THE RELATIONS OF THE INDIVIDUAL AMPULLÆ OF THE SEMICIRCULAR CANALS TO THE INDIVIDUAL EYE MUSCLES.

I. The Horizontal Canals.*

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It has long been known that the eye movements resulting from the stimulation of any ampulla correspond very closely to the compensatory movements brought about by rotation of the animal in the plane of the semicircular canal of which that ampulla forms a part. In the dogfish this correspondence has been shown by the work of Lee (1894) and of one of us (Maxwell, 1910) to be very exact. It seems desirable to determine just what part each of the six extrinsic muscles of the eyeball takes in the response to stimulation of a single ampulla.

The methods of our experiments were as follows: The dogfish was tied down on the operating board and its respiratory needs were provided for in the usual way; namely, by bringing a stream of aerated sea water into its mouth through a rubber tube from an elevated receptacle. The desired muscles were isolated and the bulb of the eye enucleated by a method essentially similar to that of Bartels (1911). On account of the delicacy of the muscles we have not attempted to tie threads to them directly but instead we have in each case cut out that portion of the sclera which includes the insertion of the muscle, and have then with a small surgical needle passed the thread through this bit of sclera and tied it. The writing levers used were very light and were right-angled so that a horizontal pull caused

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an upward movement of the lever. In this way records could be made on a long roll kymograph.

It would have been possible by the above method to have recorded simultaneously the responses of all six muscles to a single stimulation, but since in any case all the muscles were completely isolated from one another, the presence or absence of any particular muscle could in no way influence the movement of another, it was found best to avoid too many complications by recording the action of two or at most three muscles at once.

We have in every instance employed mechanical stimulation, a light touch to the ampulla with a bristle tipped with wax, or with a smooth blunt-pointed seeker. Electrical stimulation is less satisfactory, although it has the obvious advantage of permitting the use of a time signal. We have used an electric signal to mark, not of course the exact, but the approximate, moment of touching the ampulla. This record was made by a key in the hands of the assistant. The need of this was obvious because a small simultaneous contraction of two muscles might otherwise be indistinguishable from the effect of a slight movement of the head, an occurrence which could not always be avoided and also because of possible confusion with the rarely occurring spontaneous movements. The time record is in seconds.

For the stimulation of the horizontal ampullæ we might have mounted the entire outfit on a rotating table as was done by Bartels and by those who have followed his method, and have depended upon the rotation to effect the stimulation. For the vertical canals rotational stimulation would have presented insuperable mechanical difficulties, but in addition, would have involved the influence of other structures, the otoliths, the effects of which we wished finally to differentiate.

The procedure which we have employed has not been free from difficulties, but has proved on the whole satisfactory. Among our records are good instances of reciprocal innervation, but it requires a much more careful adjustment of tension to show the relaxation of the antagonist than the action of the contracting muscle, and in this study we have thought it best to concentrate effort upon the positive effects, the actual contractions which occur. We have freely assumed that in those cases where a muscle regularly and consistently remains unresponsive to a given stimulus, more careful adjustment would have shown a relaxation. Even if this assumption is incorrect it does not in the least invalidate the statement of the positive findings herein communicated. All our tracings are of the action of muscles of the left eye. Both ears, of course, were operated and stimulated.

Stimulation of the Ampulla of the Horizontal Canal.—From the positive movements of the intact eyeball when the horizontal ampullæ are stimulated it was to be inferred that the principal actors in these movements are the *rectus externus* and the *rectus internus*. Our tracings show that on stimulation of the *right* horizontal ampulla the *rectus externus* of the *left* eye contracts strongly. Stimulation of the *left* horizontal ampulla evokes a strong contraction of the *rectus internus* of the left eye (Figs. 2 and 3).

The movements of the eyeball in response to stimulation of these ampullæ gives, indeed, the appearance of rotation of the bulb around a fixed vertical axis in which case none other than the two rectus muscles would need to participate. The separateness of function of these muscles and of the ampullæ under consideration is further suggested by the fact that compensatory eye movements for rotations in the planes of the vertical canals are mediated through two sets of structures in the ear, each of which is alone competent to excite the appropriate muscles (Maxwell, 1923) but in the case of the horizontal ampullæ this duplication does not exist. It is also suggestive that the *rectus externus* gets its innervation through a separate motor nerve, the abducens. Indeed, it has also been suggested that the central pathways concerned in the reflexes from the horizontal ampullæ are different from those of the remainder of the equilibrial portion of the labyrinth (Jones, 1918).

It is obvious, however, that no such vertical axis as that which is assumed above has any anatomical existence, a fact which has recently been very clearly and forcibly stated by de Nó (1924). Either the eyeball must be pulled about on its fatty cushion in the orbit in an unsure way or else some or all of the other ocular muscles must by appropriate tonic contraction serve as fixation muscles. It was, then, a matter of particular interest to see how these other muscles respond to stimulation of the horizontal ampullæ when isolated from their connections with the eyeball and left free to act with complete independence.

