

THE RELATION BETWEEN VISUAL ACUITY AND ILLUMINATION.*

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I.

Visual Acuity and Intensity.

1. *Data.*—It is common experience that the fineness of detail which the eye can distinguish varies with the intensity of illumination. A measure of the capacity for distinguishing details is visual acuity. This is defined as the reciprocal of the angular distance which must separate two contours in order that they may be recognized as discrete. The relation between visual acuity and illumination was first investigated in 1754 by the astronomer Tobias Mayer. He believed to have found that visual acuity increases as the sixth root of the intensity of illumination.

Since Mayer many investigators have tried to find the exact nature of the relationship between visual acuity and illumination. Uhthoff (1886), who reviewed the data 40 years ago, records about twenty contributions to this particular phase of vision. Most of these data cover only a very small range of illuminations, and therefore merely confirm daily experience. Nevertheless, even a small range enabled Posch (1876) to conclude that visual acuity varies very nearly as the logarithm of the illumination intensity. This relation is borne out by the more comprehensive data of Klein (1873) and Cohn (1883), though neither of these authors drew such a conclusion.

Uhthoff (1886; 1890) himself investigated the matter further by using white and colored lights covering a great range of illuminations.

* A preliminary account of these results was presented to the XIIth International Physiological Congress at Stockholm, August 3 to 6, 1926. Cf. *Skand. Arch. Physiol.*, 1926, xlix, 146.

From his data it is apparent that in a general way visual acuity varies in proportion to $\log I$; the relation between the two is not strictly rectilinear, but sigmoid. His data are excellent, and would suffice

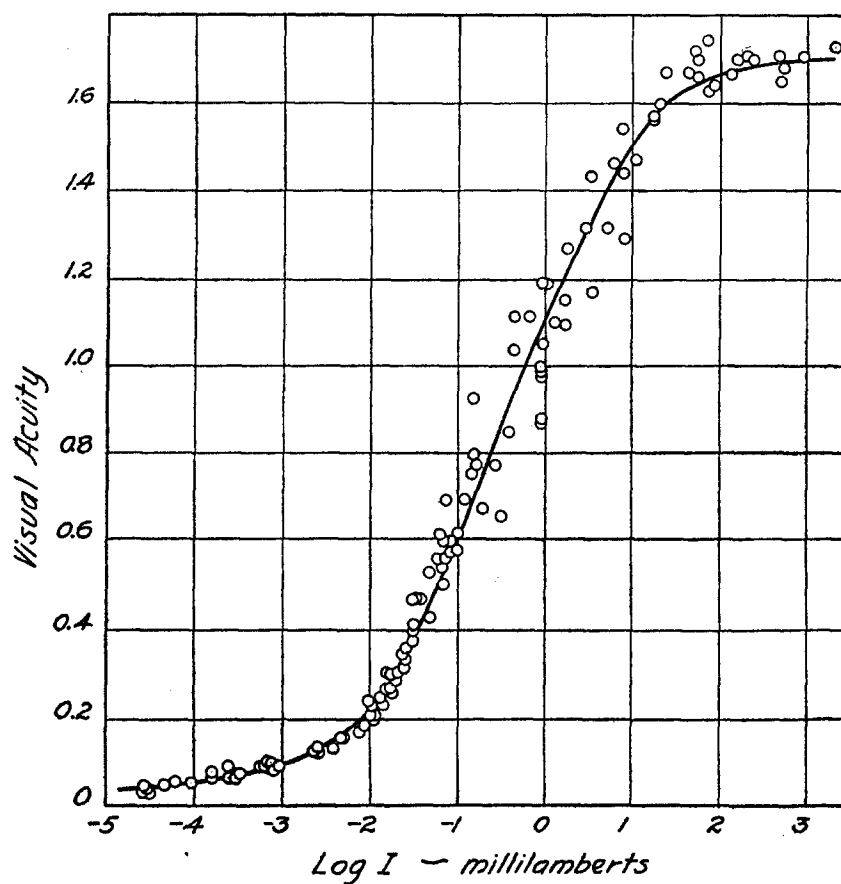


FIG. 1. Relation between visual acuity and illumination. Data of Koenig (1897). The original intensities have been multiplied by 0.072 to convert them into millilamberts. The curve is a theoretical one derived as explained in the text.

for an accurate statement of the relationship, were it not for the fact that a few years later Koenig (1897) redetermined the influence of illumination on visual acuity in such comprehensive detail that his

data have become classic. The measurements for white light are reproduced in Fig. 1. Koenig drew three straight lines through his data: one line with a small slope through the low points; another line with a steep slope through most of the points; and finally a horizontal line at very high intensities, representing a condition, known since Tobias Mayer, in which visual acuity no longer increases with illumination. For each of these straight lines Koenig wrote that visual acuity varies directly as the logarithm of the illumination.

Since Uthoff's and Koenig's experiments the number of people who have measured this relationship is not large. Up to 1912 they are recorded in an excellent memoir by Löhner (1912); an earlier review is by Zoth (1905). After that, with the recent exception of Roelofs and Zeeman (1919) there have been no significant contributions to this subject. All combined, the investigations since Koenig (*e.g.* Rice, 1912 and Ferree and Rand, 1923) have not covered the range of illumination necessary for a complete statement of this function of the eye. None the less, scattered as they are, the data indicate clearly that the relationship between visual acuity and illumination is of the form found by Koenig.

