

# INFLUENCE OF LIGHT OF VERY LOW INTENSITY ON PHOTOTROPIC REACTIONS OF ANIMALS.\*

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## INTRODUCTION.

Animals exhibiting phototropic reactions often orient equally strongly to light throughout a wide range of intensity. However, every stimulus to which an animal responds has a threshold of intensity below which that stimulus fails to elicit any response from the animal. It is therefore important to study the reactions of animals to stimuli which in intensity are in the region of this threshold in order to determine the nature and extent of the response.

The animals used in the investigation of these features were land isopods, which exhibit strong negative phototropism. These forms have been studied by Torrey and Hays (1914) and Cole (1907), but the most extensive work is that by Abbott (1918-19), who made a comparative study of several species, and found that they were equally negative in turning away from a light source in illuminations ranging from several hundred meter candles to 0.01 meter candle. Obviously the threshold of stimulation must lie at a very low value. It has been the object of this work to determine this threshold and to observe the nature of the responses to light in the region of this intensity.

## *Method.*

The isopods were collected in the immediate vicinity of Easton, Pennsylvania. No accurate identification was attempted, but with

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the assistance of Dr. Kunkel the following forms were recognized: *Oniscus asellus* L., *Porcellio scaber* Latreille, *Porcellio rathkei* Brandt, *Armadillidium vulgare* Latreille. These were kept in a healthy condition for several months confined in a covered glass dish containing moist loam, dead leaves, and rotting wood. Individuals used in experiments were separately confined in small glass vials, each containing a bit of loam and leaf stuff, and stoppered with cotton. The vials were set in the dish and the whole kept in a dark cupboard.

The method of studying the responses of these animals was essentially the same as that used by Abbott (1918-19). The isopod was placed on a dead-black table top in the center of a circle 10 cm. in radius, and stimulated by horizontal illumination. The point on the circumference at which the animal left the circle was recorded. Several such responses were obtained from each animal, and several animals were used for each intensity of light.

Two factors should be considered in providing a field of illumination. First, since the intensity gradient of a given path rapidly changes with change in the distance from the source, and since Cole's work (1907) indicates that the angle subtended by the light source may influence the response, it is necessary to find some way of changing the illumination other than by changing the distance of the animal from the source.

The field of illumination in which the animals were placed was obtained by means of the very small image of a Mazda filament, formed by a converging lens. This image, which was a fine, very bright horizontal line 1 cm. long, served practically as a point source, and gave a wide, even field. At the point where this image was formed a diaphragm was arranged with an aperture 1 cm. by 1 mm., which cut off all the rays that were not focused at that point. To eliminate the unevenness caused by the cheap lens, a diffusing screen, consisting of a piece of frosted glass, was inserted between the lamp and the lens. Placing it here instead of at the slit in the diaphragm eliminated the side area of weak illumination, and made it possible, by moving the screen closer to the lens, to decrease the intensity of the image. By inserting another such screen and two light blackened photographic plates in various combinations and positions, an unbroken range of intensity could be obtained, from 0.228 to

0.000005 c.p. This furnished a method of changing the illumination on any given point without changing the distance from the image to that point. A large number of determinations of the intensity of the image for various screens at different positions were made with a Lummer-Brodhun photometer, use of which was obtained through the kindness of the Electrical Engineering Department of Lafayette College. Measurement of the low intensities was very difficult, and involved considerable error. The extent of the error could, however, be determined by setting the photometer distinctly off balance on first one side and then the other. Lamp, lens, and screens were enclosed in a light-proof box, the diaphragm forming one end, and allowing the light to shine on the experiment table. The illumination at the center of the circle was calculated (in meter candles) in the usual way. On the whole, this scheme proved highly satisfactory, and, except for the labor of making a large number of measurements, is to be recommended where a wide, even field of illumination is required, and where it is necessary not to change the distance from the source of light to the point.

The experiment table was covered with dead-black cloth which is often used in making blackboards. This gave an even surface which was rough enough so that the animals could walk with ease. A circle 10 cm. in radius was drawn in chalk with its center 39 cm. from the source of light. Two diameters, one coinciding with the axis of the cone of light, and the other at right angles to it, referred to as the zero line, were drawn lightly. The circumference of the circle was marked off, in divisions of  $5^\circ$  each, in both directions from the zero line to the axis on each side. The quadrants toward the light are referred to as positive, those away from the light as negative. The quadrants were numbered, and the thirty degree divisions indicated, so that any point could be quickly determined at a glance in degrees + or - from the zero line. The box containing the light was set up so as to give horizontal illumination over the circle, the slit being 5 mm. above the table top.

