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Prosomal width ♂ 20-60 mm, undoubtedly juveniles even ad. Wood Hole, MA

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# CIRCUS MOVEMENTS OF LIMULUS AND THE TROPISM THEORY.

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As a result of asymmetric photic stimulation of many animals locomotion follows a circular path. If the animals are positively phototropic the path bends predominantly towards the stimulated side; if they are negative, towards the non-stimulated side. In such cases crossed innervation from the photoreceptors to the muscles of the locomotor organs on the opposite side must exist, which causes the tonus of the muscles on the two sides to be different (Garrey, 1918–19). For an analysis of animal orientation to light, circus movements are of importance since they furnish evidence to the mechanism of orientation when other movements do not. Or they may furnish evidence confirmatory of that derived from other kinds of movement. In the majority of animals whose circus movements have been analyzed (see Minnich, 1919, for a review of the literature), it has been found that the diameter of the circle turned varies inversely with the light intensity. This is what would be predicted from the tropism theory of Loeb, formulated in 1888, and is contrary to Mast's (1922) most recent theory that orientation is regulated by localized stimulation. A quantitative study of the positive circus movements of *Limulus* herewith presented shows that the photic orientation of this animal accords with the tropism theory, adding therefore one more link in the chain of evidence.

In the experiments[1] adult *Limuli* (from 20 to 60 mm. in diameter) were used, since it was found impractical to use the larval forms. Having determined that the normal animals are positively phototropic

[1] The experiments were performed at the Marine Biological Laboratory, Woods Hole, Mass., and I wish to express my appreciation for the courtesies shown me by the Director and others in charge of the laboratory.

under laboratory conditions, and that the eyes are the important receptors for photic stimulation, the next step was to test animals with a single functional eye. It should be noted that young *Limuli* possess four compound eyes, two large lateral eyes on opposite sides of the cephalothorax, and two small median, anterior eyes, one on either side of the median line. For testing circus movements, it was deemed best to remove or cover both median eyes and one of the lateral eyes, leaving only the opposite lateral eye functional. The removal was accomplished by a fine, sharp scalpel, and the covering by the use of asphaltum. Both kinds of asymmetric animals were allowed recovery periods varying from 4 hours to 2 days, according to whether the eyes were covered or removed. They were then subjected to the photic stimulation of three intensities. A cylindrical glass dish (inside diameter 295 mm.) lined on the inside with tissue paper, and surrounded on the outside by five 40 watt Mazda lamps, contained the single experimental animal. Underneath the dish was a circular cardboard marked off with 4 concentric circles and 4 diameters to facilitate the tracing of the animal's path. The intensity of the light at the center of the dish was not accurately determined, but was approximately 8,000 candle meters. When the lamps were moved outward so that they were 300 mm. from the center the intensity was approximately 2,000 candle meters, and when 450 mm. distant, approximately 900 candle meters. With this arrangement the intensity inside the dish was very nearly constant in all parts, and the illumination was diffuse and non-directive, the only conditions under which circus movements should be tested. The temperature of the water was 24° ± 3°C. Individual trials, usually of 3 minutes duration, were recorded separately on charts like the cardboard described above, except one-fourth smaller. After some practice it becomes easy to trace the path of an animal on the small chart as locomotion occurs in the dish. After the trial with the lowest intensity a test with the highest intensity was repeated to determine whether or not the animal was regular in its reaction. The paths of the animals were measured with a map measurer, and the number of degrees turned per centimeter was calculated, as will be described later. 135 trials on 38 different animals completed the observations.

Before proceeding to a consideration of the results obtained it is necessary to call attention to the fact that *Limuli* freshly collected show a high percentage (about 25 per cent) of irregular reactions to photic stimulation; *i.e.*, some animals will be indifferent to light, others will show a mixture of positive and negative movements, and still others will be definitely positive for a time, and then become the opposite. Among the reasons for such irregularity are the following: (1) the ease with which some individuals are "frightened" by handling; (2) the state of nutrition, "hungry" animals showing rapid movements in many directions; and (3) unknown causes due to previous stimuli. It becomes clear after observing *Limuli*, however, that they are fundamentally and primitively positive to light, but that many factors may modify or mask the phototropic reaction. Such behavior illustrates very well the fact that a primitive reaction of an animal, such as that to light, may be profoundly modified or even obliterated by other reactions occurring simultaneously. The idea of an inclined plane of behavior may be extended to the whole series of animals. Between the lowest forms, whose reactions to light and other stimuli are machine-like in character, and man, whose reactions to the same stimuli are nearly always modified or entirely suppressed by reason, there are all gradations of tropistic behavior. It is not surprising, therefore, to find that *Limulus*, the anatomy of whose nervous system has led to the belief that the animal corresponds closely with the hypothetical ancestors of the vertebrates, shows a modified response many times in respect to light. That this is actually the case is shown by the following experiment which was repeated several times. A normal individual was tested and found to be positive to light; then it was taken up in the hands, turned over, and handled in various gentle ways, and tested again. For several hours afterward this animal was distinctly negative to light, creeping away into the dark as fast as possible, and showing strong stereotropism. On the next morning, however, it showed an equally distinct positive reaction. The effects of handling or "frightening" the animal set up other reactions, including a stereotropic one, which reversed the phototropic reaction. As soon as those effects had disappeared, the primitive positive response to light became again apparent. Before testing animals for circus movements the normal reaction

TABLE I.