Since it is proposed to use Koenig's data as a basis for a study of this relationship, it may be well to give for comparison an example of the more recent data which cover the largest range of illuminations. Roelofs and Zeeman measured the visual acuity of their own eyes, using four different types of test objects covering only a part of the visual range with each. Their measurements are in terms of the distance which the test object (parallel lines, small squares, etc.) must be in order that it may be recognized as discontinuous. It has been necessary to convert these distances into units of visual acuity comparable to those used by Koenig, which are practically the common ones of ophthalmological practice (Koenig (1897)).¹ In order to bring the results of the four separate series of Roelofs and Zeeman together it has been necessary to multiply each by a factor. The data recalculated in this way are given in Fig. 2. It is only necessary to compare Fig. 2 with Fig. 1 to realize that they are an excellent corroboration of Koenig's work; and that Koenig's data are still the best and most com-

¹ Koenig (1897), p. 379.

plete statement of the manner in which visual acuity varies with the intensity of the illumination.

2. *Statement of Problem.*—The phenomenon that visual acuity varies in a definite way with illumination has been known for about 150

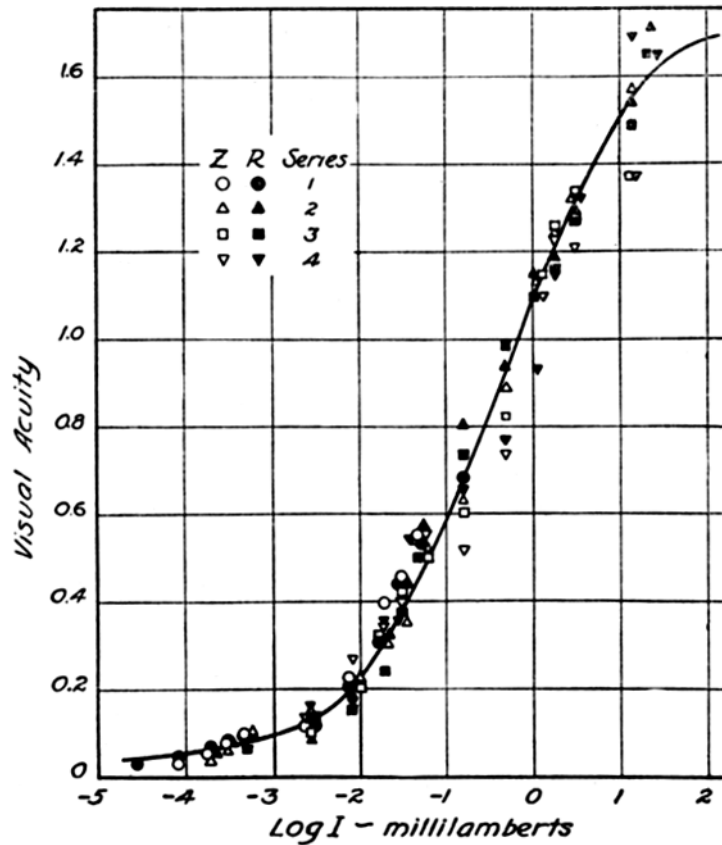


FIG. 2. Relation between visual acuity and illumination. Data of Roelofs and Zeeman (1919). The intensities have been multiplied by 0.18 to convert them into millilamberts. The measurements in Series 1 were made with black stripes; in Series 2 with large squares; in Series 3 with small squares; and in Series 4 with parallel lines. To bring them into conformity with each other and with Koenig's units of visual acuity as given in Fig. 1, it has been necessary to multiply the distances as given in Series 1 by 0.000823; in Series 2 by 0.00201; and in Series 3 and 4 by 0.00329.

years. An exact description of the relationship has been in existence for about 30 years. Nevertheless, an extensive search through the literature of vision has revealed only two occasions on which this relation has elicited any critical comment.

Helmholtz (1896) made the astute suggestion that poor visual acuity at low intensities might be related to the coarseness of intensity discrimination under similar conditions. Later, Broca (1901) supposed that a part of the increase of visual acuity with illumination could be accounted for on the assumption that at high illuminations the retinal pigment migrates between the cones, compresses them and thus decreases their diameter. For the decreased visual acuity at low illuminations Broca further supposed that the connection between retinal elements and nerve fibers is not fixed, but that the number of elements which communicate with a single fiber increases as the intensity decreases. Broca failed to realize that decreasing the diameter of the cones does not alter their average distance apart. Moreover, there is no evidence for retinal pigment migration in man (Arey, 1915).

The only real contribution to an understanding of the data in Fig. 1 was made by Koenig himself on the basis of the duplicity theory. Koenig interpreted the lower points, which he connected with a straight line of small slope, as the expression of the function of the rods in the periphery; the rest of the points, connected by a line of large slope, as the expression of the activity of the cones in the fovea. This can be verified by anyone who makes the observations. At low illuminations fixation is peripheral; at high, it is foveal.

This division of the data into rod visual acuity and cone visual acuity is positive contribution, and on it rests the present paper. However, there still remains the central, all important fact that visual acuity, as mediated either by rods or by cones, varies in a very definite manner with the illumination. It is my purpose here to propose an explanation of this relationship, and to show how it accounts for the data in quantitative detail.

II.

Nature of Explanation.

1. *Retinal Basis of Visual Acuity.*—The fineness of detail which a surface can register depends upon the number of receiving elements

present in a unit area of the surface. In other words, its resolving power varies in inverse proportion to the average distance between the centers of the sensitive elements. This is very evident in such a case as the photographic plate.

