THE REACTION OF CERIANTHUS TO TWO SOURCES
OF LIGHT.

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(Received for publication, January 19, 1924.)

When heliotropic animals are simultaneously exposed to two lights
of the same intensity the animals turn directly to neither light but
orient themselves so that their longitudinal axis is in a line which
bisects the angle between the two lights. If the lights are unequal in
intensity, negative animals deviate toward the weaker light, while
positive animals deviate toward the stronger light. The tropism
theory demands that when the animal comes to rest, the effective
illumination on the two sides of the animal shall be equal, since the
muscles on each side are then contracted to the same extent.¹

When the lights are unequal in intensity the physical intensity of the
lights may be equalized when the photosensitive areas of the animal
are inclined toward the lights at certain angles. The angle at which
equal illumination occurs, with two lights of a given difference in
intensity, varies with the angle at which the two beams of light cross
each other. For instance, equal illumination is possible for positive
animals when the beams cross each other at 90°, while at 180° equal
illumination is not possible as long as the animal deviates toward
the stronger of the two lights. The following summary may help
to make this relationship clear.

Conditions under Which Physical Illumination on Two Sides of
the Animal is Equal or Unequal.

1. Lights shining at 90°.—(A) When the lights are equal, equal
illumination is possible only at 45°, (whether the photosensory sur-
faces are parallel or non-parallel, the animal positive or negative).

¹Loeb, J., Forced movements, tropisms, and animal conduct, Monographs on

The Journal of General Physiology
(B) When the lights are unequal, equal illumination is possible only at certain angles physically determined by the ratio of the intensities (whether the photosensory surfaces are parallel or not, the animal positive or negative).

(C) Whether the lights are equal or unequal, the illumination is unequal at all other angles.

2. Lights shining at 180°.—(A) Equal illumination is possible:
   (a) At all angles when the lights are equal, the photosensory surfaces are parallel, the animal positive or negative.
   (b) At certain angles when the lights are unequal, the photosensory surfaces not parallel, and the animal is negative.

(B) Unequal illumination occurs:
   (a) At all angles when the lights are unequal, the photosensory surfaces are parallel, the animal positive or negative.
   (b) At all angles when the lights are unequal, the photosensory surfaces are not parallel, and the animal is positive.

The orientation of animals when subjected to two lights of varying intensities has been studied only in those cases in which there might occur equal illumination on the two sides of the animal. The angle of orientation for positive Balanus larvae has been determined by Loeb and Northrop, the two unequal lights shining at 90°. The same authors have measured the angle of orientation for negative Limulus, the lights again at 90°. Crozier found that in holothurians whose photosensitive areas are parallel, no orientation could be obtained when equal lights are opposed at 180°. When one light is much stronger than the other the animals turn away from the stronger light. Patten measured the angle of orientation for negative blow-fly larvae, the lights of varying intensities being reflected to shine at 180° across the larvae. In all these cases the animals might be considered to have taken such a position that the effective illumination was equal on their two sides. The case for the positive animal which orients when the two lights are opposed at 180° has not up to this time been considered.

It therefore seemed of interest to study the positions assumed by a positive animal such as Cerianthus, since it is evident that equal external illumination on two sides of the animal is impossible as long as the lights are unequal and the animal is positive. As has been stated in a former paper, if this animal is illuminated from one side only, it turns the oral end toward the light. The angle turned which in this case I have not yet determined quantitatively, depends in some way upon the intensity of the illumination. At weak intensities if no turning occurs within about 20 seconds the animal never reacts to the light at all. If after an interval in the dark the animal is again tested with a light of stronger intensity, the head turns part way. Only with relatively strong lights did the head region turn through the whole 90° toward the light. In the experiments with two lights, these effective intensities were used, and not the weaker lights. If Cerianthus is allowed to remain in the dark the oral end tends to lie in the same straight line as the tail. This is then the normal position of the body of the animal. If, however, two lights of equal intensity shine across the animal, the oral end takes up such a position that it lies perpendicular to the line connecting the two lights. This position is held, whether the tail of the animal be bent toward the left or right, and it may be called the neutral position. When the lights are turned on, the immediate effect upon the animal is an increase in the muscle tone, so that the oral disk is not so far extended from the tube as in the dark. Three animals, one much larger than the other two, and all living in glass tubes, were used to find the relation between the angle turned and the ratio of the intensities of the two lights.

