The Effect of Polarized Light on the Growth of a Transparent Cell

A theoretical analysis

L. F. JAFFE

From the Biology Department, Brandeis University, Waltham

ABSTRACT It is shown that light lost by reflection before entering a clear and homogeneous sphere or infinite cylinder is precisely compensated by light retained within these bodies by internal reflection; compensation means that the total rate of light absorption by infinitely dilute photoreceptors as integrated through the whole of these bodies or even through any concentric or coaxial shell making them up is independent of surface reflection. In the *Phycomyces* sporangiophore this theorem precludes a reflection explanation of R, the polarization dependence of the light growth response.

An alternative explanation based upon anisotropic absorption by the receptors is explored and found tenable. Formulae are derived for R in any transparent cylindrical cell as a function of the constants of anisotropic absorption by the photoreceptors taken as a group (C_H' and C_L'), of the radial position of the receptors, and of the refractive indices of the cell (n) and of the medium (N). It is inferred that the photoreceptors in the *Phycomyces* sporangiophore are most absorbent for light vibrating in the direction of a hoop around a barrel. Orientation of the receptors by linkage to the cell wall is then shown to be a plausible explanation of the inferred anisotropy. On the basis of anisotropic reception, it is predicted that R should be constant for any $N > n$, and it is shown how C_H', $C,_L'$ and the radial position of the receptors may all be obtained from a careful determination of R as a function of N.

INTRODUCTION

In 1934, Castle reported that a horizontally directed light beam vibrating *along* the axis of an upright *Phycomyces* sporangiophore must be 10 per cent brighter than a *cross*-vibrating counter beam to balance its tropic effect. Recently, Shropshire has observed a similar disadvantage of long-vibrating light in effecting a straight growth response in this cell. Thus with 450 mμ

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radiation, he found that long-vibrating light must be 24 ± 5 per cent brighter than cross-vibrating light to produce the same straight growth response. Moreover, when the sporangiophore was grown immersed in a liquid of a refractive index of 1.29 instead of in air, the polarization effect fell to 6 ± 9 per cent. These observations were interpreted by Shropshire as supporting Castle's view that the lesser effectiveness of long-vibrating light lies in its greater reflection before penetrating the cell.