The retina is a surface of this kind since it is composed of discrete rods and cones which function as individual units or as groups of units. The way in which visual acuity varies with illumination indicates the way in which the resolving power of the retina varies. A low visual acuity means that the average distance between the retinal elements is large; whereas a high visual acuity means that the distance is relatively small. To account for the large variation in visual acuity with illumination, one must suppose that the number of sensitive elements per unit area of retina can and does vary nearly a hundred-fold. But the number of rods and cones in the retina is fixed anatomically. Therefore it is necessary to assume that the number of these elements is variable functionally.

2. *Assumptions.*—To accomplish this, I have made the almost obvious supposition that in a given retinal area, the sensitivity of the individual rods or cones is not uniform, but is distributed in relation to the intensity of illumination in the manner of populations, errors, and the like, familiar from the work of statisticians. Fig. 3 gives the sensibility distribution which has to be assumed for the cones in the fovea and for the rods in the periphery in order to describe the data of Figs. 1 and 2. The curves are absolute in their abscissa values, but are relative in their ordinate values, since these depend on the size of the unit area concerned. The rod and cone curves are identical in shape, but are different in position and in relative height of ordinates.

These sensibility distribution curves of Fig. 3 may be considered as differential curves. They represent the relative number of rods and cones whose threshold is to be found at a given retinal illumination. As such the curves show that the distribution is typically skew. What we wish to know, however, is not merely the number of elements whose threshold lies at a specific illumination, but the total number of elements which are functional at a given illumination. This is given by the integral form of the curves in Fig. 3, and corresponds at any value of I to the area under the curve to the left of that value. The integral forms of these two curves are given in Fig. 4.

Visual acuity measures the resolving power of the retina; and since this depends on the number of elements functioning in a given area, it follows that visual acuity varies directly with the number of functional rods or cones in a unit area of illuminated retina. Since the size of this "unit area" is not known, the ordinates in Fig. 4 are arbitrarily chosen to read directly in units of visual acuity. Conversely

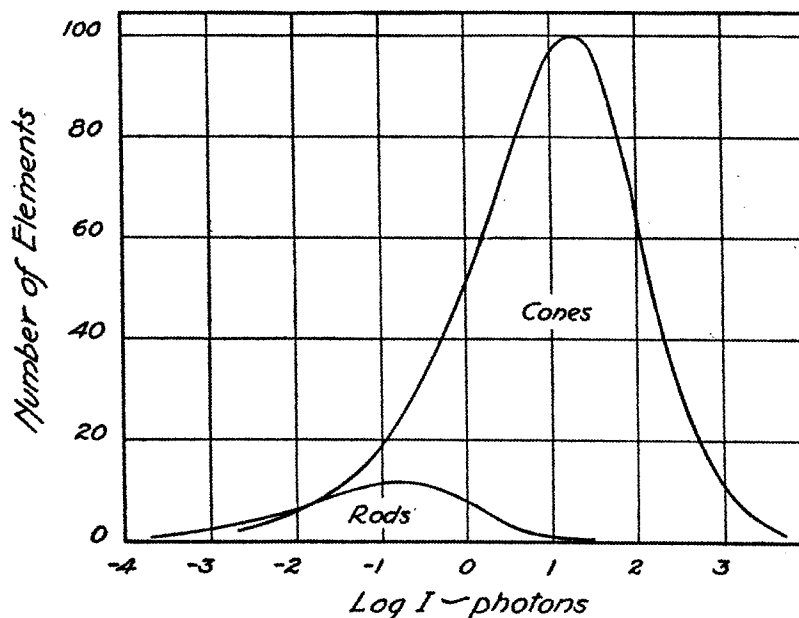


FIG. 3. Distribution of thresholds of rods and cones. The intensities are in photons, a unit introduced by Troland to represent the retinal illumination produced when the eye looks at a brightness of 1 millilambert through a pupil of 1 sq. mm. The two curves are identical in form, but different in position and in size of ordinates.

this will furnish a method of finding what the dimensions of a unit retinal area are.

3. *Explanation.*—The explanation of the variation of visual acuity with illumination in terms of these two curves in Fig. 4 is then as follows. Beginning with the lowest illuminations, vision is a function of the rods. The number of rods which are active is very small; this amounts to having a resolving surface with the receiving elements

sparsely distributed. The retinal distance between two just discriminable contours must be large, and visual acuity is very low. As the

