

## THE PHOTOCHEMICAL BASIS OF ANIMAL HELIOTROPISM.

BY JOHN H. NORTHROP AND JACQUES LOEB.

(From the Laboratories of The Rockefeller Institute for Medical Research.)

(Received for publication, February 15, 1923.)

### I.

One of us published in 1888 a preliminary notice,<sup>1</sup> followed by a monograph in 1889,<sup>2</sup> in which it was shown by experiments chiefly on insects that the motion of animals to a source of light is not due to an attraction of the animals by the light, but is due to an automatic orientation of the animal by the light, as a consequence of which the animal is forced to move to the source of light. It was shown that if there is only one source of light, certain animals are automatically oriented by the light in such a way that their heads are turned towards the source of light and that their planes of symmetry are turned into the direction of the rays of light. In that case, the animal is automatically compelled to move to the source of light.

The action of light was ascribed by Loeb to a chemical effect on the retinae or some sensitive spots of the skin. If there is only one source of light, and the plane of symmetry of the animal goes through the source of light, the symmetrical eyes (or the symmetrical photosensitive elements of the skin) are struck by the light at the same angle, and the intensity of illumination is the same for symmetrical elements. When, however, symmetrical elements of the eyes (or skin) of the animal are no longer struck at the same angle by the source of light, *e.g.* when the animal is illuminated sidewise, the intensity of illumination by the source of light is no longer the same for the symmetrical retinae or other symmetrical photosensitive elements, and the animal is automatically compelled to change the direction of its motion in such a way that its plane of symmetry is again brought

<sup>1</sup> Loeb, J., *Sitzungsber. phys.-med. Ges. zu Würzburg*, 1888.

<sup>2</sup> Loeb, J., *Der Heliotropismus der Tiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen*, Würzburg, 1889.

into the direction of the rays of light. As soon as this happens, the animal will be compelled again to move in a straight line towards the source of light. This was explained by Loeb in the following way. The tension of the symmetrical muscles of the locomotor organs is influenced by the light in a similar way to that in which it is influenced by the action of gravity on the internal ear in the higher animals. As long as the rate of photochemical change in symmetrical parts of the photosensitive organs is the same, the tension of symmetrical muscles in the locomotor organs—legs, wings, or swimmerets—will be affected in the same way and the animal will continue to move in a straight a line as the imperfections of its locomotor apparatus permit. When, however, the rate of photochemical change is no longer the same in symmetrical elements of the eye or skin, the tension of the symmetrical muscles of the locomotor apparatus will no longer be the same and the direction of the motion of the animal will be automatically changed. This change may either bring the head towards the source of light or away from the source of light. When the head is automatically turned towards the source of light, we speak of positive heliotropism, and when the head is turned automatically away from the light, we speak of negative heliotropism. As soon as the plane of symmetry falls again into the direction of the rays of light, the symmetrical muscles again assume the same tension and the animal is automatically forced to move in a straight line either towards or away from the source of light. What appeared to the earlier investigators as a mysterious attraction of the animals by the light (in the case of positively heliotropic animals) or as a mysterious flight from the light (in the case of negatively heliotropic animals) thus turned out to have been only a case of automatic orientation of the animal due to a photochemical effect on the retina or other photosensitive elements of the surface of the animal. The phenomenon was thus amenable to a purely physicochemical analysis, according to the principles of photochemistry.

## II.

In an address delivered in 1911, Loeb suggested that the physicochemical law determining these automatic heliotropic reactions of animals was Bunsen and Roscoe's photochemical law, whereby the

photochemical effect,  $E$ , is proportional to the product of the intensity,  $I$ , into the duration,  $t$ , of illumination.

$$E = K \cdot I \times t$$

where  $K$  is a constant.<sup>3</sup> The idea was tested and confirmed in his laboratory by Ewald<sup>4</sup> on the heliotropic orientation of *Daphnia*, by Loeb and Ewald,<sup>5</sup> by Loeb and Wasteneys<sup>6</sup> on the heliotropic curvature of *Eudendrium*, by Loeb and Northrop<sup>7</sup> on the larvæ of *Balanus*, and by Patten,<sup>8</sup> in Parker's laboratory, on the heliotropic orientation of the larvæ of the blowfly.<sup>9</sup> It is intended to show in this paper that the law holds also for the orientation of the horseshoe crab (*Limulus*).

