THE NERVOUS MECHANISM OF COORDINATION IN THE CRINOID, ANTEDON ROSACEUS.

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In the crinoid, *Antedon rosaceus*, each of the five rays is branched into two arms, the point of bifurcation being 3 or 4 mm. from the central disk (Fig. 1). The branches or arms are invested with two rows of pinnules oppositely placed, thus giving to the animal its characteristically feathery appearance. On the dorsal or aboral side of the central disk are about twenty cirri by means of which

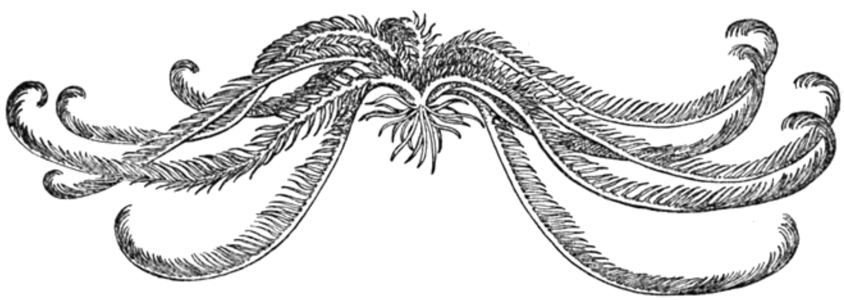

FIG. 1. Normal specimen of *Antedon* with arms extended in the resting position

the animal when at rest attaches itself to some inert object. Hence, *Antedon*, unlike the starfish and sea urchins, rests with the aboral side in contact with a surface, the oral face free. We shall use as synonymous the terms oral and ventral, aboral and dorsal.

Reaction of the Arms to Excitation.

The righting and swimming movements of *Antedon* are rapid and seemingly complex. Although one of these animals may remain in the same position for weeks if undisturbed, any strong stimulation causes the cirri to loosen their grasp, following which the animal swims through the water until another object is found to which the cirri may be attached. Swimming is accomplished by alternate motions of the arms; the first phase of each movement is oral flexion followed by extension and an aboral stroke. Two arms of a given ray, move alternately so that while one is executing the aboral stroke its mate is flexing ventrally. If the animal is laid oral side down in the aquarium, righting is accomplished by vigorous ventral flexion of the arms.

In a resting specimen, mechanical stimulation of a single arm causes one of two types of reaction depending upon whether stimulation is weak or strong. Weak or moderate stimulation causes ventral flexion of the arm, strong stimulation as by pinching with the forceps, results in dorsal extension of the arm stimulated (*a* in Fig. 2). and

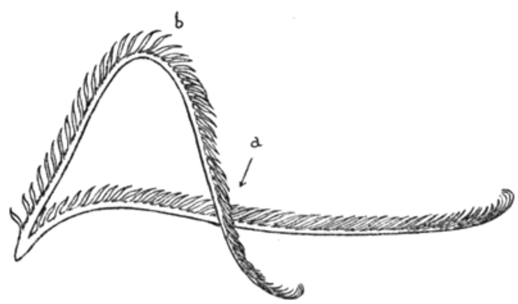

FIG. 2. Isolated ray consisting of arms *a* and *b*. As a result of strong stimulation of *a* that arm shows dorsal stroke while its mate, *b*, bends ventrally.

ventral flexion (*b* in Fig. 2) of the adjacent arms. This last reaction is followed by the swimming rhythm of the whole animal. In the case of a fatigued specimen, however, strong stimulation produces the same result as does weak stimulation of a normal individual. This is analogous to the situation in dogfish described by Maxwell (1) in which weak stimulation gave a positive and strong stimulation a negative stereotropic reaction when normal animals were employed, while in fatigued animals strong stimulation was followed by a positive reaction. Results of a similar character have been reported for the stereotropic reaction of the tube feet of *Asterias forbesii* (2), and by von Uexküll for the tension of the radial muscles of the spine of sea urchin (3). It seems apparent, therefore, that Maxwell's conclusion regarding the locus of the reversal mechanism is also correct for *Antedon*, namely that the character of the reaction is determined centrally and is not referable to the stimulation of different sets of sense organs, since strong stimulation acts upon the same sensory elements to produce opposite results depending upon the degree of fatigue in the animal.

Coordination Between the Arms of One Ray.

