

## STEREOTROPIC ORIENTATION OF THE TUBE FEET OF STARFISH (ASTERIAS) AND ITS INHIBITION BY LIGHT.\*

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Recently Maxwell has shown that the reactions of sharks to contact stimuli are due to changes in the relative tension of the antagonist muscles similar to those taking place in the galvanotropic, heliotropic, and geotropic reactions of animals.<sup>1</sup> The writer has recently made observations on the starfish which show that contact stimuli applied to the sides of a ray bring about changes in the orientation of the tube feet which are comparable to heliotropic reactions. These stereotropic reactions of the starfish gain especial significance since they can be inhibited by the reaction to light.

In order to demonstrate the stereotropic orientation of the tube feet, the starfish is laid on its back in a dish of sea water. If the animal is prevented from righting itself for 1 or 2 minutes it becomes comparatively quiet; if now a contact stimulus is applied to one of the rays by pressing a foreign body such as a piece of cork, a glass rod, or a finger tip against the side of the ray, a retraction of the tube feet and closure of the ambulacral groove occurs. Next, the groove opens and the tube feet move toward the stimulated area. The reaction is especially marked in the immediate vicinity of excitation but in the more sensitive individuals it involves the entire ray. The average length of time which elapses between the moment of contact excitation and the protrusion of the tube feet is 2.8 seconds. The contact stimulus may be applied momentarily and removed before the reaction begins, but the series of reactions proceeds as

\*The experiments described in this paper were done in the Botany Laboratory at Woods Hole, and the writer wishes to express his thanks to Professor Osterhout for many courtesies extended to him during the progress of the work.

<sup>1</sup> Maxwell, S. S., *J. Gen. Physiol.*, 1920-1921, iv, 19. von Uexküll, J., *Z. Biol.*, 1900, xxxix, 73.

described. This gives confirmatory proof of the machine-like character of the reaction. It is also worthy of note that the circumoral nerve ring plays no part in the reaction, but only the radial nerve through which the tube feet receive their impulses since these experiments can be made on isolated rays. Fig. 1 is a diagram showing the orientation of the tube feet which are extended toward the point of contact stimulation.

If two points on the same side of the ray but at a distance from each other are touched, then the tube feet turn to that side (Fig. 2). The tube feet midway between the two loci of stimulation bend neither toward the one nor toward the other but at right angles to a line

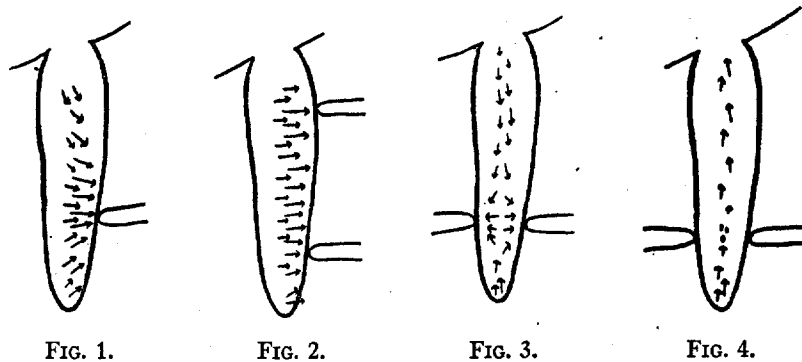


FIG. 1. Arrows indicate the direction in which the tube feet are bent, the arrow tip being put for the terminal disks. This diagram shows the tube feet all inclined accurately to the locus of contact excitation indicated by the U-shaped outline.

FIG. 2. Two loci of contact excitation on the same side of the ray result in the tube feet orienting themselves at right angles to the axis of the ray and to a line joining the two loci of stimulation. The median tube feet do not incline to either point of excitation but orient like a phototropic insect placed midway between two lights of equal intensity.

FIG. 3. Slight contact excitation has been applied at two points on opposite sides of the ray. Only the tube feet in the immediate vicinity are directed toward the points of excitation. The other tube feet are directed along the median axis of the ray at right angles to a line joining the two loci of stimulation.

