THE ORIENTATION OF ANIMALS BY OPPOSED BEAMS OF LIGHT.*

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I.

To investigate the mechanism whereby central nervous organs function as adjustors in the control of behavior, there are at least two methods of approach at present very little utilized. Something may be gained by the measurement of suitable phenomena presumed to be direct manifestations of central nervous activity, such as states of tonic immobility (Crozier, 1923–24, a, 1924, a, b, 1924–25; Crozier and Federighi, 1923–24). It is also desirable to measure in some way the resolution of conflicts between opposed or incompatible modes of response, themselves expressible quantitatively but differing in peripheral (sensory) origin (Crozier, 1923–24, b; Crozier and Federighi, 1924–25; Crozier and Stier, 1926–27; Crozier and Pincus, 1926–27). A simple instance of the second sort is given by the phototropic movements of animals under the influence of opposed beams of light. Notwithstanding its apparent simplicity, the theoretical interpretation of orientations in compound fields of light is in a state far from satisfactory although a good deal of attention has been given to it.

It is proposed to derive formulae which may be adequate for several cases of special moment, and to indicate their connection with the theory of phototropism.

For certain Protista moving in a field illuminated by beams at an angle of 90°, Buder (1917–19) found that the angle between the path of progression and the axis of one beam was given very precisely by the relation

\[ \tan \theta = \frac{I_2}{I_1} \]

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For both this case and that in which the beams are directly opposed, M. M. Moore (1923–24) found that the relationship

$$\tan \theta = K \log \frac{I_1}{I_2}$$

gave a satisfactory account of the observations with several forms. It is of interest to discover why these empirical formulae give so good a fit for various series of data, and it will be indicated why they do so. In particular, it can be shown that Buder's formula, where it applies, need not depend upon regarding the orienting power of a source of light as directly proportional to the intensity, although this would be an obvious interpretation of the equation as the formula of a force diagram for certain cases (e.g., a photopositive animal moving as in Fig. 2).

II.

Consider first the case in which a negatively heliotropic organism, located on the line connecting two sources of light, begins creeping in a direction perpendicular thereto. Under the influence of equally intense opposed beams, creeping continues in unaltered direction (Loeb, 1890, 1897, 1918; Gross, 1913; Patten, 1914, 1915, 1917, 1918–19). (This will also be true of certain positively heliotropic forms, namely those which do not turn the head from side to side during progression; cf. Crozier and Mangelsdorf, 1923–24; for the usual result with photopositive organisms cf. Alverdes, 1924.) But if the acting intensities are unequal, orientation occurs toward the weaker light and the path of creeping is deflected (Loeb, 1897; Patten, 1914). The equilibrium position of orientation, according to the tropism doctrine, is one in which excitation is the same on the two sides (Loeb, 1897; Patten, 1914; Loeb and Northrop, 1917; Northrop and Loeb, 1922–23).

It need not be assumed that the forces responsible for excitation will in all cases take the same mathematical expression. In some instances, as given by a suitable measure of the photosensory effect, the intensity of excitation is exactly or very nearly proportional to the logarithm of the intensity (Hecht, 1919–23); it may also appear so

\[1\] Compare, also, Bennitt's (1924) data on velocity of photomechanical movement in retinal pigment cells of crustaceans, which, although said by this author
when the photosensory effect is measured by the orienting posture during circus movements (Cole, 1922–23; Crozier and Cole, 1923), or by the amplitude of the act of turning under the influence of one source of lateral light (Hartline, 1923–24). In other cases the results might be understood by assuming that the excitation is primarily proportional to the intensity directly.

In this discussion it will be assumed that the beams are of parallel rays. Certain accidental consequences of the form of the organism, such as the shading of photosensitive areas by other parts of the body, may be neglected. But the angular inclination of the photoreceptive areas must enter into the calculation. An organism with parallel photosensory surfaces does not suffer definite orientation when acted upon by beams of light opposed at 180° (cf. Crozier, 1917).