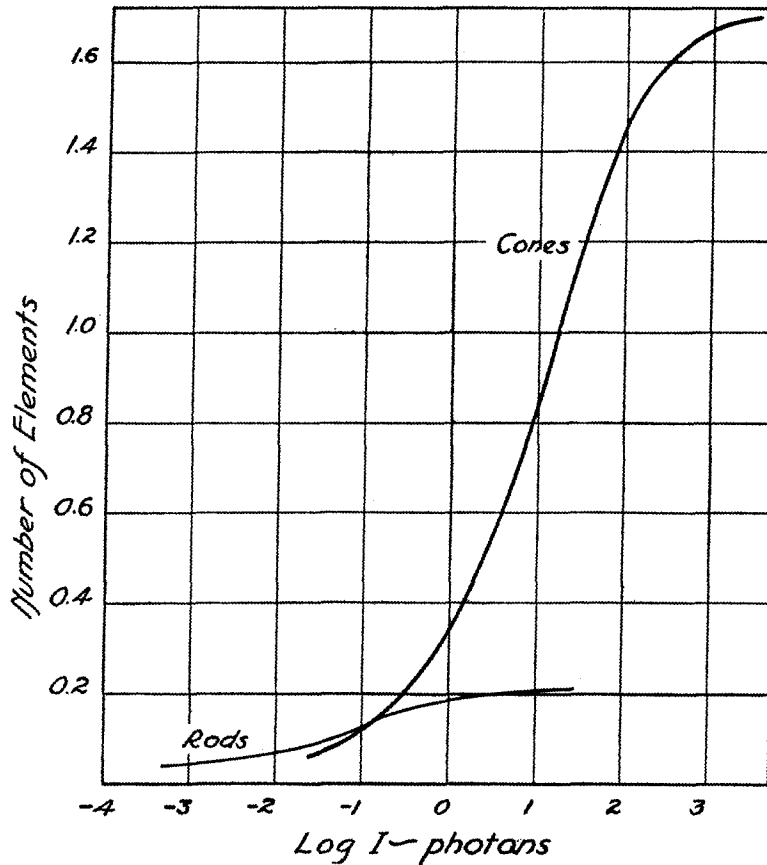


FIG. 4. Statistical distribution of sensibility of rods and cones. These curves are the integrals of those in Fig. 3, and give the relative number of elements per retinal area functional at any intensity. The curves may be described by the common Gram series of the statisticians. However, the equation here used is $KI = x^2/(a - x)$ where K and a have different values for the two curves as given in Tables I and II, and in Section IV. The ordinates read directly in units of visual acuity.

illumination increases, more and more rods reach their threshold and become functional. The average distance between the active elements becomes smaller, and visual acuity larger.

Presently an illumination is reached when the first cones begin to function. Visual acuity will still be mediated by the rods because there are already more functional rods present than cones. But as is apparent from Fig. 4, the rate at which the cones come into play with increased illumination is nearly ten times as great as the rate of the rods. Therefore at a certain point the number of cones functioning in the fovea will be equal to the number of rods in the periphery. As the intensity increases beyond this, the number of active foveal cones per unit area will be greater than the number of active peripheral rods in an equal area, and visual acuity will now be determined by the cones. This augmentation of the number of functional cones and the concomitant increase in visual acuity will continue until all the cones are active, and no further change in visual acuity is possible.

It is apparent that such a description of the relation between illumination and visual acuity is qualitatively acceptable. It remains to be shown that it is quantitatively adequate.

III.

Calculation of Normal and Color-Blind Visual Acuity.

1. *Pupil Area.*—The measurements of Koenig given in Fig. 1 were made with the natural pupil. Since the size of the pupil varies with the illumination, the sequence of intensities as given does not correctly describe the sequence of intensities falling on the retina. The outside illumination must be corrected by means of measurements relating brightness and pupil area. This correction will introduce a slight inaccuracy because it assumes that visual acuity is independent of pupil size. While this is not so (Cobb, 1914–15), it is better to neglect this slight source of error in comparison with the very large error which would result if there were no correction made for pupil area.

Fig. 5 gives the relation of pupil area to brightness calculated from the data of Reeves (1918, *b*). Reeves' illumination is given in millilamberts of brightness, whereas Koenig's data are in Hefner candles falling on white paper. Assuming a reflection coefficient of 0.8 (*cf.* Hecht, 1924–25),² one can convert Hefner candles into millilamberts by multiplying Koenig's values of *I* by 0.072. Koenig's data and

² Hecht (1924–25), p. 259.

Reeves' values for pupil diameter then become comparable and the illumination on the retina for any value of I in Koenig's data is secured by multiplying it by the corresponding pupil area at the brightness taken from Fig. 5. The pupil area is in sq. mm.; therefore the resulting retinal illumination is in photons (Troland, 1920).

In Fig. 1 there are 121 points. Their numerical values are given by Koenig in his original paper, and need not be reproduced in tabular

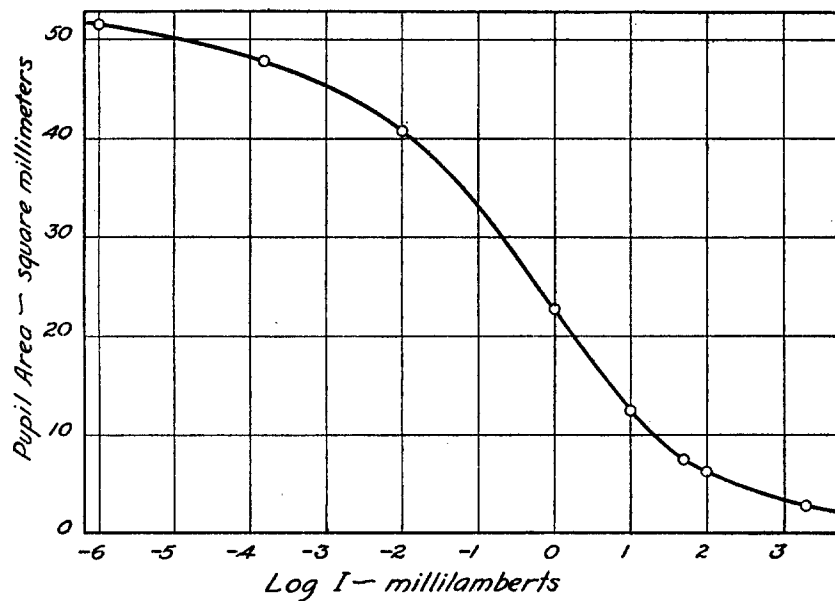


FIG. 5. Relation between pupil area and illumination calculated from the data of Reeves (1918, *b*).

form here. In working with them I have found it convenient to combine these data in consecutive groups of five readings, averaging their visual acuity and their $\log I$ values. Though not differing much from the average of the intensity values themselves, the average of the logarithms of the intensities is to be preferred because of the almost linear relation between $\log I$ and visual acuity. These averages are given in Columns 1 and 4 of Table I. In Column 2 are the pupil areas corresponding to the outside illuminations recorded in Column 1.