Since the ampulla of the anterior vertical canal lies very close to the horizontal ampulla and its excitation is known to produce elevation or depression of the eyeball and wheel turning at the same time, it might be inferred that the mechanical stimulation of the horizontal ampulla had also excited the anterior vertical. For this reason all our tracings were made after the removal of the anterior vertical ampulla. The contractions evoked then can have had no other origin than the excitation of the horizontal ampulla.

Fig. 2 shows a tracing of the contractions of the *rectus externus* of the left eye following a mechanical stimulus applied to the right horizontal ampulla. In Fig. 3 is seen the contraction of the *rectus internus* of the left eye when the left horizontal ampulla was stimulated. No importance is to be attached to the apparent difference in height of contraction in the two cases. The differences in size and in physical condition of the experimental animals make comparisons of contractions of no value except when they have been taken from the same animal and on the same record. We are unable to say whether a muscle responds more or less vigorously to stimulation of the homolateral or the contralateral ampulla. Comparison of tracings in Figs. 4 and 5 would seem to show that stimulation of a horizontal ampulla causes the *rectus superior* to contract more strongly than the *rectus inferior* on the homolateral side, while on the contralateral side the conditions are reversed. Such a difference of response on the two sides has been implied by Bartels (1911) but on the whole we are strongly of the impression that the influence of a horizontal ampulla is not unequal on the two sides. It is at least perfectly clear that stimulation of a horizontal ampulla causes simultaneous contraction of the two superior and the two inferior recti.

In Fig. 6, *a* and *b*, it is seen that stimulation of the right horizontal ampulla causes contractions of both the oblique muscles of the left eye; a like result follows stimulation of the left horizontal ampulla (Fig. 7).

It may be mentioned incidentally that occasionally stimulation of a horizontal ampulla was followed not by a single contraction of an external or internal rectus muscle, but by series of rhythmic contractions which could be seen as a horizontal nystagmus of the right eye while the muscles of the left eye were making their graphic record. Fig. 6, *a*, was selected to illustrate this phenomenon.

We have said that little importance could be attached to differences in size of contractions made from different animals of different size and condition. This is not true, however, when the contraction of an external or internal rectus muscle is recorded simultaneously with that of a superior or inferior rectus muscle or with one of the oblique muscles. It may be stated in general that stimulation of either horizontal ampulla evokes in addition to a strong contraction of a *rectus externus* of one eye and a *rectus internus* of the other a simultaneous contraction of all the other four muscles of each eyeball, namely the superior and inferior recti and the superior and inferior oblique muscles.

The anatomical arrangement of the extrinsic muscles of the eye of the elasmobranch is somewhat different from that which exists in the human eye, the greatest difference being in the shape and attachment of the superior oblique. This muscle like its counterpart, the inferior oblique, has its origin on the anterior medial wall of the orbit.

Inspection of Fig. 1, which is a drawing, after Daniel (1922), of the arrangement of the eye muscles of *Heptanchus maculatus*, shows that notwithstanding the morphologic difference from the corresponding muscle groups in the higher vertebrates the general physiological action of the individual muscles must be much alike in the two. Contraction of one oblique alone must produce a wheel turning movement but at the same time an upward or downward rotation. Contraction of a superior or inferior rectus must in addition to a rotation upward or downward also tend to drag the bulb backward in the orbit. On the other hand the external and internal recti each, unopposed, would in addition to its primary function of producing rotation in a horizontal plane, also tend to drag the eyeball backward in its orbit, since there is no actual vertical axis for the ball to turn upon.

Our experiments show that each excitation of a horizontal ampulla calls forth, in addition to the response of the appropriate external or internal rectus muscle, a smaller but very definite contraction of each of the other four muscles. Since the superior oblique and the superior rectus are attached to nearly the same point of the upper side of the bulb, and the inferior oblique and inferior rectus are similarly attached to the lower side of the bulb, the simultaneous contraction of all four must have a fixation effect with the result that the mechanism acts as if a real vertical axis had been provided with its upper pole in the neighborhood of the region marked + in Fig. 7.

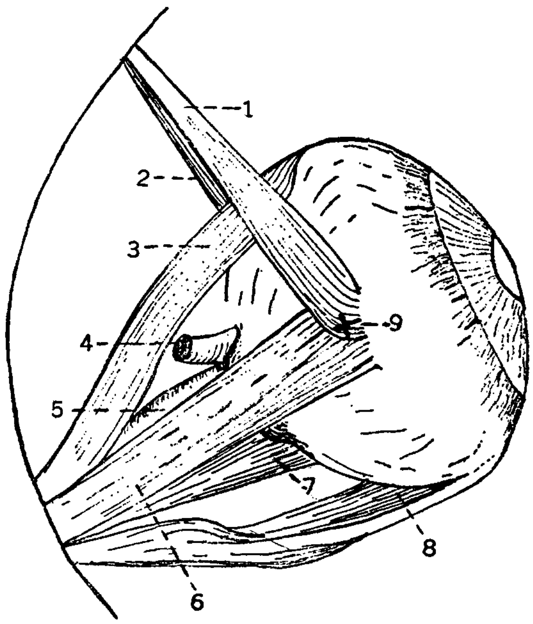

FIG. 1. Muscles of the eye of an elasmobranch, *Heptanchus maculatus*, dorsal view (after Daniel).