In terms of the theory of phototropism, when orientation is attained the excitation is the same on the two sides, and proportional to a function of the illumination: referring to Fig. 1,

\[ K_1 \log (K' I_1 \sin \alpha) = K_2 \log (K' I_2 \cos \beta), \]

where excitation is taken as proportional to the logarithm of the illumination per unit of receptive surface. From the method of recording orientation paths in such experiments (Patten, 1914), \( K_1 \equiv K_2 \). \( K' \) is
to disagree with the Roscoe-Bunsen rule, are in fact satisfactorily accounted for by the law, as \( \log I \times \text{time} = \text{const.} \), since both time and intensity were varied (cf. Hecht, 1919–20, 1920–21, and 1922–23).

2 It is of course possible to derive the equation for a perfectly general case; but the formula is extremely clumsy and discussion of it may be reserved until certain deductions from it have been tested experimentally.
a constant determined by the units in which \( I \), the intensity of the light, is measured.

It is to be observed that this formulation is independent of any attempt to measure the amount of orientation as a difference between two opposite “turning tendencies” (Hartline, 1923–24; M. M. Moore, 1923–24). The assumption of such a procedure would indeed take for granted one of the very things which it is desired to investigate, and in practice gets into difficulties because of the dimensions of the units in which the “tendency to turn” is measured (Crozier and Federighi, 1924–25).

Since

\[
90^\circ - \theta = \alpha + H/2
\]

and

\[
\theta = \beta + H/2
\]

where the angles are defined as in Fig. 1, we obtain by substitution in (1)

\[
\log I_1 + \log \sin \alpha = \log I_2 + \log \cos \beta,
\]

\( \log K' \) disappearing from each side;

then

\[
\frac{I_1}{I_2} = \frac{\cos \beta}{\sin \alpha} = \frac{\cos (\theta - H/2)}{\sin (90^\circ - \theta - H/2)} = \frac{\cos \theta \cos H/2 + \sin \theta \sin H/2}{\cos \theta \cos H/2 - \sin \theta \sin H/2},
\]

dividing by \( \cos \theta \sin \frac{H}{2} \),

\[
\frac{I_1}{I_2} = \frac{\cot \frac{H}{2} + \tan \theta}{\cot \frac{H}{2} - \tan \theta},
\]

whence,

\[
\tan \theta = (\cot \frac{H}{2}) \frac{(I_1 - I_2)}{(I_1 + I_2)},
\]

or

\[
\cot \frac{H}{2} = (\tan \theta) \frac{(I_1 + I_2)}{(I_1 - I_2)} \tag{2}
\]

It is of interest that if the photosensory effect be taken = \( KI \), the final formula, (2), is identical. Thus it is immaterial whether we at the start assume the photosensory effect = \( KI \), or = \( K \log I \).

The angle \( H \) of course need not correspond to any obvious feature
in the morphology of the organism. If it be one which symmetrically
swings the head from side to side during creeping, the average value of
$H$ may be expected to vary if the amplitude and frequency of the
swings is appreciable and in any way depends upon the light. In case
such movements are purely of the photokinetic type, $H$ will be ex-
pected to decrease (or even become negative) as the total acting in-
tensity is increased. If, on the other hand, through the elimination of
random movements, orientation is made more precise as the total in-
tensity is increased, $H$ will correspondingly increase. It appears that
both these types of variation in $H$ are realized, in different instances.
Moreover, $H$ will vary if the angle of convergence of the photorecep-
tive planes is alterable by means of muscles attached to the eyes, as
may be the case for example in certain gasteropods and some other
forms, and if the tension of these muscles is affected according to the
illumination.

If $I_1$ be made equal to $I_2$, from (2) then $\theta$ must be zero, which is the
experimental fact. When $I_2$ is zero, the animal is oriented until $\theta =
H/2$. When $\tan \theta = \cot H/2$, i.e. $\theta = 90 - H/2$, then $I_1 - I_2 = I_1 + I_2$,
which is possible only when $I_2 = 0$. If $I_1 \sin \alpha > I_2 \cos \beta$, and the lights
are not parallel but proceed from point sources, orientation can occur
until $\theta$ approaches $A + H/2 - 90^\circ$, where $A$ is the half angle of diver-
gence of the rays. So long as $I_2 \cos \beta > I_1 \sin \alpha$, the path of orientation
is then not a straight line but a curve, in which $\theta$ continually decreases.
This may complicate the interpretation of experiments, unless $H$
varies in a certain way, and indicates that in such arrangements
not merely the intensity of the light but also the distance from the
source to the animal is important. This result is very easily obtained
in experiments with fly larvae and with Limax.