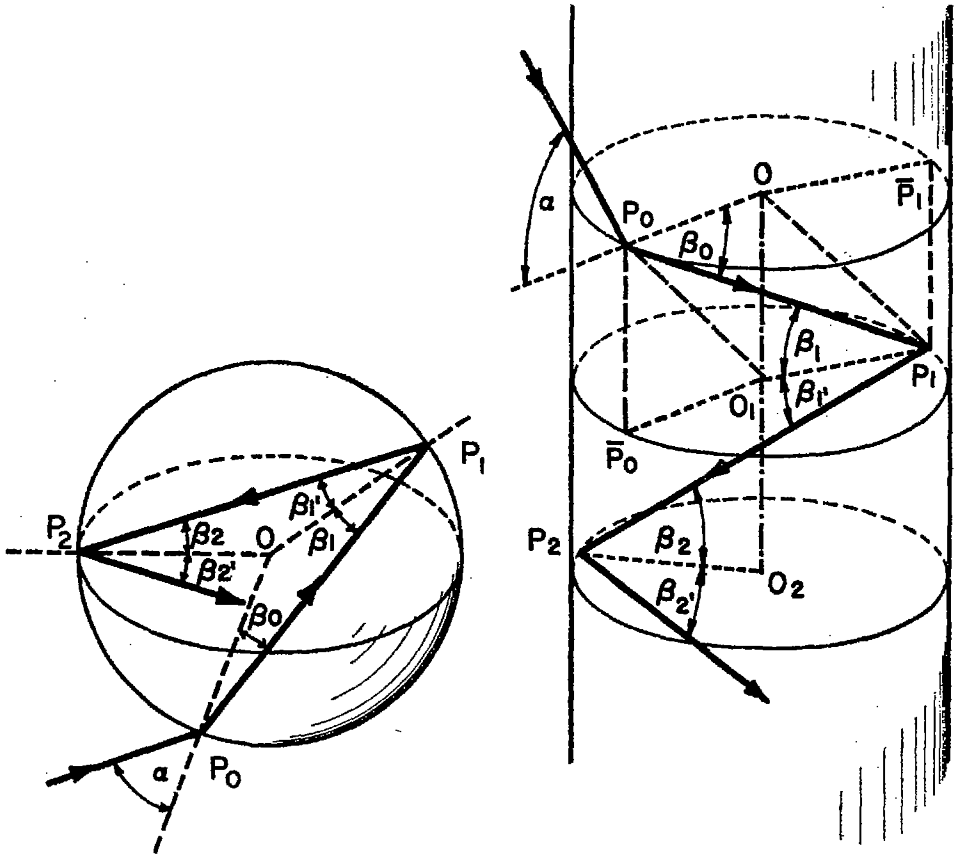

FIGURE 1. Paths of light rays which enter an isotropic homogeneous transparent sphere or infinite cylinder from an isotropic homogeneous medium. The rays kept within these bodies by internal reflection are shown; those which are refracted back into the medium are not shown.

However, Castle's analysis neglects the fact that a beam which suffers greater reflection before entering such a cell will likewise undergo greater reflection before leaving it. Thus the effect of the lower penetrance of the long-vibrating light may be counteracted by its greater retention. Pursuit of this thought leads to the theorem stated in the abstract. It is proven as follows:—

A Reflection Compensation Theorem

Consider one polarization component of a ray striking either a sphere or an infinite cylinder at any angle from the outside (Fig. 1).

In both cases, β_0, the angle of refraction, is equal to β_1, the angle of incidence at the first point of internal reflection, P_1. For the sphere this follows from the fact that the two normals, OP_0 and OP_1, are both radii. For the cylinder, it may be proven by showing that:

$$\Delta P_0\bar{P}_0 0_1 \cong \Delta P_1\bar{P}_1 0 \tag{1}$$

$$\therefore P_0 0_1 = P_1 0 \tag{2}$$

$$\therefore \Delta P_0 P_1 0 \cong \Delta P_0 P_1 0_1 \tag{3}$$

More generally, since the angle of the first internal reflection β_1', equals β_1, the angle of incidence at P_1, it follows that all internal reflections of the ray occur at the same angle of incidence, that is:

$$\beta_0 = \beta_1 = \beta_j = \beta \tag{4}$$

Let $r_e(\beta)$ be the reflecting power of the surface for the external reflection at P_0; $r_i(\beta)$, for the internal reflections at P_1, P_2, etc. Regardless of the nature of the reflecting surface, it follows from Stokes' proof (20) that:

$$r_e(\beta) = r_i(\beta) = r \tag{5}$$

Let A_1 be the rate of light absorption along the first lap of the light path, P_0P_1.

$$A_1 = K(1 - r) \text{ where } K \text{ is independent of } r.$$

Similarly,

$$A_2 = Kr(1 - r).$$

More generally,

$$A_j = Kr^{j-1}(1 - r).$$

Then,

$$A = \sum_1^\infty A_j = K(1 - r)\sum_0^\infty r^j = K(1 - r)\cdot\frac{1}{(1 - r)} = K \tag{6}$$

Thus A is independent of r for either polarization component of any ray. Hence by integrating over both components of all rays, it follows that the total rate of light absorption in these bodies is independent of reflection. Moreover, the redistribution of light effected by reflection upon a given ray is one between successive laps all of which have the same radial position. Hence the contribution made by any ray to the rate of light absorption as integrated through any concentric or coaxial shell making up these bodies is independent of r. Hence by integrating over all rays, it follows that the total rate of light absorption within any such shell is independent of reflection.

It should be emphasized that this result is independent of the relationship between reflection and either polarization or the angle of incidence as well as being independent of the pattern of external illumination.

APPLICATION TO POLARIZATION DEPENDENCE OF STRAIGHT GROWTH IN PHYCOMYCES In Shropshire's experiment, the cylindrical sporangiophore was rotated at 2 R.P.M. around its long axis, so that averaged over the period of illumination of 5 minutes, the light in the cell must have been symmetrical around this axis. Hence polarization could only have effected growth *via* an effect on the total rate of light absorption or upon the radial distribution of light. Hence, the compensation theorem shows that except for a correction for the imperfect transparency of the cell, polarization could have had no effect at all upon growth *via* differential reflection.

The following crude analysis suffices to show that the correction for imperfect transparency allows a reflection effect which is only a small fraction of the observed one: Consider the polarization effect if the transmission loss per lap were 100 per cent; that is, if only photoreceptors in the front wall were illuminated.

