STEREOTROPIC REACTIONS OF THE SHOVEL-NOSED RAY, RHINOBATUS PRODUCTUS.

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I.

It has been pointed out by Loeb[1] that our orientation in space is determined mainly by three groups of tropistic influences; namely, light, gravitation, and contact. Light and gravitation cause the orientation of organisms through effects upon muscle tonus. When the lines of force strike the animal obliquely, as for example, when light rays fall unequally on the two eyes, the unequal stimulation causes differences of tonus on the two sides, and the symmetrically placed muscle groups acting with unequal strength, bring about forced changes in the direction of locomotion. When the lines of force coincide with the axis of symmetry, or the plane of symmetry of the body, the effects are equal on the two sides and movement can go forward in a straight line. For the contact, or stereotropic, reactions, quantitative relations of this nature have not heretofore been described.

In my studies on the physiology of the labyrinth I have found it necessary to distinguish carefully between those eye and fin movements which result from excitations of end-organs in the ear, and movements which arise from other sources. In this way I have come to make observations on the contact reactions of the shovel-nosed ray, or guitar fish, *Rhinobatus productus*, which will, I believe, throw important light on the nature of stereotropic reactions in general.

Rhinobatus is not so broadly expanded as most of the other rays. The pectoral fins, however, have the characteristic fleshy thickened

[1] Loeb, J., Forced movements, tropisms, and animal conduct, Philadelphia and London, 1918.

base. The posterior part of the body and the tail are shark-like in appearance. The eyes are freely movable and can be elevated or retracted in a manner quite similar to the eye movements of the frog. Specimens 3 to 4 feet in length may be taken, but the reactions about to be described are better seen in the smaller animals, 15 to 18 inches long.

When this animal is placed on a shark board and supplied with plenty of aerated sea water through a rubber tube, little or no tying is necessary to keep it in position. Under these conditions a contact stimulus applied to the upper surface of the head or snout excites certain very definite coordinated movements of the fins and eyes, the particular combination of movements depending on the locus and strength of the stimulus.

II.

If the skin of a *Rhinobatus* is gently stroked with the finger or with a blunt instrument at any point along the midline of the head, for example, between *7* and *8* (Fig. 1), both eyes are retracted, the movements of the two being approximately equal. If a similar stimulus is applied near the outer margin of the upper surface of the head, as at *1* (Fig. 1), the eye on that side is retracted strongly, the other eye is moved very little or not at all. If trials are made at other places, *e.g.*, at *2* or *3*, Fig. 1, it is seen that as the point stimulated approaches the midline the amount of movement of the two eyes becomes more and more nearly equal, or in other words, the relative amount of retraction of each eye varies inversely with its distance from the point of application of the stimulus.

It was relatively easy to record these movements graphically. An Engelmann pincette was attached to each eye by a fold of the integument just where the rudimentary lid passes over into the cornea. The pincettes were connected by threads to a pair of light heart levers in such a way that retraction of an eye gave an upward direction to the curve. In the tracing here reproduced, Fig. 2, the upper lever was connected with the left eye and the lower with the right. The writing points were placed as nearly as possible in the same vertical line but in order to make the relations more certain simultaneous ordinates were marked throughout. The small rhythmical oscillations are respiratory, rather than eye movements. Spontaneous, "voluntary" movements occur occasionally, as between *6* and *7* near the end of the tracing. In this experiment the stimulus

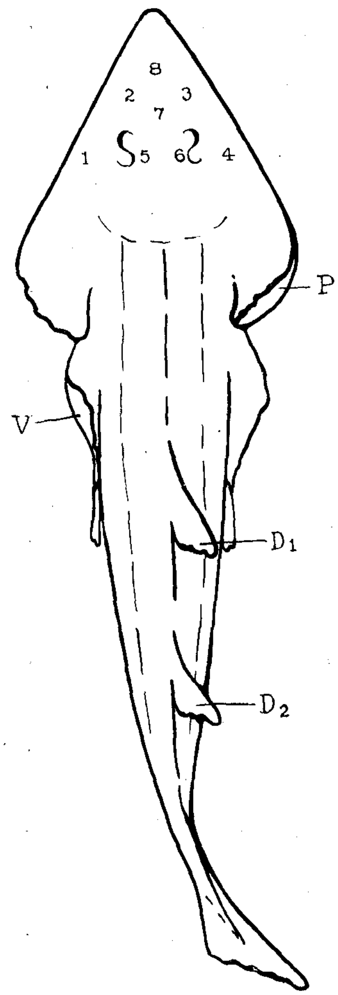

FIG. 1. Diagram of the dorsal view of *Rhinobatus productus*.