III.

When the conjoint effect of light beams crossing at $90^\circ$ is considered,
the situation is slightly different. Referring to Fig. 2, we have at
orientation, whether the primary excitation is to be taken as $KI$ or as
$K \log I$,

\[
I_1 \cos \alpha = I_2 \cos \beta
\]

\[
\beta = (90^\circ - \theta) - H/2
\]

\[
\alpha = \theta - H/2
\]
and

\[
\frac{I_1}{I_2} = \frac{\cos \beta}{\cos \alpha} = \frac{\cos (90^\circ - \theta - H/2)}{\cos (\theta - H/2)}
\]

\[
= \frac{\sin \theta \cos H/2 + \cos \theta \sin H/2}{\cos \theta \cos H/2 + \sin \theta \sin H/2}
\]

\[
= \frac{\sin (\theta + H/2)}{\cos (\theta - H/2)}
\]

(If the direction of motion is the reverse of that given in Fig. 2, or if the animal is negatively heliotropic, the complement of \( \theta \) must be used.)

Dividing in (4) by \( \cos \theta \cos H/2 \),

\[
\frac{I_1}{I_2} = \frac{\tan \theta + \tan H/2}{1 + \tan \theta \tan H/2}
\]

whence,

\[
\tan \theta = \frac{I_2 \tan H/2 - I_1}{I_1 \tan H/2 - I_2}
\]

or

\[
\tan H/2 = \frac{I_2 \tan \theta - I_1}{I_1 \tan \theta - I_2}
\]

When

\[
I_1 = I_2, \quad \tan \theta = \frac{I (\tan \theta - 1)}{I (\tan \theta - 1)} = 1,
\]

regardless of the magnitude of \( H \).

When \( H/2 \) is vanishingly small, as it may be assumed to be for small organisms swimming in a helical ("spiral") path, it is apparent from (5) that \( I_1/I_2 = \tan \theta \), which is Buder’s (1917–19) formula already referred to and found by him to describe the orientation of Chlamydomonas, Carteria, Trachelomonas, and Euglena, including photonegative and photopositive forms. As pointed out by M. M. Moore (1923–24), the action of light-beams opposed at \( 90^\circ \) differs in certain respects from that of beams opposed at \( 180^\circ \), for it is possible by the former method to orient both photopositive and photonegative organisms, whether the angle we have labelled \( H \) is zero or of any
other magnitude. When \( \tan \theta = \frac{I_1}{I_2} \), the fact that \( H = 0 \) can be checked by failure of orientation with light beams diametrically opposed.

IV.

M. M. Moore (1923–24) found that for the case of beams opposed at 90° (cf. Fig. 2),

\[
\tan \alpha = K \log \frac{I_1}{I_2},
\]

where

\[
\alpha = 45° - \theta.
\]

According to equation (6),

\[
\tan \theta = \frac{I_2 \tan \frac{H}{2} - I_1}{I_1 \tan \frac{H}{2} - I_2}.
\]

It is necessary to show why (7) and (6) can both apply, with sufficient approximation for most purposes. Let us take the case where \( H/2 \) is very small. Then

\[
\tan \theta = \frac{I_1}{I_2}.
\]

\(^2\) This formula was first found for positively phototropic bending of *Cerianthus* with lights at 180°. Consideration of the tensions existing in the wall of the actinian's body suffice to show that the formula is probably correct for this case, but of no special significance for instances of the type discussed in the present paper.
Since $\alpha = 45^\circ - \theta$, we have from (7)

$$\frac{1 - \tan \theta}{1 + \tan \theta} \equiv K \log I_1/I_2.$$

Inserting (8),

$$\frac{I_1 - I_2}{I_1 + I_2} \equiv K \log I_1/I_2,$$

which must be very nearly true if (7) is to be applicable. Now it turns out that the apparent applicability of (7) to the case of beams of light opposed at 180° (M. M. Moore, 1923–24) also depends upon the approximate numerical identity of the two halves of this expression. Thus, if it were correct that in the latter case

$$\tan \theta = \log I_1/I_2,$$

then, from (2),

$$K \log I_1/I_2 \equiv \left(\cot \frac{H}{2}\right) \frac{(I_1 - I_2)}{(I_1 + I_2)}.$$  \hspace{1cm} (10)