The retinal illumination is given in Column 3 as the products of Columns 1 and 2. Columns 3 and 4 then represent the relation between retinal illumination and visual acuity. It is these data that should be described by our assumption of the variability in threshold of the rods and cones.

TABLE I.
Relation between Illumination and Visual Acuity. Koenig's Data.

Outside illumination I	Pupil area	Retinal illumination I	Visual acuity, x		
			Observed average	Calculated, rods $0.794 I = \frac{(x - 0.03)^2}{(0.21 - x)}$	Calculated, cones $0.0906 I = \frac{x^2}{1.71 - x}$
<i>millilamberts</i>	<i>sq. mm.</i>	<i>photons</i>			
0.0000297	49.6	0.00148	0.040	0.044	
0.000130	48.0	0.00625	0.068	0.058	
0.000390	46.6	0.0168	0.075	0.073	
0.000767	45.6	0.0350	0.093	0.087	
0.00269	43.5	0.117	0.13	0.12	0.13
0.00698	41.7	0.290	0.18		0.20
0.0112	40.3	0.451	0.22		0.24
0.0153	39.5	0.605	0.28		0.28
0.0214	38.5	0.826	0.31		0.32
0.0284	37.6	1.07	0.39		0.36
0.0397	36.5	1.45	0.45		0.41
0.0678	34.5	2.34	0.56		0.51
0.0826	33.8	2.79	0.61		0.54
0.137	31.9	4.36	0.72		0.65
0.215	29.8	6.68	0.75		0.76
0.585	25.4	14.9	1.00		0.99
0.980	22.7	22.2	1.00		1.10
1.47	20.7	30.4	1.12		1.19
3.57	16.5	59.0	1.30		1.38
8.93	12.9	115.0	1.44		1.49
26.6	9.3	248.0	1.61		1.62
65.9	7.1	468.0	1.69		1.65
155.0	5.4	838.0	1.68		1.66
1096.0	3.1	3400.0	1.71		1.70

2. *Normal Eye.*—Columns 5 and 6 give the values of visual acuity taken from the curves of Fig. 4 for the retinal illuminations given in Column 3. The correspondence between experiment and theory is seen to be well within the experimental error as judged by the scatter of the data in Fig. 1.

It should be pointed out that the curve for the rods in Fig. 4 begins not at zero, but at 0.030. If the curve were to begin at zero this would mean that the average distance between functional rods at the lowest perceptible illuminations is near infinity,—which is absurd anatomically. The value 0.030 for the lowest visual acuity is found by extrapolation from the data, and gives an adequate agreement with the other measurements. This correction of lowest visual acuity is not made for the cones, first because the cones do not function at their lowest values, and second because so small a correction as 0.03 may be neglected in the much larger values of cone visual acuity.

To show the relation between the computed values of Columns 6 and 7 of Table I and the original unaveraged and uncorrected data of Koenig, I have drawn the solid line in Fig. 1. This represents the computed visual acuities referred to the uncorrected intensities of Column 1. The theory here proposed apparently gives an adequate description of these data. It is not without interest to see whether the recent data of Roelofs and Zeeman, given in Fig. 2, can be accounted for on the same basis. The solid line in Fig. 2 is drawn as in Fig. 1. It is clear therefore that the present theory forms an accurate basis for the explanation of the data of Roelofs and Zeeman as well.

3. *Completely Color-Blind Eye.*—In making the calculations I have assumed with Koenig that the lower limb of the data of Fig. 1 and of Fig. 2 represents rod vision, and the upper limb cone vision. Koenig recognized the implications which this involves, namely that in a completely color-blind individual the upper part of the curve should disappear and leave only the lower limb plus any extensions of it. He accordingly investigated the visual acuity of a completely color-blind person. The data he secured are given in the lower half of Fig. 6. They bear out his supposition that the lower limb is determined by the rods and the upper by the cones.

These data are similarly significant for us. In computing the lower part of the visual acuity data of Fig. 1, I have used only one-half of the rod population curve, on the supposition that at this point (*cf.* Hecht, 1924-25)³ the cones overtake the rods in the number of elements which are functional. If this is correct, then the data for the visual acuity

³ Hecht (1924-25), p. 252.

of the completely color-blind individual should extend to a distance beyond the inflection point of the normal eye, equal to that which has preceded it. Moreover the entire visual acuity data of the completely color-blind individual should be describable by the single rod distribution curve of Fig. 4.