Let A be the rate of absorption by the tropic photoreceptors generally; A_x, for cross-vibrating light; A_L, for long-vibrating light.

Let C be the absorption coefficient of the photoreceptors.

Let I' be the light intensity striking the cell expressed in quanta per unit area per unit time.

Let Δ be the distance traversed by a ray in passing through the photoreceptors in the front part of the cell.

Let h be the height of the photosensitive zone in the cell.

Let W be the coordinate which is perpendicular to both the cell's axis and the light's direction.

Let B be the radius of the cell.

Let $\tilde{K} = CI'\Delta hB$.

Under the conditions of Shropshire's experiment, light struck the sporangiophore perpendicular to its long axis. Hence:

$$A = \int_{-B}^{+B} CI'\Delta(1 - r)hdW = \int_{-\pi/2}^{+\pi/2} CI'\Delta(1 - r)hB \cos \alpha d\alpha$$

Ignoring the relatively small change of Δ with α, one obtains:

$$A \cong \bar{K} \int_{-\pi/2}^{\pi/2} (1 - r) \cos \alpha d\alpha \tag{7}$$

Let R be the ratio of the intensity of long-vibrating light to that of cross-vibrating light when the two beams produce equal effects. Hence R is the ratio of absorption of cross-vibrating to long-vibrating light when equal intensities are employed:

$$R = \frac{A_x}{A_L}$$

If r (α) is taken from the Fresnel equations for reflection at the boundary between isotropic dielectric media of refractive indices 1.0 and 1.5, then numerical integration gives the following result:

$$R - 1 = \frac{A_x - A_L}{A_L} = 0.08$$

Delbrück and Shropshire (10) have measured an average transmission loss per lap of about 20 per cent. Interpolating between the results for 100 and 0 per cent transmission losses, one obtains an estimate of the reflectional effect of polarization upon straight growth of 0.016, a figure which is less than 7 per cent of the observed effect of 0.24 ± 0.05.

Anisotropic Reception Fits Present Data

FRAME OF REFERENCE Fucaceae zygotes are "polarotropic." That is, their growth is oriented with reference to the plane of vibration of polarized light which strikes them. Now consider the tropic photoreceptors taken as a group in any small region of one of these spherical cells. It has been inferred that the receptors are so oriented as to have a larger absorption coefficient or cross-section, C_P, for light vibrating parallel to the nearest part of the cell surface than their cross-section, C_N, for light vibrating normal to the nearest surface (11). Moreover, observations of polarotropism in spores of a moss, a fern, and a fungus appear compatible with this interpretation (5).

These facts suggest anisotropic absorption by the photoreceptors as the cause of the polarized light response of *Phycomyces*. In this cylindrical cell, one must distinguish *three* cross-sections governing absorption by the photoreceptors at any point. As before, C_N governs absorption of light vibrating normal to the nearest part of the cell surface. C_P, however, must be subdivided into two components; the long cross-section, C_L, governs absorption of light vibrating parallel to the cell's long axis; while the hoop cross-section, C_H, governs absorption of light vibrating perpendicular to both the normal and long axes; *i.e.*, in the hoop direction, or the direction taken by a hoop around a barrel.

FALL OF R IN A MEDIUM OF REFRACTIVE INDEX 1.29 The rate of absorption of long-vibrating light will be proportional to C_L:

$$A_L \propto C_L$$

However, rays of cross-vibrating light will be refracted upon entering the cell so as to vibrate obliquely to the normal. They will, therefore, have components in both the normal and hoop axes. Hence the absorption of a certain portion, θ, of the cross-vibrating light (as integrated over-all elements of the beam) will be governed by C_H while the remaining portion, $1 - \theta$, will be governed by C_N:

$$A_x \propto \theta C_H + (1 - \theta)C_N$$

$$\therefore R = \frac{A_x}{A_L} = \frac{\theta C_H + (1 - \theta)C_N}{C_L} = \theta\left(\frac{C_H - C_N}{C_L}\right) + \frac{C_N}{C_L} \qquad (8)$$

According to Castle, n, the average refractive index of the cell, is 1.38 (see reference 8). Hence 1.29 is closer to n than is the refractive index of air, and each light ray which penetrates a cell placed in a medium of index 1.29 is refracted less than a corresponding ray which enters from air. Thus, on the average, the beam inside the cell makes a larger angle with the normal, and θ will fall in a medium of index 1.29. Hence in order to qualitatively explain the observed fall of R in this medium on the basis of anisotropy, it is necessary to assume $C_N < C_H$. Moreover, since $R > 1$, it follows from Equation 8 that:

$$C_L < \theta C_H + (1 - \theta)C_N$$

$$\therefore C_L < \theta C_H + (1 - \theta)C_H = C_H$$

Or, in words, it must be inferred that the hoop cross-section is the largest of the three.