*Length of Path, Amount of Turning, and Degrees Turned per Centimeter for Limuli under Three Intensities of Asymmetric Photic Stimulation.*

| No. | Good eye. | 8,000 candle meters. | | | 2,000 candle meters. | | | 900 candle meters. | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Length of path. | Net turn. | 0° cm. | Length of path. | Net turn. | 0° cm. | Length of path. | Net turn. | 0° cm. |
| | | *cm.* | 0° | | *cm.* | 0° | | *cm.* | 0° | |
| 9 | Right. | 664 | 3,060 | 4.6 | 476 | 825 | 1.7 | 628 | 2,690 | 4.2 |
| 10 | " | 338 | 1,735 | 5.1 | 268 | 1,440 | 5.4 | 416 | 2,565 | 6.2 |
| 11 | Left. | 404 | 2,115 | 5.2 | 372 | 1,440 | 3.9 | 260 | 1,140 | 4.4 |
| 12 | " | 476 | 2,835 | 5.9 | 424 | 1,920 | 4.5 | 408 | 981 | 2.4 |
| 13 | Right. | 460 | 2,275 | 4.9 | 346 | 1,655 | 4.8 | 208 | 810 | 3.9 |
| 14 | Left. | 584 | 6,105 | 10.4 | 536 | 4,160 | 7.7 | 596 | 1,810 | 3.0 |
| 15 | Right. | 572 | 4,190 | 7.3 | 616 | 3,135 | 5.1 | 528 | 2,380 | 4.5 |
| 16 | Left. | 612 | 3,440 | 5.6 | 664 | 3,015 | 4.5 | 496 | 1,215 | 2.4 |
| 17 | " | 528 | 3,100 | 5.9 | 424 | 1,390 | 3.3 | 476 | 1,085 | 2.3 |
| 18 | Right. | 816 | 3,980 | 4.9 | 788 | 2,390 | 3.0 | 760 | 1,530 | 2.0 |
| 19 | " | 424 | 2,500 | 5.9 | 552 | 2,550 | 4.6 | 620 | 2,560 | 4.1 |
| 20 | Left. | 380 | 2,640 | 6.9 | 428 | 2,610 | 6.2 | 240 | 1,080 | 4.5 |
| 21 | " | 264 | 2,340 | 8.9 | 308 | 1,845 | 6.0 | 386 | 1,960 | 5.1 |
| 22 | Right. | 300 | 2,090 | 7.0 | 244 | 1,080 | 4.4 | 328 | 1,170 | 3.6 |
| 23* | Left. | 512 | 3,645 | 7.1 | 400 | 1,845 | 4.6 | 456 | 2,700 | 5.9 |
| 24 | " | 420 | 3,340 | 7.9 | 412 | 2,880 | 7.0 | 300 | 1,465 | 4.9 |
| 25 | " | 432 | 4,350 | 10.0 | 528 | 3,910 | 7.4 | 432 | 3,915 | 9.0 |
| 27 | Right. | 320 | 2,090 | 6.5 | 344 | 1,800 | 5.2 | 260 | 1,350 | 5.2 |
| 28 | Left. | 300 | 1,670 | 5.6 | 264 | 180 | 0.7 | 280 | 1,080 | 3.9 |
| 29 | Right. | 308 | 1,730 | 5.6 | 288 | 1,260 | 4.4 | 208 | 990 | 4.8 |
| 30 | " | 308 | 1,930 | 6.3 | 240 | 1,440 | 6.0 | 300 | 1,540 | 5.1 |
| 31 | " | 356 | 1,710 | 4.8 | 236 | 1,080 | 4.6 | | | |
| 32 | " | 416 | 2,160 | 5.2 | 236 | 1,350 | 5.7 | 112 | 540 | 4.8 |
| 33* | " | 220 | 1,440 | 6.5 | 208 | 1,440 | 6.9 | 108 | 540 | 5.0 |
| 34 | Left. | 340 | 1,890 | 5.6 | 468 | 2,880 | 6.1 | | | |
| 35* | " | 388 | 2,260 | 5.8 | 312 | 1,170 | 3.7 | 336 | 1,800 | 5.4 |
| 36* | " | 220 | 1,460 | 6.6 | 172 | 1,080 | 6.3 | 80 | 450 | 5.6 |
| 37* | Right. | 216 | 1,260 | 5.8 | 76 | 360 | 4.7 | 128 | 720 | 5.6 |
| 38* | Left. | 212 | 2,160 | 10.0 | 220 | 1,980 | 9.0 | 276 | 2,610 | 9.5 |
| 39* | " | 204 | 1,760 | 8.6 | 180 | 1,260 | 7.0 | 144 | 540 | 3.7 |
| 40* | Right. | 356 | 2,880 | 8.1 | 256 | 1,530 | 6.0 | 384 | 2,250 | 5.8 |
| 41* | Left. | 248 | 2,700 | 10.9 | 264 | 1,980 | 7.5 | 192 | 450 | 2.3 |
| 42* | Right. | 308 | 2,660 | 8.6 | 472 | 3,060 | 6.5 | 212 | 1,890 | 8.9 |
| 43* | Left. | 84 | 720 | 8.6 | | | | | | |
| 44* | Right. | 116 | 900 | 7.8 | | | | | | |
| 45* | " | 276 | 1,800 | 6.5 | | | | | | |
| 46* | " | 376 | 2,000 | 5.3 | | | | | | |
| 47* | Left. | 464 | 3,920 | 8.5 | 312 | 2,500 | 8.0 | 300 | 1,980 | 6.6 |
| Mean..... | | 374 | 2,497 | 6.73±0.18 | 362 | 1,895 | 5.23±0.17 | 339 | 1,556 | 4.78±0.17 |
| Mean rate of creeping. | | | 178 | | | 167 | | | 157 | |