The critical illuminations to be worked with would obviously be too low to make it possible for the experimenter to see the animal. At Dr. Kunkel's suggestion, I experimented with luminous material, and found that small chips could be glued to the back of the isopod without

interfering with its movements. By this means, together with the use of luminous index points on the experiment table, the responses of the animals could be observed in total darkness and in extremely low illuminations. Three luminous index points were arranged so as to be visible from above but invisible to the animal on the table. The luminous chips which were placed on the animals were made by mixing powdered luminous material (Hammer Radium Company, Denver, Colorado) with thin collodion, and spreading the paste on tissue paper. When dry, the under side was blackened with India ink, and small chips (2 mm. by 1 mm.) were cut out. These were tough and

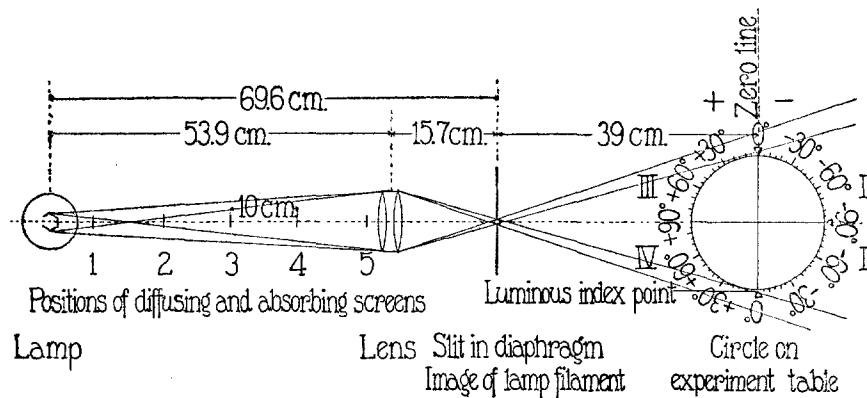


FIG. 1. Plan of apparatus. Source of illumination is image of Mazda filament made by lens. Diaphragm cuts out all other rays. Lamp, lens, and screens (diffusing and absorbing) enclosed in a light-proof box. Animals subjected to lateral illumination at the center of the circle on the experiment table.

durable, and were glued on the fourth thoracic segment by a very small drop of freshly prepared (unpoisoned) gum arabic solution. The movements of the animal could be readily seen, and when the circumference was crossed, a flashlight was used to make the reading. A wet piece of absorbent cotton would quickly remove the luminous chip after an experiment.

Cardboard frames were used to shove the animal into position in the center of the circle. When the frame was lifted, the animal was freed and at the same time exposed to light.

The apparatus was set up in a photographic dark room, the walls of which were painted dead-black to prevent reflection. The room was generally quite dry and hot, which must be noted because of the sensitiveness of land isopods to these conditions.

*Procedure.*

It is clear that an animal placed in the center of a circle will, in the absence of any directive stimulus, tend to move out of the circle on the diameter along which it is headed. Certainly, any deviations in its path which arise as the result of obscure physicochemical processes set up by either internal stimuli or uncontrollable external stimuli will be purely chance, and will be such that the average of all such deviations to one side or the other will be at the diameter along which the animal is started. This is especially true if the records are taken alternately in opposite directions to eliminate asymmetry. Thus the average of a number of responses of an isopod facing along the zero line (alternately in each direction) should, in the absence of any directive stimulus, be  $0^\circ$ . If rays of light, to which they are negative, strike the isopods from the + side, they will tend to move away from the light in a curved path, so that the average of a number of responses will be a certain number of degrees in the negative region. The same uncontrollable variations will be present and will affect the path in the same chance way, but in this case the distribution will be heavily skewed toward the negative side. The angle that this average path under the directive action of light makes with the average path in darkness ( $0^\circ$ ) can be used as a measure of the phototropism of the animal.