1, *Obliquus superior.*
2, *Obliquus inferior.*
3, *Rectus internus.*
4, Optic nerve.
5, Optic pedicle.
6, *Rectus superior.*
7, *Rectus inferior.*
8, *Rectus externus.*
9, Pole of virtual axis.

A consideration of this action of the fixation muscles will show that the paralysis or inactivity of any one of the four could give rise to an abnormal reaction of the eyeball to rotation in a horizontal plane. If the corresponding muscles of the human eye perform a similar fixation function, and there is no reason to suppose that they do not, many of the types of nystagmus seen in pathological cases could be accounted for in a similar manner.

SUMMARY.

1. The reflex effect of direct mechanical stimulation of the exposed ampulla of the horizontal canal has been graphically recorded for each of the six extrinsic muscles of the eyeball.

2. Stimulation of a horizontal ampulla evokes a strong contraction of the homolateral *rectus internus* and of the contralateral *rectus externus;* at the same time the homolateral *rectus externus* and the contralateral *rectus internus* relax.

3. A single mechanical stimulus applied to the horizontal ampulla is sometimes followed by a nystagmus resulting from a series of rhythmic contractions of the externus and internus muscles.

4. Excitation of a horizontal ampulla gives rise to weak contractions of the superior and inferior recti and of the two oblique muscles of both eyes, simultaneously with the stronger contractions of the externus and internus respectively.

5. It is pointed out that the small simultaneous contractions of the four muscles just mentioned provide a virtual axis upon which the eyeball rotates. In other words these four act as fixation muscles.

6. It is suggested that some of the abnormal responses to horizontal rotation, seen in clinical cases, are due to the inaction of one or more of the fixation muscles.

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EXPLANATION OF FIGURES.

FIG. 2. Contraction of *rectus externus* of left eye in response to stimulation of right horizontal ampulla. Reciprocal relaxation of the rectus internus is faintly indicated.

FIG. 3. Contraction of *rectus internus* of left eye when left horizontal ampulla is stimulated.

FIG. 4. Contractions of both *rectus superior* and *rectus inferior* of left eye on stimulation of right horizontal ampulla.

FIG. 5. Contractions of both *rectus superior* and *rectus inferior* on stimulation of left horizontal ampulla.

FIG. 6, *a*. Contraction of *obliquus superior* of left eye in response to a single stimulation of the right horizontal ampulla. The tracing shows the rhythmic response of the *rectus externus* and faintly the reciprocal action of the *rectus internus*.

FIG. 6, *b*. Contraction of *obliquus inferior* in response to right horizontal ampulla.

FIG. 7. Contractions of *obliquus superior* and *obliquus inferior* of left eye when left horizontal ampulla is stimulated.

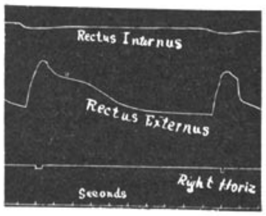

FIG. 2.

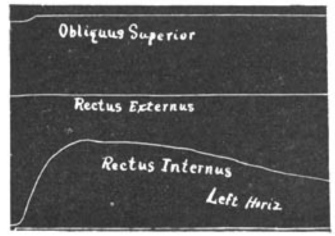

FIG. 3.

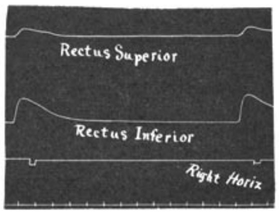

FIG. 4.

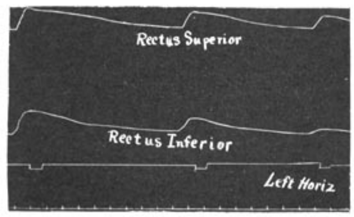

FIG. 5.

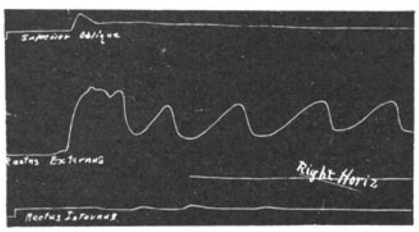

FIG. 6, *a*.

FIG. 6, *b*.

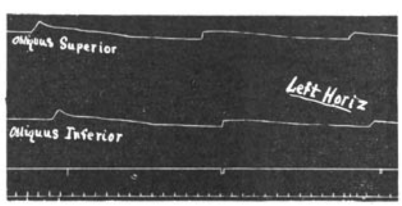

FIG. 7.