* Indicates trials of less than 3 minutes duration.

ing graph should be a straight line, according to the Weber-Fechner principle. In Fig. 3 this has been done, and it will be seen that the

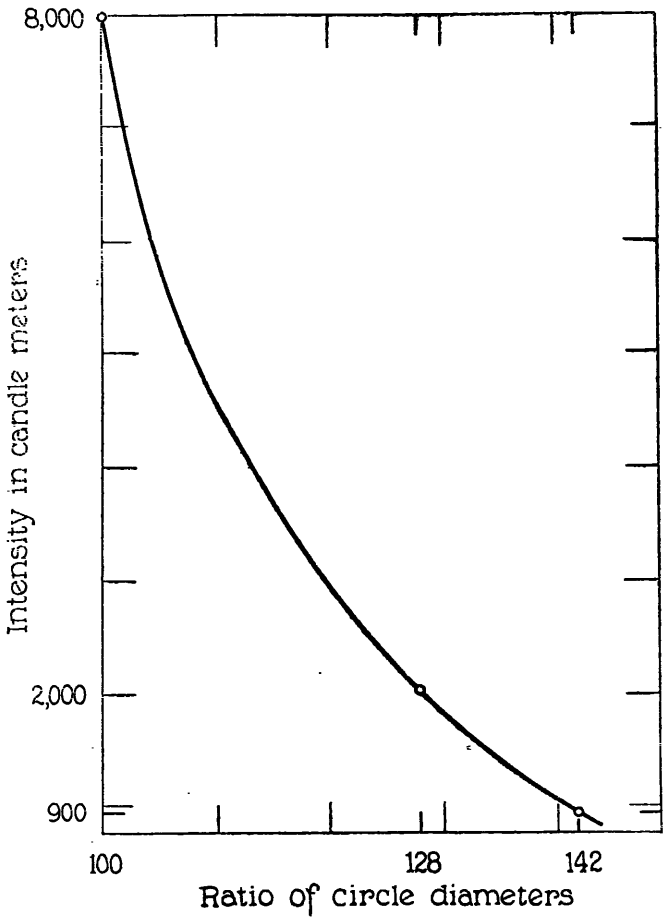


FIG. 2. Relation between the intensity of photic stimulation of asymmetric *Limuli* and the diameter of the circles turned during the circus movements. The abscissæ represent the ratios between the circle diameters, while the ordinates represent the light intensity in candle meters. Each point on the curve is the mean of 32 or more determinations.

three points lie very nearly in a straight line, and that the position of the line indicates an inverse relationship between the effect of light and its intensity, because the circle diameter is being considered, and

the action of other stimuli, probably internal, acting simultaneously with the light stimulus. This has been demonstrated not only in *Limulus* but in several other animals, and there appears no reason for doubting the reports. Modifications of tropistic behavior are to be expected, and certainly do not constitute a reason for setting up a new hypothesis in place of the tropism theory.

## SUMMARY.

1. Under laboratory conditions *Limulus* from 20 to 60 mm. in diameter are positively phototropic, and execute circus movements towards the normal side, when the median and the opposite lateral eyes are removed or covered.

2. The phototropism of *Limulus* may be modified or obliterated by (*a*) fright, (*b*) hunger, (*c*) stereotropism, (*d*) photokinesis, and (*e*) unknown stimuli.

3. Quantitative measurements of the paths of animals doing circus movements demonstrate that the amount of turning varies directly with the light intensity as follows: for 8,000 candle meters the degrees turned per centimeter were 6.73; for 2,000 candle meters, 5.23; and for 900 candle meters, 4.78. In other words, the diameter of the circle varies inversely with the light intensity.

4. The rate of ltlocomoon per minute also varies directly with the light intensity, being 178 cm. for 8,000 candle meters, 167 for 2,000, and 157 for 900.

5. These reactions are satisfactorily explained by the tropism theory.

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← locomotion

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