An isopod was removed from its bottle, a luminous chip glued on its back (fourth thoracic segment) and the animal placed on the experiment table. It was then covered with a cardboard frame and moved into position in the center of the circle, facing along the zero line. Care was taken not to expose to light and spoil its dark adaptation. The proper illumination having been set beforehand, the working light was turned out and the frame lifted. The animal's course could be followed by reference to the luminous points, and when the circumference was crossed, a flashlight was turned on and the reading taken of the angle turned. The isopod was then quickly covered with

the cardboard frame and returned to the center of the circle. Positions were alternated for each response: first the left side illuminated, then the right. Each animal was allowed to make about ten responses. The bulk of the work was done on *Oniscus*, of which only ten individuals were available. At the close of the experiment with each animal the chip was removed as described and the isopod returned to its bottle. Responses were measured in the actual number of degrees turned from the zero line in the direction headed; distributions were made of these and the means calculated.

#### RESULTS.

1. *Responses in the Absence of Light (Fig. 2, i).*—All species of isopods tried in darkness were found to move out of the circle in entirely a chance way, so that the statistical average of the paths, + and - from the zero line, is  $0^\circ$ , or very close. This shows that (a) there is no directive stimulus acting, and thus serves as a check on the apparatus and method; (b) that the stimuli initiating locomotion are not light stimuli; (c) that any internal or external stimuli setting up physicochemical processes which influence the path of the animal in any way act in a purely chance fashion. Chief among these stimuli is the stereotropism of the isopod, which causes it to remain in close contact with portions of the frame, and may be the cause of the undirected movements in the dark. Lifting the frame will almost invariably disturb the animal, and so furnish uncontrollable stimuli. Care had to be taken that the animal was headed with its axis coinciding with the zero line, as a very slight error here would give rise to a considerable angular deflection.

2. *Responses to Bright Light (Fig. 2, a).*—When subjected to rather high lateral illumination, the isopods respond by turning sharply away from the light and moving out of the circle in the negative region. The usual response is preceded by a period during which the animal remains motionless in the center of the circle—this is always definite in the normal response—and if no such pause of at least 2 seconds is made, the response is considered abnormal and discarded. Following this pause there is a period of antennary movement, followed closely by or begun immediately upon locomotion. The path with a very few exceptions is away from the light, and may be gradually curved,

or sharply broken. Usually the animal turns far enough until the curved carapace shades the illuminated eye, at which time the curving movements become less marked. Variations occur, as they do in the absence of light, but again they affect the response in a chance way. In bright light, however, the strong negative response tends to mask all these slight variations, and quickly eliminates any which tend to take the animal toward the light.

In bright light the response is maximal for a wide range of intensity with a given species. A comparison of several species was made, and the following was found. The average response of *Oniscus asellus* was  $55^\circ (\pm 2^\circ)$  for illumination of 1.50 m.c.; of *Porcellio* (*Porcellio scaber* and *Porcellio rathkei* used indiscriminately),  $31^\circ (\pm 5^\circ)$ ; of *Armadillidium*,  $16^\circ (\pm 9^\circ)$ —based on only twenty responses). In darkness *Oniscus* and *Porcellio* averaged  $0^\circ (\pm 3^\circ, \pm 5^\circ, \text{ respectively})$ . *Oniscus* is more negative and considerably more consistent in its responses, and so was used exclusively in the rest of the experiments.

The constancy of the maximal response which is elicited throughout a wide range of intensity is shown in Fig. 2, *a* to *c*, which are distributions of responses of ten individuals to three intensities of illumination ranging from 1.50 to 0.0026 m.c. For this range the action of the light is so strong as to mask other stimuli almost completely. The light rapidly turns the animal until the convex carapace shades the illuminated eye, and the active directive effect of the light is absent, although the turning movement may occasionally persist. This angle need not be  $90^\circ$ , but, due to the shape of the thorax, is such that when the animal has turned through an angle of about  $50\text{--}60^\circ$  both eyes are in the shade. Random movements occurring here might or might not bring the animal around so that one eye was again illuminated, and so bring about a reorientation—these certainly occur in a certain percentage of the cases. Because of this anatomical peculiarity, the strength of illumination required to elicit a maximal response need only be that which will produce enough photochemical product in the time of reaction to turn the animal until both eyes are in the shade in the radial distance of 10 cm.