R'S AT TWIN PEAKS Anisotropic reception is also consistent with the closeness of the R's measured at 450 and 380 mμ. For cells in air, Shropshire obtained values of 0.24 ± 0.05 and 0.21 ± 0.07 at these wavelengths. They are both action spectrum peaks (9, 10), and can therefore be assumed to be twin absorption maxima of the tropic photoreceptors. Hence it can be tentatively inferred that if the polarization dependence arises from anisotropic reception, then the dichroic ratios of the receptor at nearby absorption maxima are of similar size. Now it has been suggested, apparently on the basis of old theoretical work, that such similarity is not to be expected (16). However, the pairs of dichroic ratios measured and recorded in the literature for twin peaks of stress-oriented pigments are, in fact, quite close in value (see Table I). Thus this second observation is likewise consistent with the idea of anisotropic reception.

BENDING Finally, anisotropic reception can be reconciled with the larger value of R (as measured with visible light and cells in air) found for the light growth reaction (24 ± 5 per cent) than for the bending reaction (about 10 per cent). In speeding straight growth, one expects that the relative effectiveness of rays with different incident angles (*i.e.* different α's) should depend only on the relative rates of absorption of these rays by the photoreceptors. However, both Buder's mechanical advantage theory of bending[1] (4) and Castle's path length theory of bending[1] (6) imply that a ray's *bending* effect (per quantum of its light absorbed) rises with α.

TABLE I

AVAILABLE MEASUREMENTS OF DICHROIC RATIOS AT TWIN PEAKS IN AND NEAR THE VISIBLE

Pigment	Absorption peaks	Corresponding dichroic ratios	Authority
	$m\mu$		
Rivanol	280,375	4.4, 3.3	(13)
p-Nitrosodimethylaniline	365,440	2.8, 1.9	(18)
1,1'-Diethyl-2,2' cyanine chloride	495,527	5, 5	(12)
Congo red	505,535	24, 28	(19)
Methylene blue	612,666	3.5, 3.4	(18)

Now, as its incidence angle rises, the hoop component of a cross-vibrating

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[1] Implicit in both of these theories are the assumptions that, during steady bending, absorption of light by the receptors at any point effects an element of bending moment which is *directed* along the normal and toward the cell's axis and which is of a *size* which is a linear function of the rate of light absorption. In fact, it can be shown that the mechanical advantage and the path length effects are *both* necessary consequences of the above two physiological assumptions; while the relative weight of the two effects depends upon the radial distribution of photoreceptors. Now, sporangiophores are observed to bend away from the lighted side when subjected to grazing illumination whether the medium is air (1), water (3), or paraffin oil (2). Hence there is relatively little doubt that the direction of the bending moment of each illuminated cell element is as assumed; but it is more difficult to justify the assumption of linearity. I have made unpublished calculations of maximum steady bending rates by integrating on the basis of this assumption, and the results agree fairly well with observation. However, Dr. Delbrück has pointed out privately that this theory does not account, at least without modification, for the *continuous* decrease in wall growth rate that presumably exists in the bending sporangiophore as one passes from its most convex to its most concave point. Moreover, the calculations require the dubious assumption that almost all the transmission losses occur peripheral to the region bearing the receptors.

ray will fall. Hence, on the basis of anisotropic reception, and of the available theories of bending, the phototropic advantage of cross-vibrating light would be expected to be smaller than its advantage in speeding straight growth. Indeed, on the basis of this argument, it can be predicted that for cells in media of equal or higher refractive indices than they themselves, the polarization dependence of bending will probably be reversed. That is, long-vibrating light should be *more* effective than cross-vibrating light under these circumstances.