The experiment is as follows (Fig. 1): The animal is placed in a rectangular glass dish $OM$ filled with fresh sea water. On the table under the dish is put a piece of white paper with a line $PQ$ ruled on it in pencil. The animal is placed so that its longitudinal axis is parallel to this line, and then allowed to remain in the dark room for 1 hour. The two lights, $A$ and $B$, are arranged on opposite sides of the dish so that their beams fall in a straight line across the animal's end. The intensity of one light $(A)$ is kept constant at 6,800 meter

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candles, while the other \((B)\) is varied by increasing its distance from the animal so that the ratio is successively equal to 1, 2, 4, and \(a\), that is, extinction of the weaker light. After the lights are turned on, the animal moves from the neutral position to another position

\[\text{FIG. 1. Position assumed by Cerianthus when acted upon by two lights of unequal intensity, the rays of light falling on the animal at right angles to the longitudinal axis of the body. OM is the aquarium, PQ the longitudinal axis of the body, A and B are lights in which the intensity of A is four times the intensity of B. a is the angle which the head of Cerianthus at equilibrium makes with the axis PQ.}\]

which it maintains as long as the lights shine upon it in the same ratio. Now while the animal is in this position another line, \(QM\), is drawn parallel to the side of the anterior end of the animal, \textit{i.e.}, the longitudinal axis of the head. The angle turned is found by projecting this line to the axis \(PQ\) to intersect at \(Q\). The individual
variation on different days was very slight occasioning an error not greater than that involved in determining the angle. Between readings 1 hour was allowed for dark adaptation.

The experiments showed that if the two lights are of equal intensity, the oral disk is extended at right angles to the line connecting the lights. But if one light is twice as strong as the other, the oral disk moves approximately 27° toward the stronger light, while if one light is four times as strong as the other, the angle is approximately 43°. If only one light is used and that one of sufficient intensity, the animal turns through the whole 90° toward the light. This

<table>
<thead>
<tr>
<th>Ratio</th>
<th>( \log_{10} \frac{I_2}{I_1} )</th>
<th>( a ) (observed)</th>
<th>( a ) (calculated, ( K = 0.615 ))</th>
<th>( \tan a )</th>
<th>( K )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1:1</td>
<td>0</td>
<td>0°</td>
<td>0°</td>
<td>0</td>
<td>0.59</td>
</tr>
<tr>
<td>2:1</td>
<td>0.3</td>
<td>27°</td>
<td>26°</td>
<td>0.5095</td>
<td>0.59</td>
</tr>
<tr>
<td>4:1</td>
<td>0.6</td>
<td>43°</td>
<td>44°</td>
<td>0.9325</td>
<td>0.64</td>
</tr>
<tr>
<td>4:0</td>
<td>( \alpha )</td>
<td>90°</td>
<td>90°</td>
<td>( \alpha )</td>
<td></td>
</tr>
</tbody>
</table>

relation may be expressed mathematically by the following equation

\[
\log_{10} \frac{I_2}{I_1} = K \tan a,
\]

if \( \frac{I_2}{I_1} \) is the ratio between the two lights, \( a \) is the angle turned from the neutral position, and \( K \) is a constant. It is obvious that the tangent of the angle is directly proportional to the logarithm of the ratio between the two lights (Table 1).

This equation not only expresses the relation between the angle turned from the neutral position and the relative intensities of the two lights in the case of *Cerianthus*, but also expresses this relation as shown by the data published by Patten for blow-fly larvae, by Loeb and Northrop for *Balanus* larvae, and by Northrop and Loeb for *Limulus* (Tables II, III, and IV). Cole has shown that when

\[7\]

Limulus is acted upon by one light the logarithmic relation holds namely, $E = K \log I$, in which $E$ is the photochemical effect, $I$ is intensity, and $K$ is a constant. Assuming that the effect on each side of the Limulus is proportional to the log $I$ on that side, then

$$E_1 = K_1 \log I_1$$
$$E_2 = K_2 \log I_2$$

Then,

$$\frac{E_1}{K_1} = \log I_1$$
$$\frac{E_2}{K_2} = \log I_2$$

Subtracting,

$$\frac{E_2 - E_1}{K_1 - K_2} = \log \frac{I_2}{I_1}$$

From the experiments of Northrop and Loeb, it can be shown (Table II) that in Limulus the ratio $\frac{E_2K_1 - E_1K_2}{K_1K_2}$ is equal to $K \tan a$, $a$ being the angle turned from the neutral position. It may be pointed out that in all the cases where the angles of orientation have been measured when animals were acted upon by two sources of light, the animals did not orient themselves at angles such that equal physical illumination occurred on the two sides. Northrop and Loeb supposed that in Limulus the photosensory surfaces are