employed was a gentle stroke with the finger. These strokes were made as nearly equal as possible, but the method could hardly be expected to give perfectly uniform results. The numbers at the bottom of the tracing show the points stimulated as charted on Fig. 1.

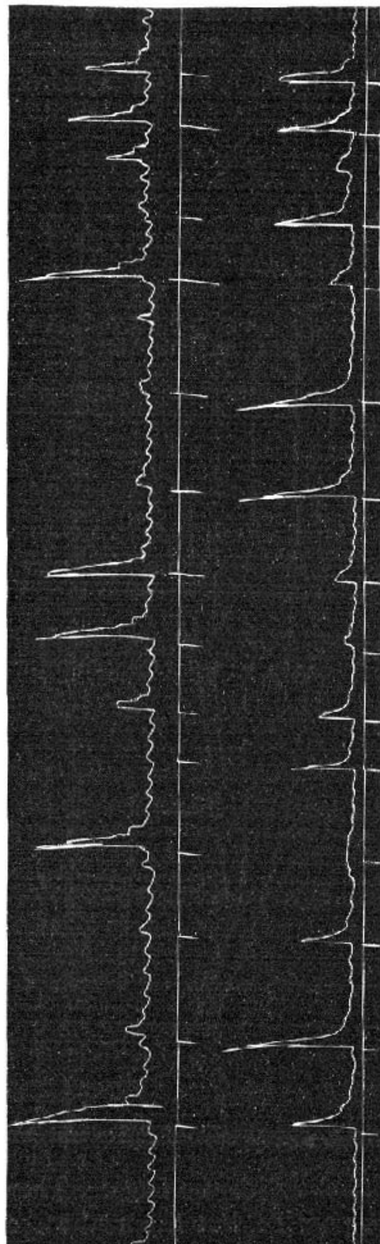

FIG. 2. Upper curve shows movements of left eye; lower curve, right eye. The numbers show the points stimulated, as indicated on Fig. 1.

Certain peculiarities remain to be mentioned. While the responses could be obtained from contact stimuli on all parts of the upper surface of the head, some parts were noticeably more sensitive than others. Also some parts were less likely than others to produce the bilateral response. Thus the strength of stimulus used in securing the tracing reproduced, rarely gave rise to a retraction of both eyes when applied at *5* or *6*, very near the inner margin of the eye. Stimuli applied to the lower surface of the snout, even near the lateral margin where the upper surface was very sensitive, were very slightly or not at all effective.

The movements which I have just described are retraction of the bulbs and partial closure of the rudimentary lids, and are not at all to be confused with the conjugate movements which result from excitation of the labyrinth.

The contact stimuli which elicit the eye movements in *Rhinobatus* bring about at the same time a remarkable group of coordinated movements of the fins and tail. An asymmetrically applied stimulus, *e. g.*, at *1* or *2* (Fig. 1), on the left side of the head, causes elevation of the posterolateral margin of the right pectoral, P, and of the left pelvic fin, V, while both dorsal fins, D_1 and D_2, are flexed to the right. A slightly stronger stimulus causes, in addition, a bending of the tail to the right and a slight elevation of the anterolateral margin of the left pectoral fin. If the stimulus is applied to the right side all the relations are, of course, reversed; the left pectoral and right pelvic fins are elevated and the dorsal fins and tail are turned to the left. If the animal was moving forward in the water the effect of the new positions of the fins would be to alter the direction so as to terminate the contact with the stimulating object. If for example the point touched was at *2*, Fig. 1, on the left upper surface of the head, the left side of the head and body would be lowered and at the same time the animal would veer off to the right; in other words a definite, negatively stereotropic, reaction would result. The fin and eye movements are as clear and characteristic in their way as are those which result from stimulation of the labyrinth.