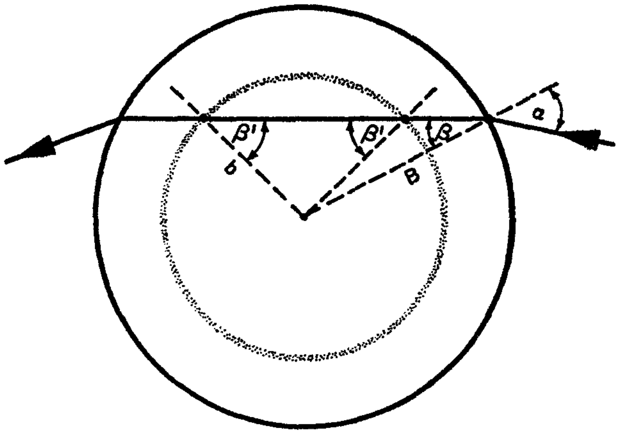

FIGURE 2. Path of one ray through a cylindrical cell containing photoreceptors in a thin coaxial shell. The ray is directed at right angles to the cell's axis. The receptors are represented by stippling. Reflection is ignored because of the compensation theorem.

Formulae Predicting Results of Anisotropic Reception

To fully expose the implications of anisotropy one must obtain θ as a function of the refractive indices of cell and medium, and of the radial distribution of the photoreceptors. Since the latter is unknown, let us deduce a formula for photoreceptors in a thin shell—an elemental case from which more complex distributions may be integrated. Consider Fig. 2. (Reflection is ignored because of the compensation theorem. This, in turn requires that transmission losses be negligible.)

Let N = the refractive index of the medium.
Let n = the refractive index of the cell.
Let B = the radius of the cell.
Let b = the radius of the shell bearing the photoreceptors.
Let $\bar{\beta}$ = the angle between the most peripheral ray to traverse the receptor shell and the normal to that shell.

It is shown in Appendix II that:

$$\bar{\beta} = \sin^{-1}\left(\frac{NB}{nb}\right) \quad \textit{for } \frac{NB}{nb} \leq 1 \tag{9}$$

$$\theta = \frac{1}{2} + \frac{\sin 2\bar{\beta}}{4\bar{\beta}} \quad \textit{for } \frac{NB}{nb} \leq 1 \tag{10}$$

$$\theta = \frac{1}{2} \quad \textit{for } \frac{NB}{nb} \geq 1 \tag{11}$$

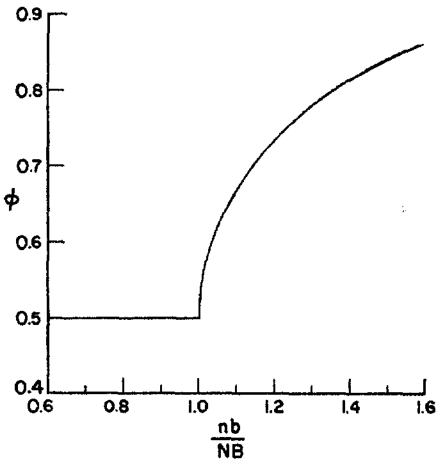

FIGURE 3. A plot of Equations 10 and 11. Consider light both directed at and vibrating at right angles to the axis of a transparent cylinder. Consider a thin coaxial shell of photoreceptors lying within the cylinder. Then θ is the fraction of light whose absorption is governed by the hoop cross-section of the receptors; $(1\text{-}\theta)$ is governed by the normal cross-section. n and N are the refractive indices of cylinder and medium respectively; b and B are the radii of the receptor shell and the cylinder's surface respectively.

On this basis, θ is plotted in Fig. 3 as a function of N. I will refer to the shape of this curve as *congé* after the molding of this name. It follows from Equation 8 and the inference $C_N < C_H$, that $R = p\theta + q$ where p and q are positive numbers independent of N. Hence R must also be a congé function of N which is constant for $N > bn/B$ if the photoreceptors are restricted to a thin shell. If they are spread out radially, then $\theta(N)$ and hence $R(N)$ will be obtained by integrating over thin shell-shaped elements each of which yields a congé curve. The resultant function will be constant for $N > \bar{b}n/B$ where $\bar{b}$ is the radius of the widest receptor-bearing shell, and will rise steadily as N falls below $\bar{b}n/B$; the more spread out the receptors are, the less abrupt will be the transition to this rising region.