Koenig's data are plotted in Fig. 6. With them are given the data previously obtained by Uthhoff (1886) for a similar case of color

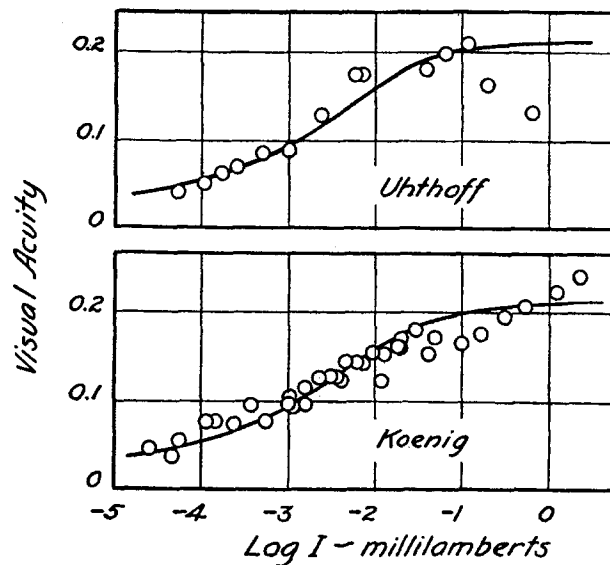


FIG. 6. Visual acuity of two completely color-blind individuals. Koenig's intensities have been multiplied by 0.072, and Uthhoff's by 0.000169 to convert them into millilamberts. In addition Uthhoff's units of visual acuity have been multiplied by 0.75 to render them comparable to Koenig's. Compare this figure with Fig. 1, but note that the ordinates here are twice as large as in Fig. 1.

blindness. To make Uthhoff's data comparable to Koenig's, the ordinates have been multiplied by 0.75. The smooth curve in both cases gives the values taken from the rod population curve of Fig. 4 but corrected for pupil area. Even though it is very likely that the behavior of the pupil is different for the color-blind eye, Reeves' values have been used again, because no other data are available. The details of the treatment are to be found in Table II, which gives, as

well, a comparison of the experimental data with those calculated in terms of the proposed explanation.⁴

IV.

Photochemical Basis of Sensibility Distribution.

1. *Independence of the Statistical Analysis.*—It is apparent from the previous section of this paper that the quantitative relation between visual acuity and the intensity of the illumination may be accurately described on the basis of a simple assumption, namely, that rods and

TABLE II.
*Relation between Illumination and Visual Acuity of a Completely Color-Blind Person.
Koenig's Data.*

Outside illumination <i>I</i>	Pupil area	Retinal illumination <i>I</i>	Visual acuity, x	
			Observed average	Calculated $0.794 I = \frac{(x - 0.03)^2}{(0.21 - x)}$
<i>millilamberts</i>	<i>sq. mm.</i>	<i>photons</i>		
0.000546	49.0	0.00268	0.054	0.049
0.000361	46.7	0.0169	0.080	0.073
0.00132	44.8	0.0591	0.101	0.101
0.00359	43.0	0.154	0.131	0.130
0.00931	40.8	0.380	0.144	0.157
0.0254	37.9	0.963	0.166	0.181
0.0991	33.1	3.28	0.185	0.199
1.75	19.8	34.7	0.234	0.210

cones vary in their threshold sensibility according to the statistical manner of other populations. Because there are certain rather extended consequences to be derived from this idea, the method of its

⁴Since this paper was submitted for publication I have found in the literature another set of data describing the relation between visual acuity and illumination for a completely color-blind individual. The measurements are again by Uhthoff (Uhthoff, W., *Z. Psychol. u. Physiol. Sinnesorgan.*, 1899, xx, 326) with still another subject, but made after Koenig's work. These data of Uhthoff's furnish extraordinary corroboration of Koenig's values, since as Koenig showed (Koenig, A., *Z. Psychol. u. Physiol. Sinnesorgan.*, 1899, xx, 425) the two possess an almost point for point agreement.

presentation has been chosen so as to render the analytical treatment independent of any previous ideas concerning the nature of the retinal process.

This having been accomplished, it becomes desirable to show how this statistical distribution is derived from, and is, indeed, a necessary consequence of the photochemical system which I have previously used as a basis for the quantitative treatment of other properties of vision. In fact the present study of visual acuity is the effort at verification of deductions made from this photochemical system; and has acquired independence only secondarily.

2. *Photochemical System.*—It has been shown that the dark adaptation of the eye (Hecht, 1921–22), and its capacity for intensity discrimination (Hecht, 1924–25), are explainable on the assumption that in the rods and cones there is present a reversible photochemical system, whose general properties may be written in the form of the equation



in which S is a sensitive substance, and P and A are materials which are decomposition products as well as precursors of S . Actually the reaction may be only pseudoreversible in that some other source of material or energy besides P and A are necessary for the regeneration of S . For the present purposes, however, equation (1) is adequate.

Let a be the total amount of S present in the system when there is no P and A ; let light of intensity I shine on it for time t ; and let x be the concentration of P and A formed and $(a - x)$ the concentration of S remaining. Then the velocity of the complete reaction will be

$$\frac{dx}{dt} = k_1 I (a - x) - k_2 x^2 \quad (2)$$

where k_1 and k_2 are velocity constants. At the stationary state of such a reaction $\frac{dx}{dt} = 0$ and

$$K I = \frac{x^2}{a - x} \quad (3)$$

where $\frac{k_1}{k_2} = K$.

Equation (3) describes the relationship between the intensity of the light to which the retina is exposed and the concentration x of the products of photolysis of S present at the corresponding stationary state of the photosensory system. The middle curve of Fig. 7 shows the relation between $\log I$ and x . The position of the curve on the abscissa axis depends on the value of the constant K ; the shape of the curve, however, remains unchanged when K is varied. The same curve applies both to rods and cones, but the value of K is different for the two (Hecht, 1924–25). This does not mean that the actual materials S , P and A are the same in the rods as in the cones, nor that they may not be three different substances in the cones or in three groups of cones. It does mean that the dynamics of the photosensory process, —its organization, —is the same in the two types of retinal cell.

