

THE STEREOTROPISM OF THE DOGFISH (*MUSTELUS CALIFORNICUS*) AND ITS REVERSAL THROUGH CHANGE OF INTENSITY OF THE STIMULUS.*

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In the preceding paper¹ I have described certain contact reactions of an elasmobranch fish, *Rhinobatus productus*, and I have shown that these reactions are definitely tropistic in their nature. I pointed out that in *Rhinobatus* the response to a particular stimulus depends upon two factors (*a*) the strength and (*b*) the location of the stimulus; that, for example, a weak stimulus applied to the right upper surface of the head causes the fins to assume an asymmetrical position of such character that the body momentarily swerves to the left, and at the same time the right side of the head is depressed; but a strong stimulus applied at the same point brings about such a change in the position of the fins as would arrest the forward movement of the animal and cause it to dive to the bottom. The effect of both these modes of reaction is to terminate the contact with the stimulating object and hence they are both to be regarded as examples of negative stereotropism.

When I attempted to find out whether analogous reactions could be obtained from other elasmobranchs I was at first greatly puzzled by the behavior of the common dogfish. A dogfish tied down on the shark board and supplied with a current of aerated sea water would respond to stroking or scratching stimuli applied to the head or snout with decided movements or changes or position of the fins; but the results were often confusing or contradictory. A contact

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¹ Maxwell, S. S., Stereotropic reactions of the shovel-nosed ray (*Rhinobatus productus*), *J. Gen. Physiol.*, 1921-22, iv, 11.

stimulus applied to the right upper surface of the snout would at one moment cause the dorsal fins to turn to the right, while at another moment a stimulation of the same region caused these fins to bend to the left. The paired fins and the tail participated in these responses, and the direction of their movements had a definite relation to the movements of the dorsal fins. It became apparent that these fin movements were always consistent among themselves; they were more than simple reflexes, and showed a coordinated adjustment of the organism as a whole. In general they could be seen to exhibit such an arrangement as would be necessary to turn the animal either in the direction of the stimulating object or away from it. That is to say, the reactions were in each case stereotropic, but the sense of the stereotropism could be positive or negative. It became then a matter of interest to determine, if possible, the conditions of the reversal, and so to control these conditions as to make the responses predictable. This proved to be indeed very simple.

METHODS.

In making these experiments on the effects of contact stimuli it would have been desirable to keep the fish in its natural position in the water. This however was impracticable because the mechanical effect of the stroke or push which constitutes the stimulus was sufficient to move the body of the fish under the unstable conditions of water support only. Moreover the stimulus excited movements of locomotion and the observer was unable to keep track of the positions and changes of positions of the different fins. If the aquarium used was large the fish was soon out of reach; if small, new stimuli were offered by collision with the walls. Another disturbing factor, if the animal is floating in the water and free to move, is the fact that each response to a tactile stimulus causes such a change of position as to excite the labyrinth and thus introduce other reflexes. It was necessary, therefore, to use the ordinary method of artificial respiration by means of a current of aerated sea water through a rubber tube in the animal's mouth.

When the dogfish is first placed in the shark board rather violent struggles occur, and tying is usually necessary until the animal be-

comes quiet. After a few minutes of immobility the cords can be gently loosened and removed and the experiment can go on for some time without any need of artificial restraint. This is important because experiments on contact stimuli should not be complicated by possible inhibitions or reinforcements from the presence of the binding cords. It is true that the ventral surface of the body is still in contact with the board, but this is not an unnatural situation since the animal when free often rests for long periods on the bottom of the aquarium. In order better to observe the movements of the paired fins the animal was usually placed above the board on a thick piece of wood no wider than the body, thus allowing the pectorals to project like wings.

The reactions about to be described were obtained by stroking or scratching the outer margin of the head from near the snout to a point just below the eye. It was not necessary that the stroke be carried the whole distance; a short stroke or sometimes a mere touch anywhere within the region mentioned gave the same result. It is not to be inferred that analogous reactions are not elicited by contact stimuli applied to other regions. I have confined this paper to reactions from the parts mentioned for the sake of definiteness of description and interpretation.

Strength of Stimulus and Sense of Reaction.