Young specimens of the horseshoe crab about 15 cm. in length were used. In each experiment one specimen was put into a square aquarium with straight glass walls (Fig. 1), and its orientation under the simultaneous influence of two lights,  $a$  and  $b$ , was ascertained. In order to permit the exact measurement of the orientation of the animal with respect to the lights, it was necessary to limit the extent of motion of the animal, without limiting its freedom of assuming a definite orientation with regard to the two lights. For this purpose the tail of the animal was fastened with the loop of a short cotton thread to a nail fixed in the bottom of the aquarium so that the animal could turn without friction in any direction without being able to move beyond the distance of the length of the thread from the nail. Loeb had found that the larvæ of *Limulus* are positively heliotropic in cold, and negatively heliotropic in warmer water.<sup>10</sup> This seems to be the case for these older specimens too, which were mostly negative at room temperature, though not all the specimens reacted to light. A small number, ten out of forty-eight specimens, could be used for the tests to be described. That not all reacted may or may not have been due

<sup>3</sup> Loeb, J., *The mechanistic conception of life*, Chicago, 1912.

<sup>4</sup> Ewald, W. F., *Science*, 1913, xxxviii, 236; *Z. Sinnesphysiol.*, 1914, xlviii, 285.

<sup>5</sup> Loeb, J., and Ewald, W. F., *Zentr. Physiol.*, 1913-14, xxvii, 1165.

<sup>6</sup> Loeb, J., and Wasteneys, H., *J. Exp. Zool.*, 1917, xxii, 187.

<sup>7</sup> Loeb, J., and Northrop, J. H., *Proc. Nat. Acad. Sc.*, 1917, iii, 539.

<sup>8</sup> Patten, B. M., *J. Exp. Zool.*, 1914, xvii, 213.

<sup>9</sup> All the work on Loeb's theory of tropisms is discussed in his book, *Forced movements, tropisms, and animal conduct*, Philadelphia and London, 1918.

<sup>10</sup> Loeb, J., *Arch. ges. Physiol.*, 1893, liv, 81.

to their exhausted condition, since they had been kept in the laboratory under unfavorable conditions.

Two Mazda incandescent lamps of equal intensity (determined with the Lummer-Brodhun photometer) were used. They were placed as indicated in Fig. 1. In order to allow the exact measurement of the