8 Hartline, H. K., *J. Gen. Physiol.*, 1923–24, vi, 137.
9 Since this paper was presented for publication Hartline has published some data on the reactions of certain isopods to one source of light which support this assumption. He also has derived an equation, $R = k \cdot \log \frac{I_2}{I_1}$ in which $R$ is the “tendency to turn.” As the author states, this equation holds for equal effective intensities. However, the left-hand member, $R$, if measured by the number of degrees turned and divided by $\log \frac{I_2}{I_1}$ does not give a constant. It therefore appears that the accurate expression for the “tendency to turn” is “$\tan a$.”
### TABLE II.
Calculation Showing That the Orientation of Limulus When Illuminated by Two Lights Follows the Same Rule as Cerianthus.

<table>
<thead>
<tr>
<th>Ratio: $I_2/I_1$</th>
<th>Log $I_2/I_1$</th>
<th>Observed angle.</th>
<th>$\theta =$ angle turned from neutral position</th>
<th>Tan $\theta$.</th>
<th>$\log \frac{I_2}{I_1} - K$.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1:1</td>
<td>0</td>
<td>45.5°</td>
<td>0°</td>
<td>0</td>
<td>1.31</td>
</tr>
<tr>
<td>2:1</td>
<td>0.3</td>
<td>60.2°</td>
<td>14.7°</td>
<td>0.2617</td>
<td>1.14</td>
</tr>
<tr>
<td>4:1</td>
<td>0.6</td>
<td>67.3°</td>
<td>21.8°</td>
<td>0.4006</td>
<td>1.49</td>
</tr>
<tr>
<td>4:0</td>
<td>$\alpha$</td>
<td>89.4°</td>
<td>43.9°</td>
<td>0.9629</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.31</td>
</tr>
</tbody>
</table>

Northrop and Loeb, *Limulus*.

### TABLE III.
Calculation Showing That Balanus Larvae Follow the Same Rule as Cerianthus.

<table>
<thead>
<tr>
<th>Ratio: $I_2/I_1$</th>
<th>Log $I_2/I_1$</th>
<th>Observed angle.</th>
<th>$\theta =$ angle turned from neutral position</th>
<th>Tan $\theta$.</th>
<th>$\log \frac{I_2}{I_1} - K$.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1:1</td>
<td>0</td>
<td>45.6°</td>
<td>0°</td>
<td>0</td>
<td>3.15</td>
</tr>
<tr>
<td>2:1</td>
<td>0.3</td>
<td>40°</td>
<td>5.6°</td>
<td>0.096</td>
<td>3.12</td>
</tr>
<tr>
<td>4:1</td>
<td>0.6</td>
<td>34.4°</td>
<td>11.2°</td>
<td>0.197</td>
<td>3.04</td>
</tr>
<tr>
<td>10:1</td>
<td>1.0</td>
<td>28.8°</td>
<td>16.8°</td>
<td>0.302</td>
<td>3.31</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.15</td>
</tr>
</tbody>
</table>

Loeb and Northrop, *Balanus* larvae.

### TABLE IV.
Calculation Showing That the Same Rule Applies to the Negative Blow-Fly Larvae.

<table>
<thead>
<tr>
<th>Percentage difference between the two lights</th>
<th>Ratio: $I_2/I_1$</th>
<th>Log $I_2/I_1$</th>
<th>$\theta =$ average angular deflection toward weaker light.</th>
<th>Tan $\theta$.</th>
<th>$\log \frac{I_2}{I_1} - K$.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>12:12 = 1.0</td>
<td>0.0</td>
<td>0.09°</td>
<td>0.001</td>
<td>(Indeterminate.)</td>
</tr>
<tr>
<td>$\frac{8}{4}$</td>
<td>12:11 = 1.09</td>
<td>0.0374</td>
<td>2.77°</td>
<td>0.048</td>
<td>0.779</td>
</tr>
<tr>
<td>$\frac{10}{6}$</td>
<td>12:10 = 1.20</td>
<td>0.0792</td>
<td>5.75°</td>
<td>0.102</td>
<td>0.776</td>
</tr>
<tr>
<td>25</td>
<td>12:9 = 1.33</td>
<td>0.124</td>
<td>8.86°</td>
<td>0.155</td>
<td>0.800</td>
</tr>
<tr>
<td>$\frac{33}{4}$</td>
<td>12:8 = 1.50</td>
<td>0.176</td>
<td>11.92°</td>
<td>0.209</td>
<td>0.842</td>
</tr>
<tr>
<td>50</td>
<td>12:6 = 2.0</td>
<td>0.301</td>
<td>20.28°</td>
<td>0.369</td>
<td>0.815</td>
</tr>
<tr>
<td>$\frac{60}{4}$</td>
<td>12:4 = 3.0</td>
<td>0.477</td>
<td>30.90°</td>
<td>0.596</td>
<td>0.800</td>
</tr>
<tr>
<td>$\frac{83}{4}$</td>
<td>12:2 = 6.0</td>
<td>0.778</td>
<td>46.81°</td>
<td>1.066</td>
<td>0.729</td>
</tr>
<tr>
<td>100</td>
<td>12:0 = (Indeterminate.)</td>
<td>0.778</td>
<td>77.56°</td>
<td>4.51</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.790</td>
</tr>
</tbody>
</table>