For most dogfish a stroke with a finger wet with sea water was sufficient to produce a definite response. As a more severe stimulus I used a scratch with the points of a small pair of forceps. The first of these usually corresponds to the designation "weak" the other "strong" stimulus.

It soon became apparent that fairly constant responses could be obtained if the stimuli were of uniform intensity. In fact under favorable conditions the movements could be repeated over and over with machine-like regularity. The following portion of the record of an experiment is typical (Table I). The pauses between the successive trials were merely the time necessary to set down the results.

Weak Stimuli.—Inspection of the results of the above experiment shows that when a weak stimulus is used the dorsal fins and the

tail turn toward the stimulated side. The effect of these as a steering apparatus would be to change the course toward the stimulated side; e.g., turning the dorsal fins or the tail to the left would cause the course to swerve to the left. But in addition to this another effect

TABLE I.

Mustelus californicus, 33 Inches Long, May 20, 1921.

Stimulus.		Reaction.				
Kind.	Side.	D1.	D2.	Tail.	Right Pectoral.	Left Pectoral.
Weak (Finger).	Left.	Left.	Left.	Left.	Down/	Up\
	Right.	Right.	Right.	0	Up\	Down/
	Left.	Left.	Left.	Left.	Down/	Up\
	Right.	Right.	Right.	Right.	?	Down/
	Left.	Left.	Left.	Left.	Down/	Up?
	Right.	Right.	Right.	?	Up\	Down/
Strong (Forceps).	Left.	Right.	Right.	Right.	Down/	Up/
	Right.	Left.	Left.	Left.	Up/	Down\
	Left.	Right.	Right.	?	Down\	Up/
	Right.	Left.	Left.	Left.	Up/	Down\
Weak (Finger).	Left.	Left.	Left.	Left.	Down/	Up\
	Right.	Right.	Right.	Left?	Up\	Down/
	Left.	Left.	Left.	0	Down/	Up\
	Right.	Right.	Right.	Right.	Up\	Down/
Strong (Forceps).	Left.	Right.	Right.	Right.	Down\	Up/

Repeated many times over with like results.

The first column indicates the strength of stimulus; the second, the side of the head to which it is applied; the third, fourth, and fifth, the direction of movement of the first and second dorsal and the tail fins respectively. The last two columns give the direction of movement of the anterior border of the right and left pectoral fins; and, in these two columns, / at the end of the word indicates that the posterior end of the fin was higher than the anterior; \, that the posterior margin was lower than the anterior.

would result. When a dorsal fin turns to the left it assumes an oblique position; that is, it is its posterior border which goes to the left most strongly. Its resistance as the animal moves forward in the water would have a screw effect, tending to rotate the body around its longitudinal axis so that the ventral side would be turned in the di-

rection of the stimulating object. This rotation effect would be increased by the new position of the pectoral fins. The pectoral on the stimulated side is elevated but its posterior margin is raised less than its anterior or is even depressed; the pectoral of the other side makes a movement which is just the converse. These fins would then also have a screw effect tending to the same direction of rotation as the dorsals, namely, ventral side toward the stimulating object. The reaction is clearly tropic and in the positive sense.

It will be seen that the total effect of a weak stimulus is to turn the ventral side of the animal, as well as to swerve the course, in the direction of the stimulating object. This accords well with what one sees on watching the dogfish swimming about in a small aquarium. They are often seen going round and round, keeping near the walls, with the body tilted to one side so that the mouth and belly are turned somewhat toward the wall. This is just the position which would be produced by the above reactions, if, on making the turn at a corner, the edge of the snout came slightly in contact with the wall. Sometimes I have been able to see such contacts actually occurring, but the asymmetrical position was often assumed when the wall was not touched. In this case it might be that the increased pressure or resistance of the water when the fish was moving near the wall could act as a stimulus. Indeed I found that a spurt of water from a pipette could be used instead of a finger stroke as a weak stimulus.

Since in the dogfish the mouth is far back on the ventral surface of the head it is not unreasonable to suppose that the positive stereotropic reaction assists in the capture of food; the response to a contact stimulus would tend at once to bring the mouth into position to seize the stimulating object.