*3. Responses to Dim Light.*—If the illumination is reduced sufficiently, it is clear that a critical point should be reached below which there

is not enough photochemical effect to turn the animal through the maximal angle in the radial distance of 10 cm. The distributions of

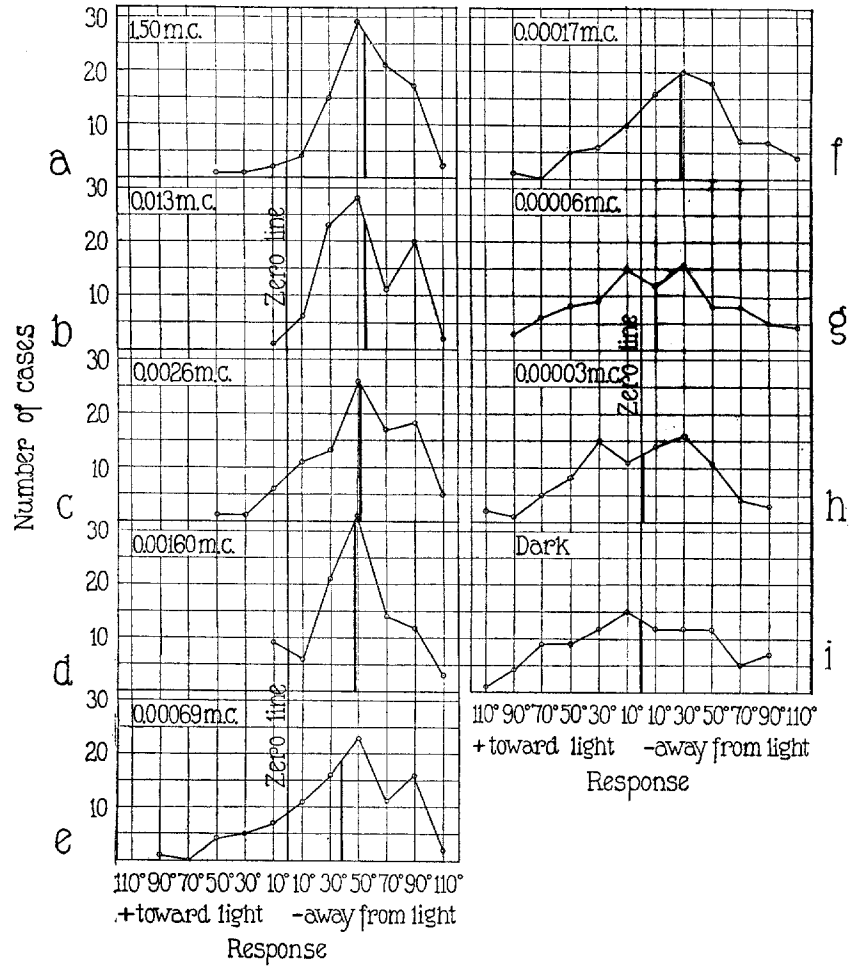


FIG. 2. Distributions of about 100 responses each of *Oniscus asellus* to light of various intensities. Responses measured as angular deflection of path from zero line, along which animals were headed. Heavy line is arithmetic mean of each distribution.

responses in illuminations below this value would be chance distributions, still skewed, with the mean at a point which would be deter-



mined by the photochemical effect of the given intensity of illumination. At these low intensities the deviations which arise from obscure causes will not be heavily overbalanced, and as a result care must be taken that they are not influenced in any regular way, such as failing to have the animal face along the zero line. The luminous material necessitated by these low intensities was used at the higher ones so that the results might be comparable.

The critical intensity was found to be somewhere in the region of 0.0026 m.c. At this intensity and above, the mean response is close to 55°. Below this value, as shown by Fig. 2, *d* to *h*, the distribution

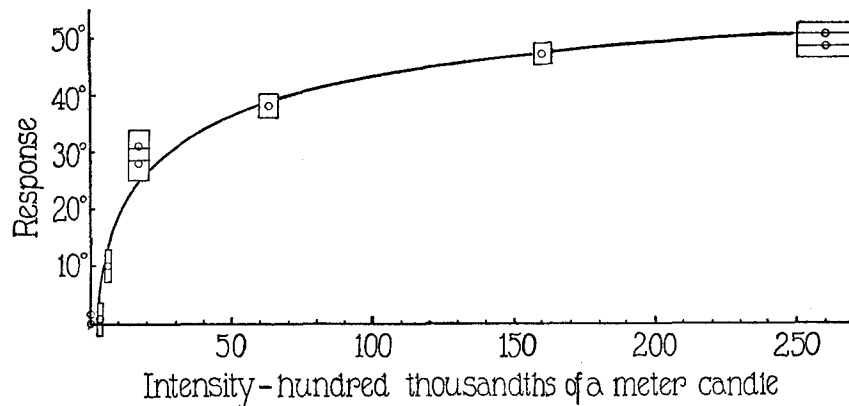


FIG. 3. Average response (angular deflection—means of Fig. 2) of *Oniscus asellus* to various intensities of light. Each point the average of about 100 separate responses. Rectangle surrounding each point indicates extent of probable error of both mean response and measurement of intensity.