It will be shown later that if $\log I_1I_2$ is practically constant then $\cot H/2$ does not vary appreciably, in which case (10) reduces at once to (9). This is of course also the case if $H$ is fixed and intrinsically independent of $I$. In certain series of experiments the product $I_1I_2$ does not vary very much; in Patten’s (1914) experiments with blow-fly larvae it happens that $I_1 \times I_2$ has the same average value for different sets in which $I_1/I_2$ varies considerably from set to set, and $H/2$ is constant. Therefore this condition is sufficiently satisfied.

The fact that in Patten’s measurements the fraction $\frac{I_1 - I_2}{I_1 + I_2}$ varies only from $\frac{1.0}{15}$ to $\frac{11.35}{16.65}$, while $\log I_1I_2$ varies from 0.0580 to 0.7235, makes it possible for $K$ in (9) to remain fairly uniform; actually it changes only from 0.868 to 0.903 (excluding the measurements for the two highest ratios $I_1/I_2$, which cannot fairly be taken with the other eight, because $I_1I_2$ differs; in these two, $K$ rises to 1.06).

Thus we may say that the formulae empirically found to describe orientation under the influence of opposed beams of light are to be
understood as approximations to the theoretical solution, and that their competence depends very largely upon the way in which the experimental variation of the ratio of the intensities of the lights happens to have been carried out, and upon the fact that the angle labelled \( H \) is either small or constant.

V.

It is desired to show how these equations serve to account for the findings in several cases.

TABLE I.
Orientation of Young Rats by Lights of Unequal Intensities Opposed at 180°; Data from Crozier and Pincus, 1926–27.

<table>
<thead>
<tr>
<th>( I_1 ) (foot candles)</th>
<th>( I_2 ) (foot candles)</th>
<th>( \theta ) (°)</th>
<th>( \cot H/2 )</th>
<th>( H/2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>8.0</td>
<td>7.0</td>
<td>5.98°</td>
<td>2.199</td>
<td>24°27'</td>
</tr>
<tr>
<td>8.6</td>
<td>7.0</td>
<td>15.8°</td>
<td>2.760</td>
<td>19°55'</td>
</tr>
<tr>
<td>8.6</td>
<td>5.7</td>
<td>22.4°</td>
<td>1.878</td>
<td>28°2'</td>
</tr>
<tr>
<td>8.6</td>
<td>4.6</td>
<td>27.9°</td>
<td>1.742</td>
<td>20°52'</td>
</tr>
<tr>
<td>8.6</td>
<td>3.9</td>
<td>32.2°</td>
<td>1.417</td>
<td>35°13'</td>
</tr>
<tr>
<td>8.2</td>
<td>3.4</td>
<td>31.1°</td>
<td>1.247</td>
<td>38°44'</td>
</tr>
<tr>
<td>9.5</td>
<td>3.1</td>
<td>41.0°</td>
<td>1.712</td>
<td>30°17'</td>
</tr>
<tr>
<td>10.3</td>
<td>2.9</td>
<td>44.3°</td>
<td>1.696</td>
<td>30°31'</td>
</tr>
<tr>
<td>12.0</td>
<td>2.67</td>
<td>47.4°</td>
<td>1.710</td>
<td>30°19'</td>
</tr>
<tr>
<td>14.0</td>
<td>2.65</td>
<td>52.0°</td>
<td>2.059</td>
<td>25°54'</td>
</tr>
</tbody>
</table>

\( \cot H/2 = \tan \theta \frac{(I_1 + I_2)}{(I_1 - I_2)} \)