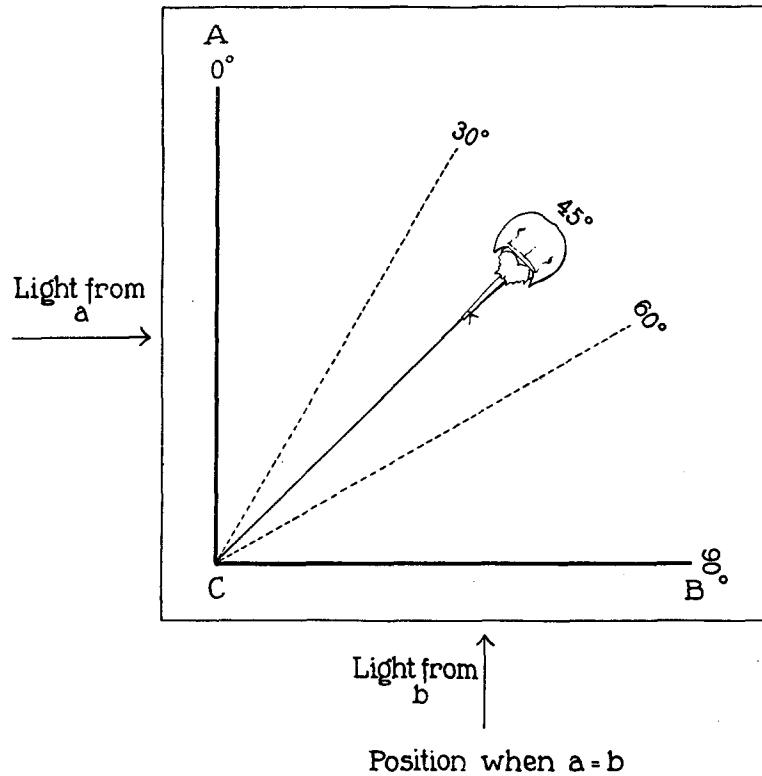


FIG. 1. Orientation of the negatively heliotropic crab with respect to two lights, *a* and *b*, when the intensity of the two lights is equal.

orientation of the plane of symmetry of the animal with respect to the two lights, a quadrant, with the nail as center, marked on the bottom of the aquarium, was divided into sectors of 5° each, the zero line being parallel to one illuminated side of the aquarium, the 90° line to the other illuminated side (Figs. 1 and 2).

When only one light was used, *e.g.* light *a*, the negatively heliotropic animal oriented itself in the path of the light, namely the line CB ( $90^\circ$ ), with its tail toward the light; when only light *b* was turned on, the animal came into the stationary position of  $0^\circ$ . In each case the animal put its plane of symmetry into the direction of the rays of

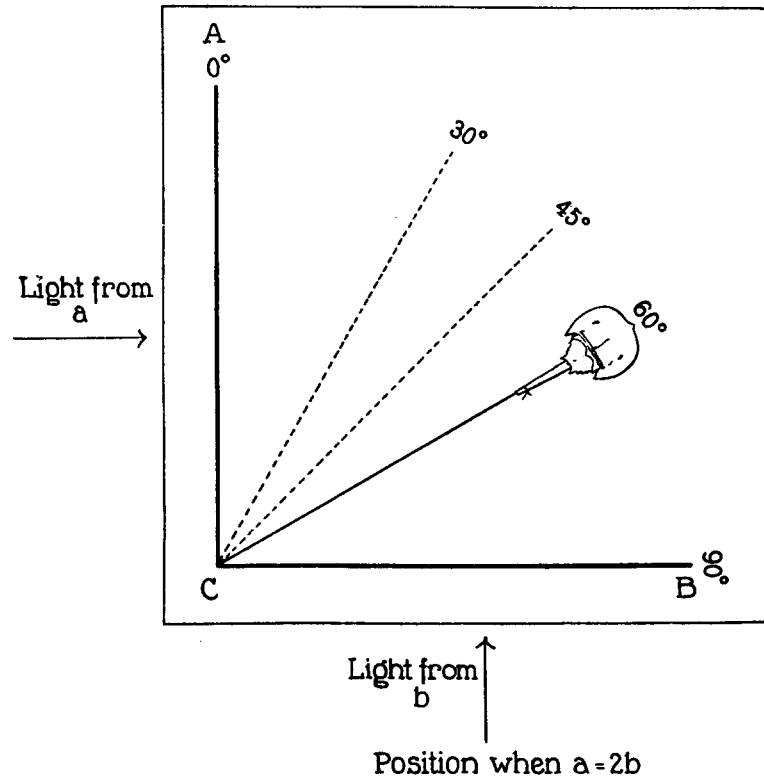


FIG. 2. Orientation of the negatively heliotropic crab with respect to two lights, *a* and *b*, when the intensity of *a* is twice as great as the intensity of *b*.

light. When both lights were turned on simultaneously and when the intensity of the two lights was equal, the plane of symmetry of the animal coincided with the angle of deflection of  $45^\circ$  from the line AC (Fig. 1). During the whole time the animal made active swimming motions, trying to escape, and these motions kept it in the stationary position of about  $45^\circ$ , as shown in Fig. 1.

In all the following experiments the intensity of light *a* remained stationary, namely 150 meter candles, while the intensity of light *b* was changed by increasing its distance from the aquarium.