As has been stated, *Antedon* swims by means of alternate ventral flexion and dorsal extension of the arms. A single ray may be isolated and the reflexes of its two arms studied. Such preparations live and show vigorous reactions for hours after being cut away from the central disk. In a preparation of this kind (Fig. 2), if one arm be strongly stimulated (*a*), extension and dorsal stroke follow while

FIG. 3. Isolated ray which has been treated with strychnine. Stimulation of one arm results in both arms assuming this position of ventral flexion and retaining it for several minutes.

the paired arm (*b*) executes the opposite phase, namely, ventral flexion. In vigorous rays a series of rhythmical movements may follow, the phases of flexion and extension alternating in the two arms. This suggests reciprocal inhibition. It should be possible to test this hypothesis by the use of strychnine since strychnine has been shown to abolish inhibitions in other echinoderms (4). For this purpose an excised ray of *Antedon* was put into strychnine sulfate dissolved in sea water 1:10,000 and allowed to remain 10 minutes. At the end of this time the ray was returned to sea water and the reflexes tested. In all cases stimulation of one arm resulted in strong ventral flexion of both arms (Fig. 3). The extension phase did not occur, both arms remaining flexed for several minutes. In other words reciprocal inhibition is abolished by strychnine, which proves that in *Antedon* the alternation of swimming movements is determined by a nervous mechanism similar to that present in the starfish arm. Nicotine in concentration 1:10,000 has an effect similar to strychnine (5). In this connection there are two exceptional features to be noted. First, strychnine acts on *Antedon* to produce a reaction similar to that brought on by weak stimulation in the normal animal, whereas the rule in other forms is that the strychnine spasm is similar to the reaction to maximal stimulation in the normal animal. Second, nicotine poisoning gives the same picture as does strychnine, although in the starfish the two alkaloids cause respectively ventral and dorsal spasms.

Coordination Between the Rays.

The crucial problem of locomotion in any animal is coordination of the muscular movements. It has been shown in the case of the starfish that coordination between the rays depends upon the fact that impulses arising from one ray travel around the circumoral nerve ring to the other rays and that an impulse decreases in effectiveness as it proceeds from its point of origin (6). This rule has been shown to hold for the annelid nerve cord (7). In order to determine whether coordination between the rays in *Antedon* might have a similar mechanism, the following experiments were carried out. If, in a normal *Antedon*, one arm be stimulated by pinching with the forceps, the arm stimulated reacts with strong dorsal bending and the other rays show varying degrees of reactivity, flexing ventrally and turning laterally toward the stimulating arm. In sensitive individuals the wave of excitation may affect all the rays, but the response is always most marked in those adjacent to the arm stimulated.

To make the point entirely clear, consider the case in which the dorsal nervous pentagon (8) (Figs. 4 and 5) which connects the rays, is interrupted at one point by an incision. Let the rays be numbered consecutively 1, 2, 3, 4, 5, and an incision be made between 1 and 5, thus breaking the nervous connection between the rays at that point, then stimulation produces the following series of reactions. Excitation of ray 1 causes strong reaction in 1 and 2, moderate reaction

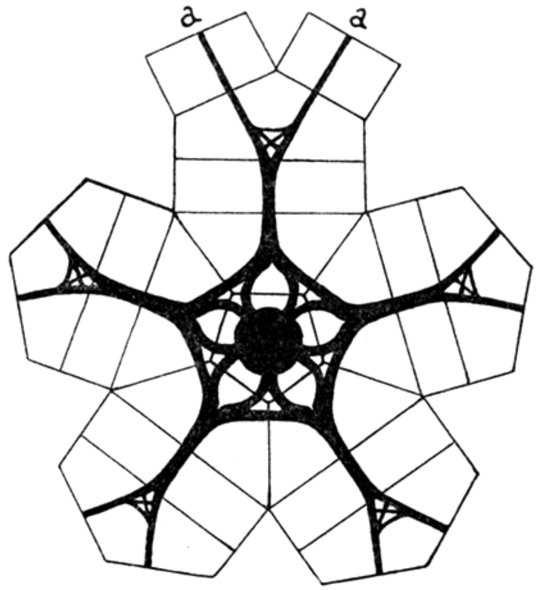

FIG. 4. Diagram (after Marshall) showing arrangement of dorsal nerve tracts of the centrum in a pentagon. Branches are shown going to each of the five rays, and further branching to each arm, *a*, *a* (axial cords).

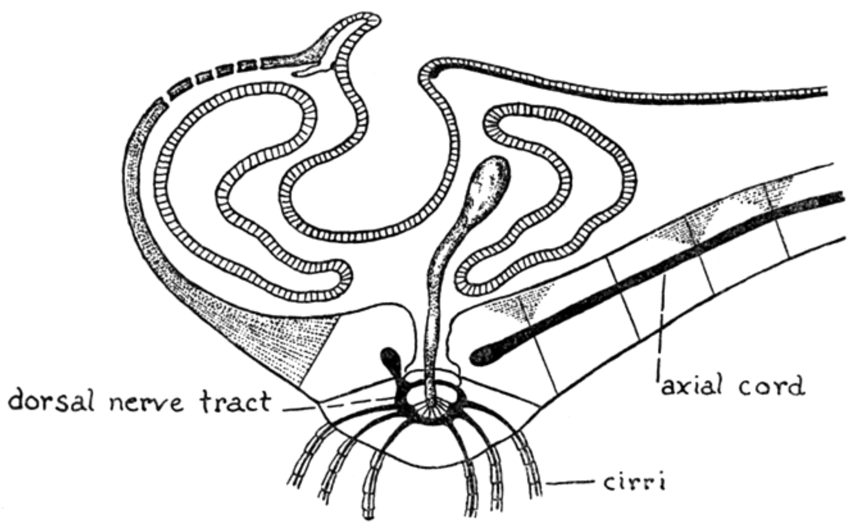

FIG. 5. Diagram (after Marshall) showing longitudinal section. Dorsal nerve tract of the centrum and distribution of branches to the cirri. Axial nerve cord of arm is shown.

in 3, weak reaction on the part of 4 and none in 5. If, on the other hand, 5 be stimulated, the wave of excitation proceeds from 4 to 3 to 2 having no effect on 1. The experiment proves that the basis of coordination between the rays in *Antedon* is in the conducting properties of the neural pentagon which connects the five rays. The fact that an impulse loses in effectiveness as it passes from the point of its origin may thus be an important factor in the coordination of movement.

