# STEREOTROPISM AS A FUNCTION OF NEUROMUSCULAR ORGANIZATION.

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When a starfish is put on its back, it rights itself and, though it has been known that this is a case of stereotropism, the details of the reaction have thus far not been accounted for. Thus it has happened that some authors have spoken of this reaction as a case of "trial and error" on the part of the animal. The experiments described in this paper show that the righting reaction of the starfish is a necessary consequence of the neuromuscular organization of the ray and that no room is left for the assumption of "trial and error."

It usually has been assumed by writers on the subject that the movements of the starfish, including those of righting, are accomplished entirely by the tube feet.[1] The writer has observed, however, that nicotinized individuals, in which all the tube feet except a few at the tip of the ray—the "feelers"—are retracted and inactive, begin righting movements, and in some cases complete the righting in course of half an hour or so. This indicates that the essential movements of righting can be accomplished by means of the nerves and muscles of the arms themselves without the use of the tube feet as locomotor organs. It therefore follows that the functioning of the *Asterias* ray in righting is based on principles similar to those which operate in the case of ophiurans. It seems probable that the principal rôle of the tube feet of *Asterias* in normal righting lies in their service as delicate sense organs, making possible quick and accurate functioning of the ray musculature. They also act as accessory locomotor organs and contribute to the speed of the somersault.

[1] Belonius, P., De Aquatibus, Paris, 1553.

### *The Musculature.*

The muscles which determine the movement of the ray are classified by position as (*a*) circular and longitudinal muscles of the dorsal sheath, and (*b*) interskeletal longitudinal muscles of the ray floor.[2] The action of the sheath muscles may be demonstrated in the intact animal by stimulating the tip of the ray with a drop of 0.1 N acid. As a result the ray shortens, due to contraction of the longitudinal muscles, and suffers a decrease in diameter from the contraction of the circular ones. Similar results are to be obtained with strong stimulation of the tube feet of any part of the ray, thereby proving the nervous connection of the sensory cells of the tube feet with the muscles of the sheath.

The most complex action of the neuromuscular system is seen in the righting response. Here certain arms bend dorsally, others ventrally, in response to reciprocal impulses.[3] Obviously it greatly aids an analysis of such reactions if the investigator can produce them at will artificially or entirely apart from their normal causation. This is made possible in the case of the starfish ray through the use of the alkaloids, strychnine and nicotine.[4] With strychnine the ray bends dorsally, with nicotine ventrally. The parts played by the various groups of muscles may be shown by separating the dorsal sheath from the floor of the ray by cutting the two structures apart longitudinally. When put into either nicotine or strychnine the dorsal sheath shows dorsal flexure and rolls together so that the cut edges meet and overlap. This demonstrates physiologically the existence of longitudinal and circular muscles in the dorsal sheath. In similar fashion the presence of dorsoflex and ventroflex musculature in the floor of the ray may be shown, since in nicotine the floor bends ventrally, in strychnine dorsally.

There are therefore four muscle groups which play a part in the movements of the ray. (*a*) The longitudinal dorsoflexors of the sheath; (*b*) the circular muscles of the sheath, effective in twisting

[2] Bronn, H. G., Klassen und Ordungen des Tier-Reichs wissenschaftlich dargestellt in Wort und Bild, Leipsic, 1899, ii, 3A, 543.

[3] Loeb, J., Comparative physiology of the brain and comparative psychology, New York, 1900, 61. Moore, A. R., *Am. J. Physiol.*, 1910-11, xxvii, 207.

[4] Moore, A. R., *J. Gen. Physiol.*, 1919-20, ii, 201.

movements; (*c*) the longitudinal interskeletal dorsoflexors of the ray floor; (*d*) the longitudinal interskeletal ventroflexors of the ray floor.

It will be shown elsewhere that limited parts of each system are independently innervated and are capable of independent action. This permits the ray to bend either dorsally or ventrally at any point, and to twist the peripheral part on its long axis through any angle up to 180°.

