previously unstimulated portion is now brought under pressure. In a previous paper² I was inclined to accept a similar explanation of the dynamic functioning of the otolith. In the light of new experiments to be reported below I am led to modify this view. I had, however, long ago given proof that in the compensatory movements of the horned toad (*Phrynosoma*) the exciting cause is not pressure, *per se*, but the torsion effect due to rotation.³

² Maxwell, S. S., Labyrinth and equilibrium. II. The mechanism of the dynamic functions of the labyrinth, *J. Gen. Physiol.*, 1919-20, ii, 349.

³ Maxwell, S. S., On the exciting cause of compensatory movements, *Am. J. Physiol.*, 1911-12, xxix, 367.

Simple and plausible as Breuer's *a priori* conception appears no one has ever been able to confirm it by direct experiment. Lee,⁴ for example, states that: "Stimulation of the otolithic parts of the ear has not been entirely satisfactory. The results were found exceedingly variable." Experiments by pressure on the otoliths or epithelium have usually been described as unconvincing or contradictory. As will be seen they are consistently contradictory to Breuer's views so commonly held.

I have now found that it is possible to stimulate mechanically the otolith organ of the recessus and to get results just as clear and consistent as those obtained from stimulation of the ampullæ. I quote the following record of an experiment.

"July 16, 1920. Large dogfish (*Galeus*).

Opened both ears and removed all six ampullæ.

Using a stiff bristle tipped with wax and the wax covered by a thin layer of absorbent cotton, applied pressure to various parts.

Right ear.

Pressed on right (lateral) side of otolith (of recessus utriculi); right eye depressed, left eye elevated.

Pressed on left side of otolith; left eye depressed, right eye elevated.

Repeated several times with uniform results. Otolith soon disintegrated: no more response.

Left ear.

Pressed on left side of otolith; left eye depressed, right eye elevated.

Pressed on right side (median) of otolith; right eye down, left eye up.

Repeated several times with same result."

Experiments made in this way gave fairly constant results, but it was not possible to repeat the observation many times without injury to the otolith organ. A new and very simple method was later found which permitted repetition of the stimulation many times before serious damage was done to the otolith and which gave absolutely constant results. The experiment is performed as follows:

A small mass of absorbent cotton is formed into a tiny cushion about the size of the otolith of the recessus and is cautiously placed on top of that otolith. The cotton is then grasped with the points of a fine

⁴ Lee, F. S., A study of the sense of equilibrium in fishes. I, *J. Physiol.*, 1894, xv, 311.

forceps and gently moved to the right or left, forward or backward at will. I quote again from my notes:

"July 23, 1920. Large shovel-nosed ray (*Rhinobatus*).

Removed ampullæ from left ear.

Exposed small otolith (of recessus utriculi) and placed on it the pellet of cotton.

Movement of pellet to left caused depression of left eye and elevation of right eye.

Movement of pellet to right caused depression of right eye and elevation of left eye.

Movement of pellet forward caused both eyes to roll forward on their axes (anterior pole of each eye depressed and posterior pole elevated).

Movement of pellet backward caused both eyes to roll backward on their axes.

When pellet was moved to one side eyes moved in same sense.

When pellet was held to any side, the eye position was retained.

Removed the three ampullæ of the right ear.

Repeated the experiment on the right ear with exactly the same results.

Repeated a score or more of times with no noticeable diminution of the response.

Holding the pellet to any side held the eyes in the corresponding position."

I have repeated these experiments on dogfish, leopard sharks, and rays. The experiments on the ray (*Rhinobatus*) were particularly striking. This fish is broad and flat and usually remains on or near the bottom of the water. It is not apparently used to much turning over or tilting of the head up or down. Taken out of the water, or rotated in the water it does not show any of the compensatory movements in so marked a degree as does the dogfish. When, however, the stimulation was applied to the recessus as described above, the eye movements were extraordinarily vigorous, much more so than in response to rotation of the body of the uninjured animal. The eyes rolled right or left, forward or backward as if on actual mechanical axes manipulated by cords.

It will be seen from the above that pressure on the *right* side of the otolith of either ear produces the same eye movement which results as the compensatory motion to rotation of the body to the *left* around the longitudinal body axis; and that pressure on the *anterior* side of the otolith gives the same effect as tilting the head *upward*. In each case the response is precisely opposite to that which would be expected if the stimulation were produced by the pressure due to the weight of the otolith; for when the body is tilted to the right the weight of the

otolith must be shifted to the right, but the reaction of this rotation is elevation of the right eye and depression of the left eye. When pressure is applied directly to the right side of the otolith as in the experiments above described the opposite result is obtained; namely, depression of the right eye and elevation of the left. It must be then that the stimulation does not result from the direct effect of the pressure but from the shifting of the otolith; a displacement to the left is brought about by pressing on its right side under the conditions of the experiment, and a similar displacement to the left results from tilting the animal to the left. In other words, it is the *displacement* of the otolith, and not the pressure due to the weight of the otolith, which is the actual stimulus and it is the *direction* of the displacement which determines the direction of the compensatory movement in response to the stimulus.

The experiments described above show that the stimulus arising from the position of the otolith is not due to the pressure as such but to the relative tensions, and is in this particular exactly similar to what I had already found for the ampullæ. The stimulus which causes the forced position (static function) is, like the stimulus which causes the compensatory movement (dynamic function), due to relative differences of tension in the organ, rather than to localized stimulation of special portions. There is therefore no evidence for a specific difference in the mode of action of the various parts of an ampulla or a macula. The relative tensions appear to determine the proportionate nerve excitation for the associated muscle groups in a manner analogous perhaps to the effects of various degrees of tension in the lungs on the vagus endings. I have made no attempt to say just where these differences of tension take effect upon the nerve endings, nor to say what part, if any, the hair cells have in the process. The arrangement of the hair cells would seem admirable for the transmission of the effects of movement or pressure to the nerve endings, but I do not at present see how the matter can be subjected to the test of experiment.

A part of the experiments on which this paper is based were performed at the Scripps Institution for Biological Research. I take great pleasure in acknowledging my obligation to the Director, Professor W. E. Ritter, for his courtesy in placing the facilities of the Institution at my disposal.