FIG. 4. The same as in Fig. 3, except that the pressure is strongly applied resulting in withdrawal of the tube feet in the immediate vicinity of excitation, and orientation of the others to the center parallel with the axis of the ray and perpendicular to a line joining the two loci of excitation.

joining the two points. In this we have a tropistic reaction analogous to that of heliotropic orientation to two sources of light.<sup>2</sup> The same principle may be illustrated in another way by gently pressing the ray between two small bodies such as glass rods. When the extension reflex takes place it will be seen that only a few of the tube feet bend laterally and they are in the immediate vicinity of the points touched. All the other tube feet bend along the axis of the ray toward the area of excitation, swaying a little from side to side, but neither markedly to the right nor to the left (Fig. 3). If the pressure is increased the tube feet central to the point of stimulation reverse their orientation and bend toward the center (Fig. 4). However, not every animal gave both phases of this reaction; *i.e.*, distal and central bending of the tube feet. In the main the results were similar to those obtained by Maxwell with *Mustelus* in which he found that weak mechanical stimulation caused bending toward the point of contact while strong stimulation produced the opposite result.<sup>1</sup> It happens therefore that when acted upon by contact on two opposite sides of the ray, *i.e.*, by two equally balanced impulses, the tube feet orient themselves along a line perpendicular to a line joining the two loci stimulated. Here again is a case analogous to that of heliotropic orientation to two sources of light, since the starfish ray like the heliotropic insect is bilaterally symmetrical with reference to right and left.

If the tube feet as a result of their extension in response to contact touch a surface, they at once adhere by means of their sucking disks. When a considerable number of tube feet have thus taken hold it is difficult to pull the animal away from a surface. Even if one succeeds in doing so some of the tube feet will be torn from the animal and left sticking to the surface, so strong is the hold they have upon it. It is, however, possible by means of the light reaction to cause adhering starfish to release their hold. This reaction may be demonstrated as follows: A starfish is placed ventral side up in a dish of sea water in a dimly lighted room. As soon as the tube feet have been thrust out, a flash of sunlight is thrown across the animal. As a result the tube feet withdraw and the ambulacral

<sup>1</sup> Loeb, J., *Forced movements, tropisms, and animal conduct*, Philadelphia and London, 1918, 75. Patten, B. M., *J. Exp. Zool.*, 1914, xvii, 213.

grooves close; the rays bend ventrally. After several seconds in this position the grooves open and the tube feet are extended. This occurs even if the illumination is continuous.

For purposes of better control all the experiments with light were made in the dark room. While the retraction is uniformly elicited in the dark-adapted starfish with white light of sufficient quantity; red light has no such effect. It was therefore practicable to observe the animals at any time by means of red light while white light was admitted by a shutter for any desired length of time. Use was made of the lamp and optical bench described by Hecht.<sup>3</sup> The source of white light was a 260 candle-power Mazda lamp. The time of exposure was measured with a stop-watch. The exposures were also checked by means of the shutter of a photographic camera. Each starfish was kept in a rectangular glass dish during a series of experiments. The test was made by allowing the light to fall perpendicularly on the side of the dish on which the animal rested. This procedure resulted in illuminating the ventral sides of one or more rays. Withdrawal of the tube feet and beginning closure of the groove were taken as the end-point of the reaction. In case it was desired to avoid contact on the part of the tube feet, the animal had to be supported vertically in the dish while the exposure was made. The starfish must be kept in the dark for an hour before beginning the experiments and they must not be excited mechanically at the time of the test. It was found that a subliminal exposure to light preceding by a few seconds an otherwise adequate exposure, completely inhibited the reflex. Therefore only one measurement could be made at a time. Accordingly after each exposure the animals were put into freshly aerated sea water and kept in the dark for 15 minutes before being tested again.

The shortest reaction time obtainable with a light intensity of 26,000 candle-meters intensity was 1.5 seconds. The longest reaction time secured with a weak light was approximately 3 seconds. If the light intensity was so low that an exposure of more than this length of time was necessary to produce the required photochemical effect, no reaction was obtained. The minimum quantity of light

<sup>3</sup> Hecht, S., *J. Gen. Physiol.*, 1919-1920, ii, 229.

which would bring about the reaction in a dark-adapted starfish, the tube feet not being in contact with a surface, was found to have an average value of 10 to 25 candle-meter seconds.