When light *b* was put so far away from the aquarium that its intensity was only 75 meter candles, *i.e.* only half the intensity of *a*, the orientation of the animal was different. It put itself into the position indicated in Fig. 2, so that its plane of symmetry formed no longer an angle of  $45^\circ$  but on the average one of about  $60^\circ$  with AC. This was presumably the angle at which the intensity of illumination of the left and right retinae was equal according to the cosine law to be discussed later.

When the intensity of light *b* was reduced to 37.5 meter candles, while that of light *a* remained constant (namely 150 meter candles), the animal oriented itself in such a way that its plane of symmetry formed on the average an angle of about  $68^\circ$  with the line CA.

### III.

In the experiments thus far mentioned only the intensity of illumination of the two lights *a* and *b* varied, while the duration of illumination was the same for both lights. The duration of illumination of the animal by light *b* can be reduced by putting a rapidly rotating opaque disc (made of thick cardboard), with one sector cut out, between the light and the aquarium.<sup>11</sup> If a sector of  $180^\circ$  is cut out from the rotating disc, light from *b* will reach the animal only during each half period of rotation of the disc, and the duration of illumination of the animal by this light will be reduced to one-half. If a sector of  $90^\circ$  is cut out from this opaque disc and put between light *b* and the animal, the duration of illumination of the animal by light *b* is reduced to one-fourth. Now if the general law of photochemistry, namely the Bunsen-Roscoe law, determines the heliotropic orientation of the animal, the animal should always put its plane of symmetry into the line bisecting the angle ACB, whenever the product of intensity into duration of illumination is the same for the two lights *a* and *b*.

<sup>11</sup> This method of varying the duration of illumination had been used by Ewald, Patten, and Loeb and Northrop in the papers referred to.

In all the following experiments the intensity of light  $a$  was kept constant, namely 150 meter candles, while the intensity and duration of illumination of  $b$  were changed.

When the intensity of light  $b$  was increased to 300 meter candles, while the intensity of light  $a$  remained 150 meter candles, it was found that the animal put its plane of symmetry into the line  $45^\circ$  (Fig. 1), bisecting angle  $ACB$ , when the open sector of the rotating disc was  $180^\circ$ . In this case the duration of illumination by light  $b$  was cut into two, so that the product of duration into intensity of illumination was for light  $a$

$$150 \times t$$

and for light  $b$

$$300 \times \frac{t}{2} = 150 \times t$$

In other words, the orientation of the animal was determined by the Bunsen-Roscoe law. When the intensity of light  $b$  was raised to 600 meter candles, while light  $a$  remained 150 meter candles, it was found necessary to reduce the open sector of the rotating disc between light  $b$  and the animal to  $90^\circ$ , to force the animal to put itself in the position of Fig. 1, where its plane of symmetry bisected the angle  $ACB$ . In this case the product of duration into intensity of illumination was again the same for the two lights, namely for light  $a$

$$150 \times t$$

and for light  $b$

$$600 \times \frac{t}{4}$$

which again conforms with the Bunsen-Roscoe law.

#### IV.

We have seen that when no rotating disc is used, *i.e.* when the duration of illumination is the same for both lights, the animal puts its plane of symmetry into an average angle of about  $60^\circ$  with the line  $AC$  when the ratio of the intensity of  $a$  to  $b$  is as 2:1. Now the law of Bunsen and Roscoe demands that this orientation should always occur when the ratio, product of  $I \times t$  for light  $a$  over that of the

same product for light *b*, is as 2:1, regardless of whether the intensity alone or the duration alone or both are changed. This was found to be the case.

When the intensity of both lights was 150 meter candles, the duration of illumination of light *b* had to be cut exactly to one-half with the aid of the rotating disc to force the crab to put its plane of symmetry into the position shown in Fig. 2, where the plane of symmetry of the animal forms an angle of 60° with the line AC.