The supposition is that P and A are “active” substances (chemically or electrically) and that the accumulation of a given concentration of them discharges the cell and sends an impulse down the nerve fiber. Very likely there is a secondary process intercalated between the accumulation of P and A and the discharge of the impulse (Hecht, 1925; Piéron, 1925), but that need not concern us at the moment. Suffice it that a given amount of P and A is required to cause an impulse to proceed along the attached nerve.

3. *Thresholds of Rods and Cones.*—Two assumptions may be made with regard to the amount of P and A necessary to discharge a cell. One is that the amount is the same for all the rods and for all the cones; the other, that the amount is different for the different rods and cones. In terms of the first, an increased concentration of these materials will then be indicated by an increase in frequency of discharge. This explanation serves as an adequate basis for intensity discrimination (Hecht, 1924–25) and agrees well with what Adrian and Zotterman (1926) have found for other sense cells. It is however inadequate as a basis for visual acuity because it supposes that all the rods and all the cones function at all intensities above the lowest thresholds. We know this cannot be true.

One must therefore adopt the other assumption,⁵ namely that the

⁵ There is, of course, the third possibility that the amount of P and A necessary for discharge is constant, but that the concentration of S varies widely in the

individual rods and cones differ in the concentration of P and A necessary to discharge them. Since there is no reason for preferring certain concentrations of P and A , it may be supposed that all concentrations of P and A have the same number of cells for which they specifically represent the threshold of discharge. The rods and cones are thus evenly distributed along the concentration axis (ordinates) of the $x - \log I$ curve of Fig. 7; and the total number of elements which are functional at a given value of I is directly proportional to the corresponding concentration x of P and A .

In relation to log I this linear dependence of the number of cells on the concentration of P and A results in a distribution resembling the integral curves of statisticians. In fact the curves of Fig. 4 are just this concentration-log I curve of Fig. 7. Moreover the skew frequency curves of Fig. 3 are nothing more than the first differential $\frac{dx}{d \log I}$ of the photochemical curve of Fig. 7. Indeed the computations of the theoretical values of visual acuity for Tables I and II, were made by means of equation (2) relating concentration and I . The equation for the cones is

$$0.0906 I = \frac{x^3}{1.71 - x} \quad (4)$$

and for the rods

$$0.794 I = \frac{(x - 0.03)^2}{(0.21 - x)} \quad (5)$$

where x is visual acuity, 1.71 is the upper cone limit, 0.210 the upper rod limit and 0.030 the lower rod limit. I is the intensity in photons.

These upper and lower limits for rods and cones will vary for different people, probably because the absolute number of retinal elements may be different. But as is apparent from the comparison of the data

individual cells. My reason for neglecting this hypothesis at present is not that it may not be correct, but that preliminary calculations in terms of it have not convinced me of its usefulness as a tool. One has to assume a rather awkward distribution of concentration among the cells in order to secure a distribution with regard to intensity which will satisfy the data of visual acuity. Nevertheless this possibility may have to be explored some day.

of Koenig with that of Roelofs and Zeeman and with that of Uthoff, the form of the equations remains adequate.

The agreement between experiment and calculation is thus much more significant than first appears. The frequency curves of statistics, both differential and integral, are largely empirical. They usually contain three or four parameters, and one can change them here and there in order to bring about an almost perfect fit. The curves in

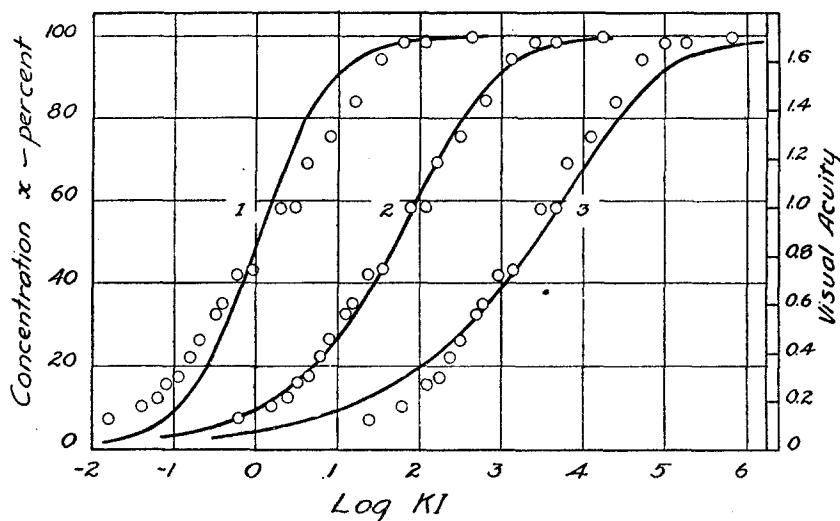


FIG. 7. This illustrates the relation of cone visual acuity to the stationary state curve $KI = \frac{x^n}{a-x}$ when n is 1, 2, and 3, and I is in photons. The visual acuity data are those of Koenig and are the averages used in Table I. It is apparent that the curve when $n = 2$ is the only one which describes the data adequately.

Figs. 3 and 4 are not derived in such a way. Their form depends on the properties of a photochemical mechanism, and is derived from previous knowledge of the behavior of the retina.