Dorsal Flexion and Inhibition of Righting.

Moderate stimulation of an arm at any point yields ventral flexion followed by swimming movements of all the arms. Even stimulation caused by contact is sufficient to elicit this reaction. This is shown by the following experiment. A specimen of *Antedon* is put oral face down on the floor of the aquarium. At once all the arms make vigorous movements of ventral flexion. This is followed by active swimming, and as a result righting follows, *i.e.* the animal turns oral side up. Since the reaction just described is a reaction of the oral face to surface contact, it follows that *Antedon* is negatively streotropic with respect to its ventral side. On the other hand, excitation of the dorsal cirri always inhibits swimming and righting movements of the arms and causes them all to flex dorsally (Fig. 6). It can be shown, furthermore, that stimulation of the cirri inhibits the effects of ventral excitation even to the extent of preventing righting. If an animal be laid ventral side down on the bottom of an aquarium and at the same time the cirri be touched with a solid object, the arms of all the rays remain in extension and execute none of the righting movements. The moment contact is withdrawn from the cirri, vigorous ventral flexion of the arms follows and the animal turns oral side up. A striking form of the experiment may be shown in the following way. If a specimen of *Antedon* attached by its cirri to a small object such as a pebble, is inverted and allowed to rest ventral surface down on the floor of the aquarium, no righting movements occur. But stimulation of the oral surface caused by contact with the bottom forces the cirri to release their grasp on the pebble. The latter now lies loosely upon the cirri but still exerts enough excitation to inhibit any movement of the arms. If the pebble is now removed from its contact with the cirri vigorous righting movements begin, since these movements are no longer inhibited by stimulation of the cirri, and the animal comes to rest oral side up.

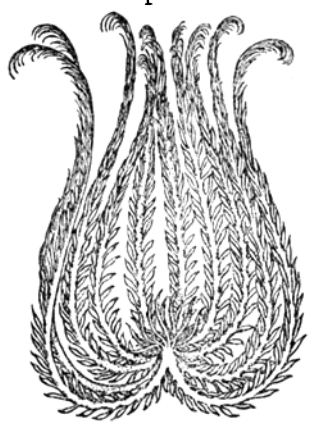

FIG. 6. Aboral bending of all the arms in response to stimulation of the cirri. In the figure the pair of arms at the front are shown drawn apart in order to allow a view of the cirri and other arms. Such a reaction always follows picking up an *Antedon* by the cirri.

The experiment proves two points, (1) stimulation of the cirri inhibits ventral flexion to the extent of preventing righting movements and (2) stimulation of the ventral surface inhibits the grasp reflex of the cirri. Thus the tropistic impulses of oral and aboral sides, respectively, act antagonistically—a case of dynamic symmetry with reference to structurally dissimilar halves (*i.e.* upper and lower halves) of the organism. This experiment disposes of the contention of Jennings (9) to the effect that tropisms are not to be found in the echinoderms since structurally bilateral symmetry is lacking in them (10).

CONCLUSIONS.

1. Stimulation causes *Antedon* to swim by means of alternate oral bending and dorsal stroke of the arms. Two arms of a given ray move alternately so that while one is executing the aboral stroke its mate is flexing ventrally. This implies reciprocal inhibition.

2. Recriprocal inhibition between the two arms of an isolated ray can be abolished by the use of either strychnine or nicotine.

3. Coordination between the rays is referable to the conducting properties of the nervous pentagon which connects the five rays. In this system an impulse loses in effectiveness as it passes from the point of origin.

4. When *Antedon* is made to rest *oral* face down on the floor of an aquarium, oral flexion of all the rays, swimming movements, and righting result. *Antedon* is therefore negatively stereotropic with reference to its ventral side.

5. Excitation of the dorsal cirri results in *aboral* bending of all the rays. Stimulation of the cirri inhibits ventral flexion to the extent of preventing righting movements while on the other hand stimulation of the ventral surface inhibits the grasp reflex of the cirri. Thus oral and aboral sides of *Antedon* exhibit dynamic symmetry although structurally dissimilar.

I take this occasion to thank Professor Bottazzi of the physiological section of the Station for giving me free use of the laboratory. I also wish to express my appreciation of the excellent service rendered by Mr. Santarelli and his staff of the collecting department in procuring material for the work.

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