A. In experiments of which details are given in another place (Crozier and Pincus, 1926–27), the deflection \( \theta \) was measured when young rats, with eyes still unopened, were acted upon by two opposed lights of unequal intensities. The necessary data are given in Table I. What may be called the head angle, \( H \), is not constant, but decreases as \( \log I_1I_2 \) increases. As Fig. 3 shows, the relationship between \( H \) and \( \log I_1I_2 \) is approximately linear, within the degree of exactness reasonably expected in such experiments. This is understood to mean that side-to-side motion of the head is more extensive or more frequent as the total acting intensity increases. This certainly agrees...
with the result of observations on the progress of oriented creeping. If excitation varies as \( \log I \), then the reduction of \( H \) as \( I_1 I_2 \) increases must be nearly proportional to the sum of the excitations on the two sides, and thus, roughly, to \( \log I_1 I_2 \). The reason for this is, that the total excitation of the organism, \( E \), should be expressible as

\[
E = K \left( \log I_1 \sin \alpha + \log I_2 \cos \beta \right),
\]

where \( K \) includes the constant introduced by the units in which \( I \) is measured. Referring to the previous substitutions (Fig. 1), this becomes

\[
E = K \left( \log I_1 I_2 + \log \sin \alpha \cos \beta \right) \\
= K \left( \log I_1 I_2 + \log (\cos^2 \theta \cos^2 H/2 - \sin^2 \theta \sin^2 H/2) \right) \\
= K \left( \log I_1 I_2 + \log (\sin^2 \theta + \cos^2 H/2) \right).
\]

The term \( (\sin^2 \theta + \cos^2 H/2) \) is small, and, particularly if \( \theta \) and \( H \) vary together, it does not alter very much as \( I_1 \) and \( I_2 \) are changed; therefore we may write

\[
E = K' \log I_1 I_2 + C',
\]

where \( C' \) is approximately constant. It will be noticed that there is obtained in this way a quantitative measure of photokinesis or of the restriction of random movements.

B. The problem of predicting the path pursued when bilaterally located photoreceptors are activated by opposed lights is particularly interesting when it is possible to study independently the effect of
light as exerted through each member of the symmetrical pair functioning singly. In the case of negatively phototropic *Limax maximus* data have been obtained by Cole and Crozier upon circus movements (Crozier and Cole, 1921–22, 1923). Subsequently, experiments were made with lights opposed at 180°. The results are collected in Table II.

In these experiments ten trails were obtained from each of a number of individuals, the animal being caused to creep first with one side and then with the other toward the stronger light. In this way asymmetry of sensitivity is automatically discounted. The animals crept upon a moistened glass plate having beneath it a card bearing a system of coordinates; on a similarly marked sheet the path of the animal is recorded from moment to moment. This organism, however, is not so well adapted to give quantitative results as the blow-fly larva. The method is not one of extreme accuracy, but errors in recording appear to be of less moment than those introduced by the fact that not all the individuals were of the same size. The last entry in Table II is probably somewhat in error from this cause, as well as because orientation was probably not in all instances complete at the cessation of the record. The trails obtained are in every respect similar to those secured with blow-fly larvae (Patten, 1914).

Calculation of cot $H/2$ from equation (2) shows (Table II) that

<table>
<thead>
<tr>
<th>$I_1$ (meter candles)</th>
<th>$I_2$ (meter candles)</th>
<th>$\theta$ (°)</th>
<th>$H/2$ (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>172.8</td>
<td>172.8</td>
<td>3.6°</td>
<td>—</td>
</tr>
<tr>
<td>126.9</td>
<td>108.6</td>
<td>5.0°</td>
<td>41.9°</td>
</tr>
<tr>
<td>227.7</td>
<td>71.48</td>
<td>20.9°</td>
<td>53.85°</td>
</tr>
<tr>
<td>184.5</td>
<td>80.65</td>
<td>20.25°</td>
<td>47.9°</td>
</tr>
<tr>
<td>400.0</td>
<td>55.6</td>
<td>36.27°</td>
<td>45.8°</td>
</tr>
<tr>
<td>649</td>
<td>47.4</td>
<td>39.25°</td>
<td>46.5°</td>
</tr>
<tr>
<td>205.2</td>
<td>75.6</td>
<td>20.96°</td>
<td>49.6°</td>
</tr>
<tr>
<td>400</td>
<td>75.6</td>
<td>24.71°</td>
<td>55.85°</td>
</tr>
<tr>
<td>660</td>
<td>65.08</td>
<td>30.86°</td>
<td>53.95°</td>
</tr>
<tr>
<td>806</td>
<td>60.1</td>
<td>50.66°</td>
<td>35.25°</td>
</tr>
</tbody>
</table>
$H/2$ does not vary markedly, except for the terminal entry in the table. For reasons already given, then, as already indicated, it should be approximately correct to state that, except for high values of $\theta$,

$$\tan \theta = K \log \frac{I_1}{I_2}$$

As Fig. 4 shows, the approximation is fair.