### *Motor Nerve Elements.*

It has been found that strychnine[5] and nicotine are without excitatory action on the neuromuscular system of the cœlenterate *Metridium*. It may be assumed then that the alkaloids in question, in the case of echinoderms and the higher forms, act on elements of the neurone especially developed in the more complex types of nervous system. The contraction of certain groups of muscles as the result of the action of nicotine or of strychnine consequently becomes an indicator of chemical excitation of the corresponding nervous elements. If we assume that the excitatory action of nicotine and strychnine is on some part of the motor neurone such as the sensory-motor junction, it would then follow as to the loci of the action of the alkaloids that (*a*) both substances excite the motor neurones of the dorsal sheath; (*b*) both sustances excite the motor neurones innervating the muscles of the ray floor which cause ventral flexure; (*c*) strychnine excites the motor neurones governing the dorsoflex musculature of the ray floor; they are refractory to nicotine.

### *Sensory Nerve Elements.*

Ordinarily when an *Asterias* is laid on its back on the floor of an aquarium the rays begin their dorsal bending quite promptly, and righting is accomplished in 1 or 2 minutes. If, however, the aquarium jar has a cone-shaped floor and the inverted animal is placed so that its central disk rests on the apex of the cone, the righting is much delayed, since in this case the rays only by chance come into contact

[5] Moore, A. R., *Proc. Nat. Acad. Sc.*, 1917, iii, 598.

with the bottom surface. Or if a specimen of *Asterias* is suspended in the water by a thread tied around the central disk, so that the rays cannot touch a surface, dorsal bending of the rays does not occur at all. The animal hangs inert for an indefinite length of time with the rays in a position of partial ventral flexure (Fig. 1). Now hold a glass rod in contact with the back of the ray. The latter bends slowly a little distance dorsalward (Fig. 2). This proves that the sensory cells of the dorsal integument, when stimulated, cause contraction of the dorsoflexors of the sheath. Ordinarily this reflex plays a part in initiating the righting by pressing the entire ray against the bottom. This enables the sensitive "feelers" of the tip of the ray to touch bottom immediately, and from the numerous sensory cells of the am-

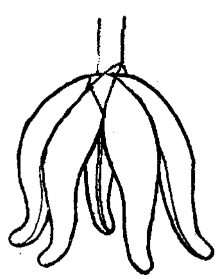

FIG. 1.

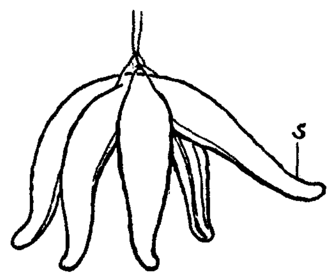


FIG. 2.

FIG. 1. Position taken by an individual *Asterias* during suspension in an aquarium. The animal is not in contact with a surface, consequently the rays are inert.

FIG. 2. A glass rod has been brought into contact with the dorsal side of the ray at the point indicated by *S*. As a result the ray has responded by bending dorsally.

bulacral disks impulses go to the musculature facilitating flexure. As the tube feet secure hold, that part of the ray straightens and actual bending occurs only centralward to the point where the last tube feet have touched bottom.

That the muscular responses of the later phases of righting are due to stimulation of the sensory cells of the tube feet may be shown in the following way. Place a medium sized *Asterias* ventral side up on a glass plate. Stimulate the sensory cells of the tube feet by touching these organs at the tip of the ray with a loop of thread dipped in 0.05 N HCl. At once the tip bends dorsally (Fig. 3). Now touch the tube feet near the middle of the ray with the acid thread. Two results appear; (*a*) the tip returns to its former position, and (*b*) the ray bends dorsally immediately central to the point of the last application of the acid (Fig. 4). Stimulation of the sensory cells of the tube feet, therefore, results in dorsal flexure of the ray central to the point of stimulation, and inhibition distal to this point. It was found as a rule that strychnine abolished this phase of inhibition, so that in a thoroughly strychninized ray stimulation of the tube feet at any point resulted in dorsal flexure of the entire ray.

