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CIRCUS MOVEMENTS OF LIMULUS

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By the symmetric and asymmetric stimulation by light of Limuli (from 20 to 60 mm. in diameter) it has been demonstrated that the animals are positively phototropic and that they show positive circus movements. It has further been found that the diameter of the circles turned as the result of asymmetric stimulation is inversely proportional to the light intensity. Because of the importance of circus movements in the analysis of orientation to light, and because there has recently appeared in these pages by Professor Mast a new explanation of orientation in insects, opposed to the tropism theory, the experiments leading to the above conclusions are briefly reported at this time. A fuller account will appear later in another journal.

In all the experiments on circus movements with Limuli the conditions were such that the animals were subjected to diffuse and non-directive illumination, the only conditions under which circus movements should ever be investigated. This was accomplished by arranging several Mazda lamps around the outside of a cylindrical glass dish lined on the inside with tissue paper. Three intensities of light were obtained by placing the lamps at different distances from the center of the dish, viz., 150, 300 and 450 mm., and although the intensities were not accurately determined, they were always in the same proportion, and were approximately 8000, 2000 and 900 candle meters. The conditions of asymmetry in the photoreceptors were produced either by removing or by blackening the two median eyes and one lateral eye, leaving the other lateral eye functional. One hundred thirty-five experiments on thirty-eight animals furnished the data presented here. The paths of the animals were transferred to record sheets, and were afterward measured as to length and number of degrees turned per centimeter. From table I it is seen that the number of degrees

TABLE 1

THE NUMBER OF DEGREES TURNED PER CENTIMETER UNDER THREE INTENSITIES OF LIGHT*

Candle Meters	Length of Path	Degrees per Centimeter
8000	374	6.73±0.18
2000	362	5.23±0.17
900	339	4.78±0.17

* Each number in the last two columns represents the mean of 45 determinations.

turned per centimeter varies directly with the light intensity, being 6.7 for 8000 cm.; 5.23 for 2000 cm., and 4.78 for 900 cm. In other words, the circles turned are larger under low intensity than they are under high intensity. To state the differences in more concrete form, it may be said that the diameters of the three circles turned are in the proportion of 100 to 128 to 142 for the corresponding intensities of 8000, 2000 and 900 candle meters.

The experimental animals were selected because of the regularity of their phototropic reactions. It was found that about 25% of normal freshly collected animals are very irregular in their reactions, some being indifferent to light, some being at first definitely positive and soon thereafter negative, and still others showing a mixture of positive and negative reactions. A higher percentage of irregularity is found in animals which have been in the laboratory several days. In spite of this irregularity in the phototropic reactions of Limulus, which may be due to several factors, such as the ease with which some individuals are frightened by handling, the state of nutrition, and unknown factors due to previous stimuli, yet it is clear that the animals taken as a whole are fundamentally positive to light, and that positive circus movements appear as a result of a symmetric stimulation. Many factors were found which modified or obliterated this fundamental phototropic reaction. Such behavior illustrates very well the fact that a primitive reaction of an animal may be profoundly modified by other reactions occurring simultaneously.

This is not at all a new idea, since it has long been known that there is an inclined place of animal behavior, beginning with the lowest forms whose reactions to stimuli, such as light, are machine-like in character, and ending with man whose reactions to the same stimuli are almost always modified or suppressed by reason, learning, etc. 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 to the hypothetical ancestors of the vertebrates, shows a modified tropistic reaction many times in respect to light.

The inverse relation between the light intensity and the diameter of the circle turned as a result of asymmetric stimulation contributes further evidence to Loeb's theory of heliotropism formulated in 1888. It should

be pointed out that although several investigators previous to that time had proposed theories of orientation somewhat like the tropism theory of Loeb, none of them embraced all the facts, and none of them were founded upon such conclusive evidence as Loeb's. It is absurd to claim that such early workers as Ray and de Candolle had the same idea as is expressed in the tropism theory concerning the photochemical effect of light upon the eye, since the true science of photochemistry was not even begun until about the middle of the nineteenth century.

When circus movements are performed by an animal in diffuse non-directive light, the strength of the photic stimulus remains practically constant throughout a single revolution, since the rays of light enter the eye at all angles with the same intensity. This fact would vitiate any hypothesis based upon localized retinal stimulation to explain circus movements in animals with eyes. The phototropism of animals without eyes cannot of course be explained by such a hypothesis, but is subject to explanation by the tropism theory. The evidence from Limulus as well as from other forms is preponderantly in favor of Loeb's theory, and the few real exceptions so far reported are undoubtedly due to the masking of phototropism by other more complex reactions occurring simultaneously.