Strong Stimuli.—The experiments described above show that the reaction to a strong stimulus is almost exactly the reverse of the reaction to a weak stimulus. The dorsal fins and the tail are flexed to the side away from the contact. The pectoral fin on the stimulated side is elevated, its posterior margin still more than its anterior, the pectoral on the opposite side is depressed, the posterior margin more than the anterior. The whole arrangement of the fins is that of a screw whose effect in the water would be to rotate the body around its longitudinal axis in such a way as to turn the back to the stimulat-

ing object. At the same time the dorsal fins and the tail would act as a steering apparatus to alter the course to a direction away from the source of stimulation. This then is also a definite tropic reaction and in the negative sense.

Attention should perhaps be called to the fact that while the positive reaction is on the whole opposite in character to the negative it is not precisely so. A weak stimulus on the right side of the snout or a strong stimulus on the left side would each tend to turn the ventral side to the right and cause the course to veer to the right. But the mechanism is not quite the same so far as the pectorals are concerned. In the positive reaction the pectorals act feebly in comparison to the unpaired fins; in the negative reaction their movement is relatively more vigorous. In both the positive and the negative reaction the pectoral of the stimulated side is elevated; but in the one case its posterior margin is elevated less than the anterior and in the other case more. It will not do then to say that the negative reaction differs from the positive merely in the fact that the excitation is shunted from one side of the central nervous system to the other. It is certainly not so simply diagrammatic as that.

The Decerebrate Animal.

My experiments on *Rhinobatus* led me to expect that the destruction of the forebrain would have no effect on the character of the stereotropic reactions of the dogfish. In a number of instances I made transections of the brain, usually near the anterior margin of the cerebellum, with no noticeable alteration in the responses to contact stimuli. The following record of an experiment will serve as an example:

July 4, 1921.—*Mustelus californicus*, 29 inches long.

9:20 a.m. Brain exposed and cut across at anterior margin of cerebellum. Animal returned to tank, lies inert; does not right itself.

10:30 a.m. Animal swimming about normally. Taken out and placed on board. Contact reactions tested. (Table II.)

Possible Sources of Error.

Certain possible sources of error were considered and should be mentioned.

1. *Reflexes from the Labyrinth.*—I have already spoken of the necessity of avoiding any movement of the head at the moment of the experiment. It would be quite possible, if labyrinth effects were not taken into account, that the mechanical effect of the stroke used as the stimulus would turn the head enough to excite a reflex from the internal ear. I have often in the course of an experiment tried to see how much and how fast the head must be turned in order to provoke a labyrinthine response, and the amount has always been much greater than could be caused by the strongest contact stimulus employed. But in order to avoid all possibility of error from this source I have made experiments on a number of dogfish in which both labyrinths

TABLE II.

Stimulus.		Reaction.				
Kind.	Side.	D1.	D2.	Tail.	Right Pectoral.	Left Pectoral.
Forceps scratch.	Right.	Left.	Left.	Left.	Up.	Down.
	Left.	Right.	Right.	Right.	Down.	Up.
	Right.	Left.	Left.	Left.	Up.	Down.
	Left.	Right.	Right.	Right.	Down.	Up.
Finger stroke.	Right.	Right.	Right.	0	Up.	Down.
	Left.	Left.	Left.	Left.	Down.	Up.
	Right.	Right.	Right.	Right.	Up.	Down.
	Left.	Left.	Left.	Left.	Down.	Up.

Continues to respond like a normal animal.

had been previously destroyed and have found the stereotropic responses in no way altered.

2. *Tension of Neck and Trunk Muscles.*—The observation of Lyon² that eye movements can be elicited by bending the body of the dogfish, even after total destruction of the ears, can be easily repeated. Fin movements can also be obtained in the same way. It was conceivable, then, that the responses or some of them might have been due to pressure on the side of the head inducing reflexes by changes of tension in the joints of the neck region. It was easy to test this also

² Lyon, E. P., Compensatory motions in fishes, *Am. J. Physiol.*, 1900-01, iv, 77.

and I found that the amount of bending necessary to produce any reflex movement in this way was vastly more than could be caused by the contact stimuli.