In another series of experiments the intensity of light *b* was increased to 300 meter candles, while that of light *a* remained 150 meter candles. In this case it was found necessary to cut down the time of illumination of light *b* to one-fourth (by using a rapidly rotating disc with a sector of 90° cut out) in order to compel the animal to put its median plane at an angle of 60° with the line AC. In both of these experiments the value of the illumination product,  $I \times t$ , for *a* and *b*, was as 2:1.

Finally it was possible to show that in order to compel the animal to put its plane of symmetry into a line forming an angle of about 68° with the line AC, it was necessary to make the value of the product  $I \times t$  for light *b* one-fourth of the value of the product  $I \times t$  for light *a*. Thus light *a* had the intensity of 150 meter candles and no disc was put before this light. When the light *b* had the intensity of 75 meter candles, the open sector of the rotating disc between light *b* and the animal had to be 180° in order to force its plane of symmetry into forming an angle of 68° with the line AC. In this case the ratio of the illumination products  $I \times t$  for the two lights *a* and *b* was

$$I_a \times t_a : I_b \times t_b = 150 \times 1 : 75 \times \frac{1}{2} = 4 : 1$$

When the intensity of light *b* was 150 meter candles, the open sector of the rotating disc had to be 90° to compel the animal to put its plane of symmetry into a line forming an angle of 68° with AC. In this case the ratio of illumination product for *a* and *b* was again 4:1.

$$I_a \times t_a : I_b \times t_b = 150 \times 1 : 150 \times \frac{1}{4} = 4 : 1$$

These results leave no doubt that the heliotropic orientation of the horseshoe crab is determined by a photochemical reaction which follows the law of Bunsen and Roscoe.



## V.

The results of our experiments are tabulated in Table I. For the explanation of this table the following data should be remembered. The intensity of light  $a$  ( $Ia$ ) was always constant, namely 150 meter candles, and so was the duration of illumination  $t$  of light  $a$ , which was 1, since no rotating disc was put in front of this light. The illumination product for light  $a$ ,  $Ia \times ta$ , was therefore always  $150 \times t$ . The intensity of light  $b$  ( $Ib$ ) varied, as the first vertical column of the table indicates, between 0 and 600 meter candles. The relative duration of illumination,  $tb$ , varied between 0.25 and 1.0. This time is the fraction of the period of rotation during which the light could reach the animal.

The third column of the table gives the illumination product for light  $b$ , namely  $Ib \times tb$ , and the fourth column gives the ratio of the illumination products of light  $b$  and light  $a$ , namely

$$\frac{Ib \times tb}{Ia \times ta}$$

The last vertical row of the table gives the average angle of the plane of symmetry of the animal with the line AC (Figs. 1 and 2).

The table shows that the value of this angle is the same for the same value of

$$\frac{Ib \times tb}{Ia \times ta}$$

In order to give the reader an idea of the individual variations, the value of the angle of orientation of the animal is given for each of the individual specimens of *Limulus* tried.

Ten individuals were found to orient themselves to the light, practically all being negatively heliotropic. Each animal is numbered and some animals were used repeatedly on different days; e.g., Animals 1, 6, and 9.

Each individual figure is the average of ten consecutive measurements taken within 1 minute. The animal made constant swimming motions but was prevented from making any progressive motion, being held by the thread attached to the nail (Figs. 1 and 2).

All the variations in intensity and duration of illumination of light  $b$  recorded in the vertical Column 1 were tried for each animal in rapid

succession. There were variations in the orientation of different individuals but these were chance variations which were equal and opposite for different individuals. The average angular deflection of the animal from the path of light *b* (the line AC) is given in the last vertical column of Table I.

TABLE I.

*Angular Deflection of Limulus from Path AC of Light b.*Intensity of light *a* constant = 150 meter candles.Duration of illumination by light *a* constant = 1.Intensity  $\times$  duration of light *a* constant = 150.Intensity and duration for light *b* variable.