flattens out and the mean approaches 0°. At the intensity below which the light produces no measurable results, the distribution is purely chance, like that of responses in darkness (Fig. 2, *i*). This threshold is about 0.00003 m.c.

Whether or not the mean responses at various intensities may be dealt with quantitatively is open to question. If the effective photochemical substance is formed in the period before locomotion starts, and its quantity little affected by changes of illumination (which would probably be rather slight due to the shortness of the period of turning and the marked convexity of the eye), then every degree

of turning would be an equal measure of the effectiveness of the light, whether it be a degree close to the zero line or not. A comparison is made on this assumption, using the mean response as a measure of the reaction of the animal.

If the average responses to the lower intensities are plotted against their respective intensities, the curve shown in Fig. 3 is obtained. The nature of this curve is indicated by Fig. 4, in which the average response is plotted against the logarithm of the respective intensity. Between the threshold and the critical value for maximal response the points lie fairly close to the line drawn through them. The equation of this line is  $R = k \cdot \log I - K$ , in which  $k = 27$  and  $K = 10.8$  ( $I$  in hundred thousandths m.c.).

TABLE I.

Responses of *Oniscus asellus* to light of various intensities. Response measured by average angular deflection (in radial distance of 10 cm.) from direction headed, under lateral illumination. Each the average of about 100 separate responses (ten individuals). Calculated response given by the equation  $R = k \cdot \log I - K$ ,  $k = 27$ ,  $K = 10.8$ ,  $I =$  intensity of illumination in hundred thousandths of a meter candle.

Intensity of illumination. $I$	Error of measurement. $\pm$	Average response. $R$ (observed)	Probable error of mean. $E_m \pm$	Calculated response. $R$ (calc.)
<i>meter candles</i>	<i>meter candles</i>			
1.50	0.01	{ 55.0° 52.4°*	2°	(55°)
0.013	0.001	54.4°	2°	(55°)
0.0026	0.0001	{ 51.2° 48.6°*	2°	54.5°
0.00160	0.00003	47.3°	2°	48.6°
0.00069	0.00003	38.1°	2°	38.9°
0.00017	0.00003	{ 30.4° 27.7°*	3°	22.4°
0.00006	0.00001	10.0°	3°	10.3°
0.00003	0.00001	1.1°*	3°	2.2°
Dark		{ 1.9° 0.0°*	3°	(0°)

\* Check experiments carried out under carefully controlled voltage of lamp. Time measurements mentioned in text (below) made for these.

Table I gives the average responses of *Oniscus* to the various intensities tried, and also the calculated values of the responses in the range between the threshold and the critical value for maximal response, on the basis of the above equation.

The photokinetic effect is probably quite small, and the factors concerned with the time of response are probably other than light. The actual time required for the entire response from the time of lifting the frame until the animal crossed the circumference was measured by a stop-watch for the entire range of intensity, including darkness. The average was found to vary independently of the intensity between 22.0 and 32.7 seconds—differences scarcely significant. The individual time of each response was correlated with

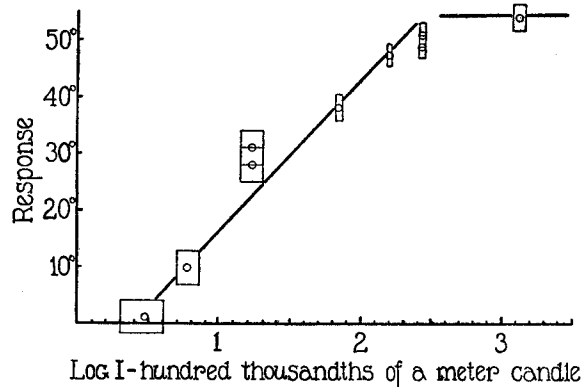


FIG. 4. Response of *Oniscus* plotted against logarithm of intensity.

the magnitude of turning, for each intensity, and the coefficient of correlation was found to vary between  $+0.17$  and  $-0.10$  ( $\pm 0.07$ ), indicating clearly that there is no relation between time taken to make a response and amount of angular deflection.