In the preceding paragraph I have described the effect of a moderate stimulus. If a more severe stimulus is applied, whether to the midline or to a point asymmetrically situated on the upper surface of the head, a different reaction results; the margins of all four of the paired fins are elevated strongly. The effect of this would be to check the forward movement in the water and at the same time to steer the fish downward to the bottom. This is plainly also an example of a negatively stereotropic reaction. (It is necessary to bear in mind that a stimulus on the upper midline of the head is symmetrically placed with reference to the median plane of the animal but not with reference to the horizontal plane.)

All of the above reactions occur with great regularity and may be called forth over and over again by appropriate stimuli, but it is important to remember that the character of the response depends not only on the location but also on the nature of the stimulus. A stimulus at a given point may cause a change of direction of locomotion in the horizontal plane with a slight rotation of the body around its longitudinal axis, while a stronger stimulus at the same point may cause a change of direction out of the horizontal plane, that is, a movement toward the bottom.

III.

The above described reactions occur equally well in animals in which the forebrain has been destroyed. I have made repeatedly transsections of the brain as far back as the optic chiasma without affecting them in the least. Complete destruction of the two labyrinths is equally without effect. Since these movements occur in the absence of the forebrain it would be illogical to speak of them as "voluntary," or "purposeful," or "instinctive." On the other hand they illustrate beautifully the tropistic conception of animal behavior since they are very evidently reactions of the organism as a whole in response to asymmetrically applied stimuli. The effect of these stimuli is to bring about sudden changes of tonus in those groups of muscles which in their state of resting equilibrium hold the eyes and fins in a position of symmetry. The change of tonus causes an unsymmetrical action of the corresponding muscle groups on the two sides of the body with the result that the new position induced, terminates the contact with the stimulating object.

At first sight it might appear that these reactions differ in their nature from the other tropisms because in the latter we are concerned with the influence of forces acting along definite lines, while in the contact reaction the stimulus is applied to a single spot or a limited area of the skin. It is hardly necessary to point out that in heliotropic animals with two eyes the light rays act upon two very limited areas, namely, portions of the retinas, and in the geotropic reactions, gravitation acts upon very limited areas in the internal ear to bring about or maintain orientation. While ordinarily the two eyes or the two ears come into play in the heliotropic and geotropic reactions respectively, experiments show that marked effects are produced by stimuli applied to one eye or one ear alone. Another apparent difference is that contact stimuli may act from moment to moment in different directions. This, however, would be paralled by the effect of an intermittent, moving light upon a heliotropic organism.

It is of interest to picture the behavior of the organism under the play of two tropistic influences. Instead of a direct response to either, the position or movement which occurs may be the simple resultant of the two, as in the case of barnacle larvæ exposed to two lights from different directions.[2] On the other hand the one stimulus suddenly applied may for the moment inhibit the effect of the other. The free swimming fish, for example, reacts to gravitation by definite compensatory movements and positions of the eyes and fins through which it maintains a definite course and a horizontal position. If now suddenly a foreign body comes in contact with a certain portion of the head, say a point on the left upper surface, a negatively stereotropic movement occurs; the fins are thrown into an unsymmetrical position causing the left side of the head to be lowered and the course to be changed to the right. These changes terminate the contact and the stereotropic reaction ceases. But the sudden swing to the right has excited the ampulla of the right horizontal canal and a compensatory movement to the left, *i.e.*, to the original course, is produced while at the same time the rotation around the longitudinal, body axis has stimulated the otolith organs and the ampullæ of the vertical canals in such way that the horizontal position is again attained. The resulting behavior of the animal would in this way

[2] Loeb, J., and Northrop, J. H., Heliotropic animals as photometers on the basis of the validity of the Bunsen-Roscoe law for heliotropic reactions, *Proc. Nat. Acad. Sc.*, 1917, iii, 539.

give the appearance of volition and purpose, where a more exact analysis shows its purely mechanical nature. In case more than two sets of influences come into play simultaneously the behavior becomes more variable, the analysis becomes more difficult, and the behavior gives the appearance of purpose or caprice, although its correct interpretation would involve no new factors such as "will" or "intelligence," but merely the recognition of a larger number of variables.