3. *Retinal Stimuli.*—I have already mentioned the fact that dogfish swimming about in the concrete tank often keep close to the wall, with the dorsal fins slightly flexed and the body tilted so that the belly is turned slightly outward toward the wall. It was possible that this position was induced by the moving image of the wall upon the retina. In making the strokes used as contact stimuli I naturally passed my hand close to the eye of the stimulated side. It was possible that the flexion of the dorsal fins might be due in reality to the image (or the shadow) of the hand upon the retina. I found in fact that when the fish was placed on the board parallel to the window, so that the left eye was toward the light, passing the hand between the window and the animal's left eye often caused a definite flexing of the first dorsal fin to the left, but I could never by this means get a movement of the other dorsal or of the paired fins. In order, however, to test this matter farther I made many experiments in which the eyes were covered with thick pads of wet absorbent cotton and found no apparent change in the responses to contact stimuli.

CONCLUSIONS.

In the majority of instances the regularity of the responses to the finger strokes and to the forceps scratches is no more remarkable than the definiteness of the change from the one kind of response to the other. The two kinds of stimuli mentioned differed sufficiently to give reactions of opposite sign. An occasional animal, however, reacted very feebly or not at all to the finger stroke, and gave "positive" reactions to fairly strong forceps scratches, in fact in a few instances no negative reaction was obtained. Other specimens gave positive reactions to moderately strong forceps scratches (stimuli which in the great majority of specimens would cause a lively negative reaction), but gave the negative reaction when still more force was applied. On the other hand a few gave only the negative reaction to any effective stimulus.

It was noticeable, too, that what constituted a "weak" or a "strong" stimulus depended upon the physiological state of the individ-

ual animal. Specimens were usually less sensitive and less responsive immediately after the struggles connected with capture and immobilization were over than they were ten or fifteen minutes later. In fact an occasional animal remained unresponsive until roused to excitability by an unusually hard scratch or a pinch or twist of the tail, when it suddenly began to react in the regular way. These instances forcibly reminded one of the awakening from a nap. Immediately after the "awakening" all the responses, even to strong stimuli, were likely to be positive, although occasionally just the reverse was the case. Then after a few strokes the reactions would become normal, that is, positive to weak and negative to strong stimuli.

Naturally one raises the question: How is the reversal brought about? The phenomena described in this paper seem to present a close analogy to the observation of Sherrington³ that in a spinal dog the reaction to a stimulus applied to the plantar surface of the hind foot differs in a way dependent on the nature of the stimulus; a firm gentle pressure causes extension, a sharp prick causes flexion. Sherrington apparently assumes the existence of one kind of nerve endings, nociceptors, which are excited by harmful stimuli, and which give rise to flexion, and another kind which respond to bland stimuli by extension. The analogy in the case of the dogfish is quite marked, except that the stimulus which is "bland" in one animal or in one state of the animal, is "nocuous" in another animal or in another state of the same animal.

There appears to me to be a yet closer analogy between these reactions and the reversibility of the heliotropic reactions of certain organisms; namely, those which are positive to weak and negative, to strong light. All the phenomena seem to me to indicate that the reversal of the stereotropic reactions of the dogfish is a central process. It has been objected to the idea that the heliotropic reversals are brought about in the nervous system that such reversals occur in unicellular organisms where no separate nervous system exists; but it has been pointed out by Loeb⁴ that even in unicellular organisms

³ Sherrington, Charles S., *The integrative action of the nervous system*, New Haven, 1906.

⁴ Loeb J., *Forced movements, tropisms, and animal conduct*, Philadelphia and London, 1918.

structures could exist which would have the effect of synapses. It must be admitted, however, that notwithstanding the closeness of the analogy, the reversal of the heliotropic and of the stereotropic reactions may be due to totally different mechanisms.

SUMMARY.

1. The dogfish responds to certain contact stimuli by definite stereotropic reactions. These reactions can be positive or negative.
2. The sense of the stereotropic response depends on the strength of the stimulus; a "weak" stimulus, produces a positive and a "strong" stimulus, a negative response.
3. The strength of stimulus necessary to cause a reversal of the reaction depends in part on the physiological state of the animal.
4. The stereotropic reactions occur equally well in the absence of the forebrain.