Patten, blow-fly larvae.
placed at such angles as to make the effective illumination the same on the two eyes of the animal although they were unable to calculate what these angles may be. Patten calculated the angle at which the photosensory elements in the blow-fly larvae would have to be inclined, if the animals took such a position that the illumination on the two sides were equal. However, it has not been determined whether the photosensory areas in the blow-fly larvae are actually so inclined. It therefore appears that in all these experiments on heliotropic turning of animals illuminated by two lights, the apparent agreement of the results with the tropism theory rests upon an assumption which may or may not be valid.

The theory has assumed that the amount of photochemically changed substance is the same on the two sides of the animal when a position of equilibrium has been reached. Even if the effective physical illumination is not the same on the two sides, as is the case in these experiments with Cerianthus, yet possibly the photochemical effect inside the animal may be equalized in some way not determined. The intensity outside the animal is greatly modified by sense organs so that we only know that the photochemical effect inside the animal varies with the light outside. That equal amounts of light may not have the same effect in opposite sides of the same animal was demonstrated by Patten who found blow-fly larvae which were unsymmetrical with respect to their photosensitive areas. These animals when illuminated equally on their two sides turned toward the side of less sensitivity, since they were negative. Garrey also found that it is possible to produce differential sensitivity in the two eyes of the robber-fly by removing the covering from one eye after it has been covered for 2 or 3 days. Such an animal circles toward the more sensitive side.

Another possible explanation of the seeming contradiction to the basic assumption of the theory of phototropism is that here we may have not a final orientation such as may be the case with free moving animals, but a tropistic bending comparable to the experiments of Garrey on insects in which unequal illumination in the two eyes was produced by blacking one eye. In these animals forced positions

were assumed as a result of unequal illumination. The same forced unilateral tension occurs when certain animals are subjected to a constant electric current.\textsuperscript{11-13}

In the experiments on \textit{Cerianthus} the two sides of the animal were unequally illuminated, and like Garrey's flies, the muscle tone on the two sides of the animal was correspondingly unequal. But on the other hand it has been shown that not only in sessile animals like \textit{Cerianthus} but also in moving animals the same relation holds between the intensity of the two lights, and the angle turned from the neutral position where the physical illumination is the same. May we not, therefore, conclude that in all cases of heliotropic bending in animals differences in illumination cause corresponding differences in muscle tonus which in the free moving animal tend to bring the animal into a position where equal illumination occurs? The equation is a mathematical expression of the fact that the muscle tonus on a given side is proportional to the logarithm of the intensity of illumination on that side. Therefore, since the angle turned is the result of muscle tonus, the tangent is proportional to the logarithm of the ratio between the two intensities.\textsuperscript{14}

\textbf{CONCLUSIONS.}

1. In case \textit{Cerianthus} is acted upon by two lights of unequal intensities the relation between the angle turned and the ratio between the intensities of the two lights is mathematically expressed by the equation \( \log_{10} \frac{I_2}{I_1} = K \tan a \), in which \( \frac{I_2}{I_1} \) is the ratio of the two lights, \( a \) is the angle turned from the neutral position, and \( K = 0.615 \).

2. According to published data from experiments on other animals, the relation between the angle turned and the ratio between the intensities of the two lights may be expressed by the same equation.

I wish to thank Professor S. E. Brasefield, of Rutgers College, for helpful advice.

\textsuperscript{12} Loeb, J., and Maxwell, S. S., \textit{Arch. ges. Physiol.}, 1896, lxiii, 121.
\textsuperscript{13} Loeb, J., and Garrey, W. E., \textit{Arch. ges. Physiol.}, 1896-97, lxv, 41.