#### DISCUSSION.

The constant maximal response which these forms make to light above a certain critical intensity can be accounted for on purely anatomical grounds, being determined by the convexity of the carapace and the position of the eyes. The specific differences among the isopods can be explained on these grounds, *Porcellio* being more variable

and having a slightly more convex carapace, *Armadillidium* having a considerably more convex thorax.

Below this critical intensity the responses fall off regularly with decrease in intensity. Variations which are caused by obscure processes due to uncontrollable stimuli—"random movements"—are here no longer masked by the light reaction, but are still affected so that the distribution is skewed. The mean response will then be determined by the light, in accordance with the muscle tonus theory of Loeb. According to this theory, the amount of turning is determined by the difference in tonus of body muscles on opposite sides of the body, and this difference is in turn due to a difference in the amount of photochemical product in the two receptors. This amount is determined according to the laws of photochemistry. These experiments seem to show the relation between certain photochemical laws and the phototropism of animals.

Weber's law states that the amount of sensation necessary to produce a barely noticeable difference from a former sensation is a constant fraction of the intensity of the stimulus producing the first sensation. Fechner has expressed this in the form of an equation

$$dS = c \cdot \frac{dI}{I},$$

in which  $S$  is the magnitude of the sensation,  $I$ , the

intensity of the stimulus producing the sensation, and  $c$ , a constant. Integrating,  $S = c \cdot \log_e I + K$  (see Moore and Cole, 1920-21).

The results of my experiments seem to indicate that the phototropic responses studied follow at least this form. This is not at all singular, since Moore and Cole (1920-21) found that the beetle, *Popillia*, follows this relation, and Cole (1922-23) found that the ratio of circle diameters of the movements of asymmetric *Limulus* is proportional to the logarithm of the intensity of illumination—the higher the intensity the smaller the circles. Moreover, this same kind of a response takes the logarithmic form in the whip-tail scorpion (Patten, 1917). I have replotted Patten's data, putting response (angular deflection) against logarithm of intensity, and find that the points lie roughly on a straight line, indicating that *Mastigoproctus* also follows this form.

The similarity between Cole's results for *Limulus* (1922-23) and mine for *Oniscus* indicates that the amount of turning in *Oniscus* is a

measure of exactly the same thing as the circle diameters of *Limulus* and that the negative response is in reality an arc of a limited circus movement.

Hecht (1919-20), has pointed out that a logarithmic relation may be merely a coincidence with the Weber-Fechner law, and that the real basis is probably a photochemical one. He has found the reactions of *Mya* to be definitely of a photochemical nature, and explains

them on the basis of the reaction  $S \xrightleftharpoons[\text{dark}]{\text{light}} P + A$ , in which  $S$  is the

amount of photosensitive substance present, and  $P$  is the photochemical product with its accessory  $A$ . The photochemical effect is produced by  $P$  and  $A$  (through a simple reaction which they catalyze), and is proportional to the logarithm of the intensity and the time,  $E = k \cdot t \cdot \log I$  (Hecht, 1920-21). Weigert (1911) states that the amount of blackening,  $S$ , of a photographic plate in a given time is  $S = k \cdot \log I$ . Hecht has pointed out the similarity of the two, indicating the basic photochemical nature of the responses of *Mya*.

My results with *Oniscus*, as far as they go, indicate that this same general relation holds when the photochemical effect is measured by the phototropic response. Here the actual length of time during which the light is acting is about the same, and the amount of photochemical product formed in this time is dependent upon the intensity of the light and determines the amount of turning, in accordance with Loeb's theory.