<i>Ib</i>	<i>ib</i>	<i>Ibb</i>	Ratio $\frac{Ibb}{Iaa}$	7	5	2	3	4	1	1	6	6	12	9	9	9	18	Average angular deflection.	
meter candles																			
150	1.0	150	1.0	40	46.5	45	46	46.5	46	47	50	42	50	43	41	43	42	45.1	$\pm 0.6$
300	0.5	150	1.0	45	42		44	42.5	43	48	57	41	43	41	43	46	49	45.2	$\pm 0.8$
600	0.25	150	1.0	45	45	42	44	44.5	48	50	52	40	49	46	46	46	42	45.7	$\pm 1$
75	1.0	75	0.5	60	55	65	70	69	72	54	70	46	58	58	53	56	50	59.7	$\pm 2$
150	0.5	75	0.5	61	60	59	71	70	69	58	63	55	62	63	58	57	51	61.2	$\pm 2$
300	0.25	75	0.5	60	58		68	69	68	56	61	53	50	63	64	58	51	60.0	$\pm 2$
37.5	1.0	37.5	0.25	70	61	70	74	78	79	66	78	61	71	64	67	69	63	68	$\pm 2$
75	0.5	37.5	0.25	67	63		70	73	72	59	75	57	70	67	68	60	57	66	$\pm 2$
150	0.25	37.5	0.25	70	60	64	74		79	65	78	66	71	69	70	68	53	68	$\pm 2$
0	1.0	0	0	89.5	88	92	91	90	88	87	92	86	91	91	90	87		89.4	$\pm 0.6$

## VI.

An animal is therefore automatically oriented by the light in such a way that the illumination products  $I \times t$  are the same for the two eyes. When only one source of light exists, this is always the case when the plane of symmetry of the animal falls into the direction of the rays of light, *i.e.* goes through the source of light. When two lights of equal intensity act simultaneously on the animal, this happens when the plane of symmetry of the animal bisects the angle that its head (or rather that point of its head which we may assume to represent Hering's imaginary cyclopic eye, substituted for the retinae of the animal) forms with the two lights.

In both cases the symmetrical points of the eyes or skin of the animals are struck by the rays of light at the same angle. The importance of this angle was pointed out by Loeb in his first publications referred to above. The photochemical significance of this angle lies in the cosine law which states that the intensity of illumination of a surface element varies with the cosine of the angle of incidence of the light. If this angle be  $\alpha$ , then the expression for the orienting effect,  $E$ , of light becomes

$$E = K \cdot I \times t \times \cos \alpha$$

Now Loeb had also insisted on the fact that symmetrical elements of the eyes or of the photosensitive parts of the skin of the animal are not only equal morphologically but also chemically; *i.e.*, the same illumination will produce equal chemical effects on two symmetrical elements, but not, as a rule, on dissymmetrical elements. This explains why, when only one source of light exists, the animal is automatically oriented by the light in such a way that symmetrical elements of the retinae are struck by the light at the same angle,  $\alpha$ . In this case the rate of photochemical change in both eyes is the same when  $I$  and  $t$  are the same. The heliotropic orientation of animals by light is, therefore, such that the value of the product

$$I \times t \times \cos \alpha$$

is the same for both eyes (or any other symmetrical photosensitive elements of the animal).

It is obvious what must happen when the value of  $I \times t$  is no longer the same in both eyes. If  $\alpha$  remains the same for both eyes, the rate of photochemical change in the two retinae will be different when  $I \times t$  is different for the two eyes, and hence the symmetrical muscles of the locomotor organs will undergo a different degree of tension, a fact to which we shall return presently. If the value of  $I \times t$  is greater in the left than in the right eye (as in Fig. 2), the equality of photochemical effect in the two eyes can be restored only when the value of  $\cos \alpha$  becomes greater for the right eye ( $b$ ) than for the left eye ( $a$ ),  $\cos \alpha_b > \cos \alpha_a$  (Fig. 2), or, in other words, the animal will be automatically compelled to put its plane of symmetry into such a position that it forms a greater angle than  $45^\circ$  with the line AC which

is nearer the stronger light  $a$ . Through this change of position  $\alpha$  becomes smaller in the right than in the left eye and hence  $\cos \alpha$  becomes greater in the right than in the left eye. This is rendered evident in Diagram 3. It would be even possible to calculate beforehand the ratio of the two angles for each case if only the surfaces of the retinae were plane and parallel. According to Loeb's theory the animal must put its plane of symmetry into such a position that the product of