In any case, $\bar{b} \leqq B$. Hence, if for any $N > n$ (that is, for a medium of a refractive index greater than that of the cell), experiment shows that R is *not* approximately constant, then receptor anisotropy must be rejected as a mechanism of the polarization effect. If, however, experiment shows R to be approximately constant for $N > n$, then the effect can be tentatively attributed to such anisotropy.[2] Inferences can then be drawn as to the radial position of the receptors from the transition region of $R(N)$ as indicated in the paragraph above. For this, $\theta(N)$ can be calculated *via* Equations 9 to 11, and then measures of receptor anisotropy, *e.g.* C_H/C_N and C_L/C_N, can be inferred from the observed $R(N)$ and Equation 8. Some of this will be illustrated in the last section.

Are the Receptors Oriented by Linkage to the Wall?

It will now be shown that if Shropshire's data are taken at face value, then they fit that particular pattern of receptor anisotropy which would arise if the receptors were uniaxial, positively dichroic molecules linked to the cell wall and were thus oriented by the anisotropic stress which originates in turgor pressure.

In the wall of a turgid cylinder, stress in the hoop axis is twice that in the long axis (8) while in the radial axis the wall is necessarily under compensating compression. Moreover, Roelofsen (14) has shown that the bulk components of the wall being considered, like that of some other growing cylindrical walls, actually show a pattern of orientation in qualitative conformance to this stress pattern: The polarizing microscope indicates, that as averaged through the wall, more fibrils lie along the hoop axis than the long axis; electron micrographs confirm this (though the anisotropy is confined to the inner layer of the wall), and do not appear to show *any* fibrils along the radial axis.

Now, pigment molecules are usually oriented by linkage to a stress-oriented polymer film so as to lie with their axes of greatest absorption in the axis of greatest stress (12, 13, 15, 17, 18). Hence according to the hypothesis being tested, about two-thirds of the receptors should lie in the hoop axis, about half this, or one-third in the long axis, and few or none in the radial axis. It will now be shown that if Shropshire's data are attributed to uniaxial positively dichroic receptors lying in or near the wall that the pattern of receptor orientation must be of this very sort.

For the case considered, $b \cong B$. Taking $n = 1.38$ from Castle's measure-

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[2] Not only does an anisotropy mechanism require such constancy but *all* alternatives in which refractive index dependence arises from reflection preclude it. Thus this test offers a means of excluding such subtle alternatives as one in which differences in scattering direction within the cell result in differences in the angles of incidence of scattered rays with the cell surface which in turn results in differences in the degree of retention of scattered rays by internal reflection and thus finally in differences in light intensity within the cell.

ment (6), and using Equations 9 and 10, one can then calculate θ for cells immersed in air ($N = 1.00$) and in totally fluorinated tributylamine ($N = 1.29$), the two media employed by Shropshire. The results are $\theta = 0.809$ and $\theta = 0.638$ respectively. Let

$$C'_L = \frac{C_L}{C_N} \text{ and } C'_H = \frac{C_H}{C_N}.$$

Then Equation 8 can be put in the form:

$$RC'_L - \theta C'_H + (\theta - 1) = 0 \tag{12}$$

R and θ are known for each of two media. Hence one has two linear equations with two unknowns and can readily obtain, $C'_H = 3.7$ and $C'_L = 2.6$. Thus measures of receptor anisotropy are inferred. Now let us draw the desired inferences at the molecular level.

TABLE II

THEORETICAL LIMITS OF THE RECEPTOR* ORIENTATION AND DICHROIC RATIO REQUIRED TO FIT SHROPSHIRE'S DATA

f_H	f_L	f_N	D
0.63	0.37	0.00	5.3
0.50	0.36	0.14	∞

* The receptors are assumed to be uniaxial, positively dichroic molecules lying in or near the cell surface.

Let D be the dichroic ratio of the receptors; that is, D is the absorption coefficient for light vibrating parallel to a receptor molecule's axis divided by this coefficient for light vibrating perpendicular to this axis. Note that $D \geqq 1$ since it has been assumed that the receptors are positively dichroic.

Let f_H, f_L, and f_N be the fractions of the receptors oriented in the hoop, long, and normal axes respectively.