C. The most complete series of measurements is that made by Patten (1914) with larvae of the blow-fly. Calculation from the data in Patten's tables shows that while $\theta$ changes from $3^\circ \pm$ to $30^\circ \pm$, $\log (\sin^2 \theta + \cos^2 H/2)$ changes only from 1.8797 to 1.9400; therefore any change in $H$ with intensity of light should, if apparent, be pro-

![Fig. 4. Limax maximus, lights opposed at 180°. The straight line shows the degree to which the observations agree with the simplified formula for orientation, at low values of the angle of orientation ($\theta$); the nature of the correction implied by the dashed line is discussed in the text.](image)

portional to $\log I_1/I_2$. But the data show that $H/2$ is constant until, at very high angles of orientation ($46.81^\circ$), $\log (\sin^2 \theta + \cos^2 H/2)$ falls to 0.0864, and $H/2$ to $34^\circ$; this is probably due in part to the fact that shading of the head end by the rest of the body introduces complications. The constancy of $H/2$ makes it possible to use the formula $\tan \theta = K \log \frac{I_1}{I_2}$ with reasonably satisfactory results; and also to construct, as Patten did, diagrams giving the angle $H$ geometrically. By calculation from equation (2), $H$ is found $= 85^\circ$; Patten, by constructions based upon $I_1/I_2$, obtained $H = 83^\circ$.−.
A good test of the present analysis is given by measurements of $\theta$ with the same organism, under lights opposed at 180° and again at 90°. For such an animal as the blow-fly larva, $H$ should be identical in the two cases. These experiments will be discussed separately.

The fact that $H$ does not change appreciably makes it possible to average, as Patten (1914) did, the closely agreeing values of $\theta$ which result for a given magnitude of the ratio $I_1 - I_2 / I_1$, which if constant means that $I_1 + I_2$ is constant also $I_1 - I_2 = c$, then

$$\frac{I_1 + I_2}{I_1 - I_2} = \frac{2 - c}{c}.$$  

This removes the force of the argument, which as Patten (1915) showed might be advanced, to the effect that the constancy of the orienting deviation for a given ratio of the acting light intensities is an example under the Weber-Fechner rule. A related question is that arising in the discussion of phototropism of plants, as to the applicability of Weber's rule for cases of orientation obeying the Resultantengesetz (as in Buder's work (1917-19) already cited; cf. Lundegårdh, 1922; Pringsheim, 1926). As pointed out earlier in this paper, the "resultant" formula appears, with light beams crossing at 90°, if the excitatory surfaces are practically parallel, whether excitation be proportional to $I$ or to $\log I$; hence the discussion as to the applicability of Weber's rule is quite without point.

**SUMMARY.**

When orientation is attained under the influence of beams of parallel light opposed at 180° the deflection $\theta$ from a path at right angles to the beams is given by $\tan \theta = (\cot H/2) \frac{(I_1 - I_2)}{(I_1 + I_2)}$, where $I_1$ and $I_2$ are the photic intensities and $H$ is the average angle between the photoreceptive surfaces. This expression is independent of the units in which $I$ is measured, and holds whether the primary photosensory effect is proportional to $I$ or to $\log I$. When photokinetic side-to-side motions of the head occur, $H$ decreases with increasing total acting light intensity, but increases if higher total light intensity restricts the amplitude of random movements; in each case, $H$ is very nearly proportional to $\log I_1 I_2$. 
For beams of light at 90°,
\[ \tan \theta = \frac{I_2 \tan \frac{H}{2} - I_1}{I_1 \tan \frac{H}{2} - I_2} \]

The application of these equations to some particular instances is discussed, and it is shown why certain simpler empirical formulae previously found by others yield fair concordance with the experimental data. The result is thus in complete accord with the tropism theory, since the equations are based simply on the assumption that when orientation is attained photic excitation is the same on the two sides.

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