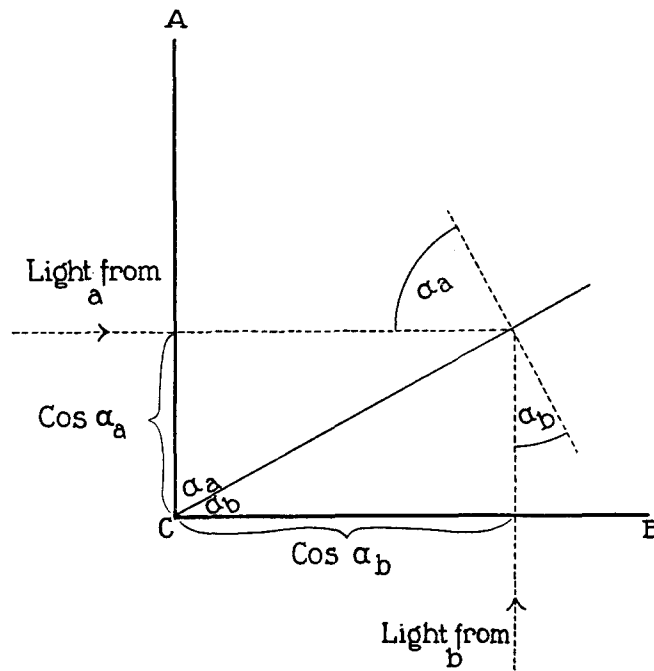


FIG. 3. Diagram illustrating the variations of the intensity of illumination with the cosine of the angle of incidence.

$I \times t \times \cos \alpha$  is the same for the two eyes. If now  $I \times t$  is twice as great for the left as for the right eye,

$$2 \times \cos \alpha_a \text{ (left eye) } = \cos \alpha_b \text{ (right eye)}$$

In other words, the cosine of the angle of incidence of light on the left retina,  $\cos \alpha_a$ , must be only one-half of the cosine of the angle of incidence in the right eye,  $\cos \alpha_b$ . The animal must change its position

in such a way that the angle of incidence,  $\alpha_a$ , for the stronger light on the left retina is greater than the angle of incidence,  $\alpha_b$ , for the weaker light on the right retina (Fig. 3), a result which is actually observed. On account of the curvature of the retinae of the horseshoe crab and on account of the fact that it possesses in addition to two lateral, also median eyes, it is impossible to test this postulate of Loeb's theory quantitatively for *Limulus*. Patten's<sup>8</sup> observations on the heliotropic orientation of the larvæ of the blowfly may be used as an approximate quantitative confirmation of this part of the theory. Qualitatively, however, the theory is supported by all the observations of the heliotropic reactions of animals.

## VII.

Finally the question arises as to why it happens that the animal is automatically oriented in such a way that  $I \times t \times \cos \alpha$  has the same value for the symmetrical eyes or the symmetrical elements of its photosensitive surface. The answer to this was given by Loeb by the suggestion that the products of decomposition of the photosensitive substance act on the sensory nerves connected with the eye and thereby influence the tension of the muscles. The connection between the rate of photochemical change and muscular reaction of the animal has been investigated by Hecht<sup>12</sup> from a physicochemical viewpoint in the case of reactions of *Mya* and *Ciona* to light, and he has been able to define the nature of the reaction. On the basis of his measurements it is safe to say that the rate of decomposition of a photosensitive substance in the eye or skin of an animal influences the tension of muscles. Now experiments on the influence of gravity on the ear of higher animals leave no doubt that the tension of the symmetrical groups of muscles which move the eyes or head and subsequently the whole body to the right or left is acted upon as a unit; and also that these two units are linked with the two symmetrical halves of the photosensitive or the geotropically sensitive elements of eyes or internal ear respectively. Experiments have shown that upon asymmetrical illumination animals are either compelled to move to that side where the product  $I \times t \times \cos \alpha$  is greater or where it is smaller;