Then:

$$3.7 = C'_H = \frac{Df_H + f_L + f_N}{Df_N + f_L + f_H}$$

$$2.6 = C'_L = \frac{Df_L + f_H + f_N}{Df_N + f_L + f_H}$$

$$1 = f_H + f_L + f_N$$

Since we have three equations with four unknowns, no unique solution is possible. However, it can be shown that all four unknowns have their extreme values at $f_N = 0$ and at $D \rightarrow \infty$. These extreme values are given by:

$$(i) \qquad f_H = \frac{C'_H - 1}{C'_H + C'_L - 2} \qquad f_L = \frac{C'_L - 1}{C'_H + C'_L - 2} \qquad f_N = 0$$

$$D = C'_H + C'_L - 1$$

$$(ii) \qquad f_H = \frac{C'_H}{C'_H + C'_L + 1} \qquad f_L = \frac{C'_L}{C'_H + C'_L + 1} \qquad f_N = \frac{1}{C'_H + C'_L + 1}$$

$$D \rightarrow \infty$$

The numerical results appear in Table II.

It is seen that the required pattern of receptor orientation is of the sort predicted for wall-linked molecules.

APPENDIX I

Glossary of Symbols Not Always Defined in Context

A, A_x, and A_L = the rates of light absorption by the tropic photoreceptors of light vibrating in an unstated direction, across the cell's long axis, and along it, respectively.

b = the radius of a shell bearing the photoreceptors.

B = the radius of the cell's surface.

β = the angle between a ray within the cell and the normal at the cell's surface.

β' = the angle between a ray and the normal at a shell bearing the photoreceptors.

$\bar{\beta}$ = the maximum value of β'.

C_H, C_L, C_N = the photoreceptors' cross-sections or absorption coefficients for light vibrating in the direction of the hoop, long, or normal axes, respectively.

$C'_H = C_H/C_N$

$C'_L = C_L/C_N$.

n, N = the refractive indices of the cell and medium, respectively.

θ = the fraction of the intensity of a beam of cross-vibrating light whose absorption is governed by C_H, the residue being governed by C_N.

r = the coefficient of reflection at the cell-medium interface.

R = the ratio of the intensity of a beam of light vibrating in the direction of the long axis of the cell to that of a beam vibrating across this axis when the two beams produce equal effects.

APPENDIX II

Derivation of Formulas 9, 10, and 11

Consider Fig. 2. In the photoreceptor shell, an element of cross-vibrating light of amplitude, dE, will have a component, $dE_H = \cos \beta' dE$ in the hoop direction and

$dE_N = \sin \beta' dE$ in the normal direction. Hence such an element of intensity, dI quanta per unit time, will have intensity components:

$$dI_H = \cos^2 \beta' \, dI \qquad dI_N = \sin^2 \beta' \, dI$$

Let the element considered be of width, dW, height, h, and intensity, I' quanta per unit time per unit area. Then:

$$dI = I'hdW = I'hB \cos \alpha \, d\,\alpha$$

By Snell's law:

$$\sin \beta = \left(\frac{N}{n}\right) \sin \alpha$$

By the sine formula:

$$\frac{B}{\sin \beta'} = \frac{b}{\sin \beta'}$$

$$\sin \alpha = \left(\frac{nb}{NB}\right) \sin \beta'$$

Hence for

$$\frac{NB}{nb} \leq 1, \bar{\beta} = \sin^{-1}\left(\frac{NB}{nb} \sin \pi/2\right) = \sin^{-1}\left(\frac{NB}{nb}\right) \tag{9}$$

Moreover,

$$\cos \alpha \, d\,\alpha = \left(\frac{nb}{NB}\right) \cos \beta' \, d\,\beta'$$

$$\therefore \; dI = \left(\frac{I'hnb}{N}\right) \cos \beta' \, d\,\beta'$$

$$\therefore \; dI_H = \left(\frac{I'hnb}{N}\right) \cos^3 \beta' \, d\,\beta' \qquad dI_N = \left(\frac{I'hnb}{N}\right) \cos \beta' \sin^2 \beta' \, d\,\beta'$$

Let A_{xH} and A_{xN} be the rates of absorption of the two components of cross-vibrating light. Then:

$$dA_{xH} = \left(\frac{C_H \, lI'hnb}{N}\right) \cos^3 \beta' \, d\,\beta' \qquad dA_{xN} = \left(\frac{C_N \, lI'hnb}{N}\right) \cos \beta' \sin^2 \beta' \, d\,\beta'$$

where l is the path length of a ray in traversing the photoreceptor-bearing shell. Since this shell is thin:

$$l = 2\Delta \sec \beta'$$

where Δ is the shell's thickness.

$$\therefore\ dA_{xH} = \left(\frac{2C_H\,\Delta I'hnb}{N}\right)\cos^2\beta'\,d\beta' = K'C_H\cos^2\beta'\,d\beta' \tag{13}$$

$$dA_{xN} = \left(\frac{2C_N\,\Delta I'hnb}{N}\right)\sin^2\beta'\,d\beta' = K'C_N\sin^2\beta'\,d\beta' \tag{14}$$

where K' is independent of β'.