Illumination of the dorsal surface of the starfish does not cause the retraction of the tube feet nor closure of the ambulacral groove. This shows either that the dorsal surface is insensitive to light or that nervous connection between the sensory cells of the dorsal surface and the tube foot musculature is lacking. Since, as we know from the effects of mechanical stimulation<sup>4</sup> there is nervous connection between the stereosensitive cells of the dorsal surface and the tube feet, the first hypothesis is probably correct; *i.e.*, the dorsal surface has no light receptor cells.

The "feelers" of the tips of the rays are relatively insensitive to light since they show no retraction upon illumination. Only tube feet with well developed terminal pads are strongly photosensitive. Illumination of a limited number of tube feet causes reaction only in that area, or at most, in the most sensitive individuals, only in the ray illuminated. The light reaction is therefore local in character.

It was noted in the experiments that tube feet which were not in contact with a surface retracted much more readily in response to illumination than did those which were in contact with a surface. But by the use of more intense light it was found possible to force the retraction of those in contact with a surface. This antagonism between stereotropism and the reaction due to light gives a means of quantitative treatment of stereotropism by the method of indirect measurement. It is therefore only necessary to illuminate the animal with a known quantity of light just sufficient to neutralize its stereotropism, as shown by the withdrawal of the tube feet from the surface, in order to have a measure of stereotropism in terms of light quantity. Although 10 to 25 candle-meter seconds is sufficient to cause retraction of tube feet which are simply extended in the water without touching a surface, this quantity of light has no apparent effect upon the tube feet which are in contact with the glass side of the aquarium. But if exposed to a light sufficiently powerful, starfish clinging to the side of a glass dish frequently release their hold en-

<sup>4</sup>Moore, A. R., *J. Gen. Physiol.*, 1919-20, ii, 319.

tirely and drop to the bottom. The least quantity of light which will cause the retraction of the tube feet from a surface may be regarded as the photic equivalent of stereotropism.

In making determinations of the photic equivalent of stereotropism the apparatus and procedure were the same as noted above except that the exposures were made on the ventral side of the starfish while it clung to the vertical wall of the dish. It was thus possible to measure the distance of the receptors from the light source with accuracy. Exposures were made on each animal at 5 cm. intervals (Table I). The letters in the table indicate the individual animals. The figures under the letters are the distances in centimeters at which the 260 candle-power light acting for the time interval stated in the first column will just cause the tube feet to be withdrawn from the wall and the ambulacral groove to begin to close. At a distance

TABLE I.

Exposure time.	A	B	C	D	Average $i$ .	$t \times i^*$
<i>secs.</i>						
0.5	70	60	75	60	609	305
1	85	90	110	90	304	304
2	125	130	160	140	139	278

\*  $i$  represents intensity in candle meters;  $t$ , exposure time in seconds.

of 5 cm. farther away from the light an exposure of the length designated caused no significant response. Each figure is the result of repeated trials.

While there is a considerable variation in the values when different individuals are compared, each animal yields fairly consistent results. For example, *C* has higher sensitivity than the others and shows the fact in each of the three exposures. The desirability of more extensive studies is apparent, but the end of the season cut short the progress of the experiments and the data given are submitted for the purpose of illustrating the possibilities of the method.

As a result of the measurements made, it can be stated that the average photic equivalent for stereotropism in *Asterias* is between 250 and 350 candle-meter seconds. This is a value 10 to 20 times as great as is required to cause retraction of the tube feet when they are

not in contact with a surface. It is also clear from the figures in the table that the length of exposure is inversely proportional to the light intensity since the product of intensity by time equals a constant. This shows that a certain quantity of light is required to bring about the reaction, which is but another way of saying that the Bunsen-Roscoe law holds here as it does in other photochemical reactions.<sup>3,5</sup>

<sup>5</sup>Loeb, J., *Forced movements, tropisms, and animal conduct*, Philadelphia and London, 1918, 83.