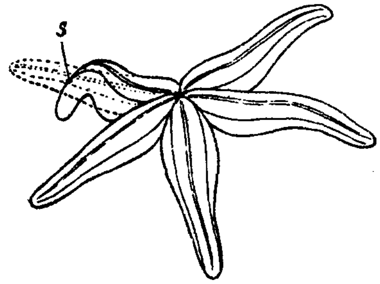


FIG. 3.

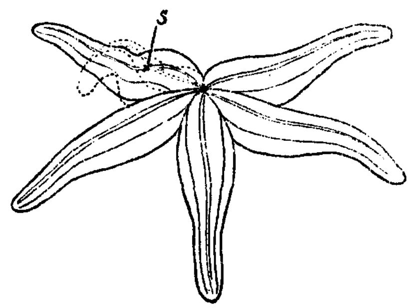


FIG. 4.

FIG. 3. The specimen lies ventral side up on a glass plate. A thread previously dipped in 0.05 N HCl has touched the extended ray (indicated by the dotted outline) near the tip as at *S*, with the result that the distal end of the ray bends sharply dorsalward.

FIG. 4. With the ray in the position of Fig. 3, shown here by dotted outline, the acid stimulus is applied to the tube feet near the center of the ray. As a result the distal half is extended to the normal position but dorsal flexure occurs central to the point of stimulation.

## CONCLUSIONS.

From what has been said concerning the neuromuscular organization of the *Asterias* ray, it is possible to arrive at certain definite conclusions regarding the nature of the stereotropism of that organ. The righting movements from the start are not haphazard; *i.e.*, they cannot be explained on any hypothesis of "trial and error." The excitation of the sensory cells of the dorsal sheath initiates dorsal flexure of the ray. This movement makes it possible for the tube feet of the tip to touch bottom and start the vigorous action which follows and completes the righting If the "feelers" by chance touch bottom they initiate the reaction *de novo*.

As to the remaining phases, the stereotropic reaction of the ray is referable to the high degree of surface sensitivity of the tube feet disks and the propagation of excitatory and inhibitory impulses, resulting from stimulation, along appropriate paths to the muscles of the ray. In this respect the tube feet may be regarded as playing a rôle similar to that of tropistic receptors in general. That is, unequal stimulation of the receptors causes a corresponding inequality of tone or of contraction in the musculature which ultimately results in an equilibrium of orientation to the factor involved.

It is evident that as a mechanism for righting stereotropism differs in one important respect from other tropisms. The latter depend for their operation upon unilateral effects in organisms which are dynamically bilaterally symmetrical. In stereotropism the sensitivity of the organism is not distributed in bilaterally symmetrical fashion. As a rule only the ventral side is stereosensitive; *i.e.*, the sensitivity is unilaterally distributed. There is a tropistic action in such cases because of the fact that when the sensitive surface is only partially stimulated an unequal contraction of the musculature follows and this as a result brings the sensitive surface into such a position that it is all equally stimulated. Equal muscle tone follows and the organism is in equilibrium with its environment.[6]

[6] Jennings (Jennings, H. S., *Univ. California Pub., Zoology*, 1907–08, iv, 156) believes that he has discovered in *Asterias* a capacity for learning in connection with this reaction; that is, a ray ordinarily passive during righting could be induced by repeated suppression of the other more active rays to undertake righting movements. In describing his experiments Jennings states that the active rays were prevented from taking part in the righting by "stimulating their tube feet with a glass rod." In 1910 (Moore, A. R., *Biol. Bull.* 1910, xix, 235), I called attention to the fact that Jennings' result did not prove the use of memory or hysteresis of any kind in this functioning of a previously passive ray, because strong stimulation or a slight injury of any sort to the other rays renders them inactive and forces the use of the ray in question. By "stimulating with a glass rod," Jennings simply diminished the reacting capacity of the active rays, or, in other words, raised their threshold either to a point equal to or above that of the ray he was seeking to "teach." The experiment may be much simplified by making a single stroke with a glass rod in the ambulacral groove of each of the four active rays. Animals treated in this way have been kept under observation and found to resume the use of the treated rays only after 1 or 2 weeks. In the interval righting is always performed by the previously inactive ray which, however, had not been stroked along the groove with a glass rod.