To integrate Equations 13 and 14, one must consider two cases, and use Equation 9 to obtain limits:

Case 1:

$$\left(\frac{NB}{nb}\right) \leq 1$$

$$A_{xH} = K'C_H\int_{-\bar{\beta}}^{\bar{\beta}}\cos^2\beta'\,d\beta' = \tfrac{1}{2}\,K'C_H\,(2\bar{\beta} + \sin 2\bar{\beta}) \tag{15}$$

$$A_{xN} = K'C_N\int_{-\bar{\beta}}^{\bar{\beta}}\sin^2\beta'\,d\beta' = \tfrac{1}{2}\,K'C_N\,(2\bar{\beta} + \sin 2\bar{\beta}) \tag{16}$$

Case 2:

$$\left(\frac{NB}{nb}\right) \geq 1$$

$$A_{xH} = K'C_H\int_{-\pi/2}^{\pi/2}\cos^2\beta'\,d\beta' = \tfrac{1}{2}\pi K'C_H \tag{17}$$

$$A_{xN} = K'C_N\int_{-\pi/2}^{\pi/2}\sin^2\beta'\,d\beta' = \tfrac{1}{2}\pi K'C_N \tag{18}$$

By definition:

$$A_{xH} = I\theta C_H \qquad A_{xN} = I(1 - \theta)C_N$$

Eliminating I and solving for θ:

$$\theta = \frac{C_N A_{xH}}{C_H A_{xN} + C_N A_{xH}} \tag{19}$$

Substituting Equations 15 to 18 in Equation 19, one gets Equations 10 and 11. Q.E.D.

REFERENCES

1. Banbury, G. H., J Exp. Bot., 1952, **3,** 77.
2. Banbury, G. H., *in* Encyclopedia of Plant Physiology, (W. Ruhland, editor), Berlin, Springer, 1959, **17,** pt. 1, 552.
3. Buder, J., *Ber. bot. Ges.*, 1920, **38,** 10.
4. Buder, J., Uebersicht über Ergebnisse einiger noch ungedruckter Arbeiten aus

den Botanischen Anstalten der Universität Breslau (mimeographed private communication), 1946.

5. BÜNNING, E., and ETZOLD, H., *Ber. bot. Ges.*, 1958, **71**, 304.
6. CASTLE, E., *J. Gen. Physiol.*, 1933, **17**, 41.
7. CASTLE, E., *J. Gen. Physiol.*, 1934, **17**, 751.
8. CASTLE, E., *J. Cell. and Comp. Physiol.*, 1937, **10**, 113.
9. CURRY, G., AND GRUEN, H., *Proc. Nat. Acad. Sc.*, 1959, **45**, 797.
10. DELBRÜCK, M., and SHROPSHIRE, W., data to be published.
11. JAFFE, L., *Exp. Cell Research*, 1958, **15**, 282.
12. LAND, E. H., and WEST, C. D., *in* Colloid Chemistry, (J. Alexander, editor), New York, Reinhold Publishing Corp., 1946, **6**, 160.
13. POPOV, K. R., *Opt. Spectroskopiya*, 1957, **3**, 579.
14. ROELOFSEN, P. A., *Biochim. et Biophysica Acta*, 1951, **6**, 357.
15. SCHERER, H., *Z. Naturforsch.*, 1951, **6a**, 440.
16. SHROPSHIRE, W., *Science*, 1959, **130**, 336.
17. SMIRNOV, L. V., *Zhur. Eks. Teort. Fiz.*, 1952, **23**, 68.
18. SMIRNOV, L. V., *Izvest. Akad. Nauk, Ser. Fiz.*, 1953, **17**, 695.
19. SMIRNOV, L. V., *Opt. Spectroskopiya*, 1957, **3**, 123.
20. STRONG, J., Concepts of Classical Optics, San Francisco, W. H. Freeman and Co., 1958.