Hecht (1922-23) has pointed out that the amount of freshly formed photochemical product in excess of the amount already present in sensory adaptation is what determines the muscular response, rather than a ratio between the two. This is also found to apply to a tropic response. The amount of product present in the shaded eye of *Oniscus* (if completely dark adapted) would be zero. The amount in the illuminated eye is the photochemical effect,  $E$ , and is determined according to the equation  $E = k \cdot t \cdot \log I$  ( $t$  is constant). The ratio  $E : 0$  is indeterminate, but the *excess* of the amount in the illuminated eye over that in the shaded eye is  $E$ , and is determined by the above equation, as indicated by results with *Limulus*, *Mastigoproctus*, and *Oniscus*. This is further borne out by the work of Patten (1915) on blowfly larva. The orientation of these animals subjected

to opposed beams of light was found to be dependent only upon the ratio of the intensities on the two sides. The photochemical treatment of these data is significant. Let  $I_1$  be the intensity of the light shining on one side, and  $I_2$  the intensity on the other. Then the photochemical effects in the two receptors will, according to the above equation, be

$$E_1 = k \cdot t \cdot \log I_1$$

and

$$E_2 = k \cdot t \cdot \log I_2$$

in which  $E_1$  and  $E_2$  are respective photochemical effects. If the tendency to turn ( $R$ ) is determined by the difference in photochemical effect in the two receptors, this will be

$$R = E_1 - E_2 = k \cdot t \cdot (\log I_1 - \log I_2),$$

or

$$R = k \cdot t \cdot \log \frac{I_1}{I_2}$$

This means that the photochemical effect is proportional to the logarithm of the *ratio* of the two intensities, regardless of their absolute values. The tendency to turn on account of the resulting muscle tonus will therefore be the same as long as the ratio of the intensities is the same. As the animal turns, the effective intensity—which is the intensity of the beam at that point times the cosine of the angle made by the norm of the surface and the ray of light—is changed until it is equal on both sides, and  $I_1 = I_2$ , whence  $\frac{I_1}{I_2} = 1$ , and  $\log \frac{I_1}{I_2} = 0$ , and so  $E_1 - E_2 = 0$ , and the animal is oriented.

Similar reasoning could be applied to the experiments of Northrop and Loeb (1922–23) on *Limulus*, if the orientation were to result regardless of the absolute value of the intensity, since in this material the validity of the equation  $E = k \cdot \log I$  has been proven by Cole (1922–23).<sup>1</sup>

<sup>1</sup> Rough experiments performed by H. S. Mayerson and myself at Woods Hole, Massachusetts corroborated Northrop and Loeb's findings, and indicated that the orientation is actually determined by the ratio of the lights, regardless of their absolute intensities.

These results and considerations throw some light on the photochemical basis of phototropism, since they link up Hecht's work on *Mya* with a phototropic response. This can best be understood on the assumption that muscular contraction determining the tropism is proportional to the amount of photochemical product formed in the illuminated photoreceptor, which in turn is determined by the intensity of illumination on the receptor in accordance with laws governing a photochemical process such as the reduction of silver salt on a photographic plate. There can, therefore, be hardly any other conclusion but that, as Loeb originally pointed out, phototropism is the result of a difference in tonic contraction of opposing muscles determined in a purely photochemical way by the excess of decomposed photosensitive substance in one photoreceptor.

#### SUMMARY.

1. The negative phototropism of certain land isopods was investigated over a large range of intensities, especially low ones. The responses were determined quantitatively by measuring the angle through which an animal turned away from a line perpendicular to the rays of light.

2. In the absence of light the undirected movements set up by obscure stimuli were such as to compensate each other statistically, the average path being a movement in the direction in which the animal was headed.

3. Over a large range of intensities (0.0026 m.c. up) the average turning is maximal, about  $55^\circ$  (*Oniscus*). This maximal response is due to an anatomical peculiarity, in that the carapace cuts off the light on the eye after the animal has turned  $50-60^\circ$ . This peculiarity probably accounts for specific differences among land isopods. Any light, therefore, which is strong enough to turn an animal through this maximal angle in a radial distance of 10 cm. will give results whose mean will be maximal.

4. Below 0.0026 m.c. the amount of angular deflection becomes less and less, in proportion to the logarithm of the intensity, until at 0.00003 m.c. the movements are the same as in darkness.

5. This proportionality between amount of turning and the logarithm of the intensity indicates the photochemical nature of phototropism

on the basis of Hecht's work with *Mya*. As a result, Loeb's theory of phototropism may then be stated in the mathematical form

$$R = E_1 - E_2 = \log \frac{I_1}{I_2}$$

in which  $I_1$  and  $I_2$  are the two intensities,  $E_1$  and  $E_2$ , their respective effects, and  $R$ , the muscular action set up by the difference in photochemical effect on the two sides.

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