<sup>12</sup> Hecht, S., *J. Gen. Physiol.*, 1919-20, ii, 229, 337; 1920-21, iii, 367, 375.

in the former case we speak of positively heliotropic animals, in the latter of negatively heliotropic animals. In the case of positively heliotropic animals the tension of muscles turning the head towards that source of light increases with the value of  $I \times t \times \cos \alpha$ , while in the case of negatively heliotropic animals the tension of the same muscles is lowered. The reason for this difference is not yet known. When the eyes of a positively heliotropic animal are struck asymmetrically by light the rudder action of the swimmerets, turning the head toward the source of light, will be stronger than that of their symmetrical antagonists, and the animal will automatically deviate towards the source of light until its plane of symmetry is again in such a position that the value of  $I \times t \times \cos \alpha$  is again the same for both eyes. In that case the influence of the light on symmetrical muscles is the same and the animal will continue to move in that direction. This part of Loeb's theory has been put to a test by a number of writers, among others Holmes,<sup>13</sup> Garrey,<sup>14</sup> Minnich,<sup>15</sup> and Cole,<sup>16</sup> and proved to be correct. Of the many experiments of these authors special attention may be called to the fact that when one eye is covered, the animal moves constantly in a circle around a source of light, the open eye facing the center of the circle when the animal is positively heliotropic. This is a consequence of the fact that in such a case the rudder action of the symmetrical organs of locomotion is no longer the same but is stronger in those muscles which turn the head of the animal towards the source of light. Moreover, it was shown by Garrey<sup>14</sup> and Cole<sup>16</sup> that the curvature of the circle in which such animals move becomes the greater the greater the intensity of light. Cole<sup>16</sup> has shown that the relation between intensity of light and curvature is logarithmic in agreement with the Weber-Fechner law. It follows further that the heliotropic orientation can only be expected in a moving animal, since when the animal rests there can only be a difference in the relative tension of symmetrical muscles. This may result in peculiar postures which have been observed by Garrey,<sup>14</sup> but it is not necessary that they should result in a definite orientation

<sup>13</sup> Holmes, S. J., *J. Comp. Neur. and Psych.*, 1910, xx, 145.

<sup>14</sup> Garrey, W. E., *J. Gen. Physiol.*, 1918-19, i, 101.

<sup>15</sup> Minnich, D. E., *J. Exp. Zool.*, 1919, xxix, 343.

<sup>16</sup> Cole, W. H., *J. Gen. Physiol.*, 1922-23, v, 417.

of the plane of symmetry with reference to the light. Thus heliotropic animals at rest may occupy any position with reference to the light, while when they move they will be automatically oriented on account of the rudder effect of the symmetrical legs or swimmerets of the animal.

Differences in the heliotropic sensitiveness of different animals will probably be found to depend upon the relative mass and nature of the photosensitive substance in their eyes or skin, in the relative quantity of decomposition products required to cause reflexly a change in the tension of their muscles, and in the nature of the nervous connection of the eyes with the symmetrical muscles of locomotion.

### VIII.

#### SUMMARY.

1. Experiments on the heliotropic orientation of *Limulus* were made which confirmed Loeb's photochemical theory of animal heliotropism proposed first in 1888 and 1889 in experiments on insects, and later in experiments on other forms of animals.

2. It is shown that these animals are oriented by light in such a way that the product

$$I \times t \times \cos \alpha$$

is the same for the symmetrical photosensitive elements of the eyes or the skin, where  $I$  is the intensity of the light,  $t$  the duration of illumination, and  $\alpha$  the angle of incidence of the light at the surface element of the photosensitive organ.

3. When this equation holds, the products of decomposition by light must be the same in symmetrical elements of the eyes or skin, and the influence of these products of decomposition on the tension of symmetrical muscles of the locomotor organs of the animal must be the same. As a consequence the animal must move in the path of light, either to or from the source of light.