4. *Kinetics of the "Dark" Reaction.*—The equation of the stationary state (3), which is the basis for the curves describing visual acuity, is written on the assumption that the "dark" reaction which regenerates S is bimolecular. It has been contended (Lasareff, 1923, *b*) that this process need not be fixed as a second order reaction, but that

a first or third order reaction give results indistinguishable from that of a second order. This may be true for the kinetics of retinal dark adaptation, though there is evidence even here (Hecht, 1925), that such is not the case. Nevertheless, kinetic equations do not give an unequivocal statement of reaction order when actual concentrations are not concerned and arbitrary constants are freely available.

Fig. 7 shows three curves of the relation between x and $\log I$ derived from

$$K I = \frac{x^n}{a - x} \quad (6)$$

where n is 1, 2 or 3, thus corresponding to the stationary state of a first, second and third order "dark" reaction respectively. The cone visual acuity data of Table I are plotted with each curve. It is apparent that a monomolecular "dark" reaction gives a curve which is too steep; and a trimolecular, one which is not steep enough to represent the data; whereas a bimolecular one corresponds accurately with the data. It may therefore be concluded that the recovery process in the retina is adequately described only by a bimolecular "dark" reaction.

V.

Related Theoretical Consequences.

1. Intensity Perception.—The assumption that the individual retinal elements have different "discharge" thresholds is sufficient as an explanation of the behavior of visual acuity with illumination, because it underlies the statistical relation between intensity and the number of functional elements per unit area. There are other properties of vision, however, which very likely take one other thing into account, namely the frequency of discharge of each cell. Consider, for example, the situation at an intensity when half the available cones are functional. The cones whose specific threshold is 50 per cent of P and A will discharge at a given minimal frequency. But the cones whose threshold is 25 per cent of P and A will discharge impulses along the nerve at twice this frequency; and so with the others. As the illumination intensity increases, two changes thus take place simultaneously in the retina. First, the number of elements functioning per unit

area increases; and second, the frequency of discharge of each of the already functional elements also increases. Visual acuity is attributable to the first of these changes. Other properties of vision such as intensity discrimination, intensity perception, and the recognition of flicker may depend on both of these changes.

In relation to the impulses travelling up the optic nerve, an increased intensity on a given retinal area will result in an increased frequency of nerve impulses, such as has been found by Adrian and Zotterman (1926) and Adrian and Eckhard (1927). This increase in frequency is due to an increase in the number of functional rods and cones and to an increase of discharge frequency of the already functional elements, because these two changes happen concomitantly.

It is well known that the same threshold effect may be produced by a small stimulus of high intensity or by a large stimulus of lower intensity (Reeves, 1918, *b*; Piéron, 1920). Intensity recognition would thus seem to depend on the total frequency of impulses in a group of closely associated fibers in the optic nerve, and may be produced either by many elements functioning in the larger area or by a few elements discharging at a higher rate in the smaller, more illuminated area.

The interchangeability of area and intensity cannot be exact. Since the spatial distribution of the thresholds of retinal elements within small areas is very likely fortuitous, the number of elements stimulated by a given intensity will vary directly with the size of the illuminated retinal area. On the other hand, the number of elements stimulated in a given area is an approximately logarithmic function of the intensity, as shown by Figs. 4 and 7. An accurately reciprocal relation between intensity and area can therefore exist only over a very limited range. This has been demonstrated by Reeves (1918, *b*) and more recently by Piéron (1920).

Such a description of intensity recognition is the logical extension of the all-or-none law to vision. This was first suggested perhaps by Brown (1913-14) and has had an interesting corroboration by Troland (1920). It is in harmony not only with what is known of the visual process but also of muscle contraction (Lucas, 1908-09), of nerve conduction (Adrian, 1913-14), of other sensory stimulation (Adrian, 1926), and of reflex contraction (Forbes and Gregg, 1915-16). It may be

deduced, as I have already pointed out (Hecht, 1924–25), either in terms of a simple statistical distribution of sensibility, or as a consequence of a photochemical mechanism, and has no need for the confusing introduction of quantum theory speculation suggested by Lasareff (1923, *a*).

2. *Unit Retinal Area*.—The term unit area has been used throughout this paper, in a purely formal manner, as descriptive of the density of cone and rod population. Is there such a thing as a unit retinal area? Is there a minimal retinal area which contains the equipment for recording the various properties such as intensity perception, color vision, visual acuity, and the like, usually ascribed to the retina as a whole? One can, in terms of the ideas presented in this paper, make a calculation of the size of such a minimal retinal area.

As a direct result of his experiments with Brodhun on intensity discrimination Koenig computed that it is possible to recognize 572 discrete steps in brightness over the complete range of intensities perceptible to the eye. By comparing his computations with an analysis of intensity discrimination (Hecht, 1924–25) it is apparent that the first 30 of these steps are mediated by the rods; the remainder, 542, by the cones. If the recognition of a minimal intensity difference represents a change from n to $n + 1$ or to $n - 1$ in the number of cones functional in a unit area, then the *minimal* retinal area in the fovea must contain 542 cones. The actual unit area may be some multiple of this; but the *minimal* area can contain no fewer than 542 cones. This number is thus derived directly from the experimental data of intensity discrimination.

The minimal retinal area should also be able to mediate all visual acuities, from the highest to the lowest. Such an area will have for its side the retinal distance between two just perceptible contours corresponding to the lowest visual acuity. The retinal distances for all other values of the visual acuity will obviously fall within this distance. Moreover, this minimal retinal area for visual acuity is by definition the same for rods and for cones, since the unit of visual acuity is taken to be the same for both. From Koenig's data in Figs. 1 and 6, the lowest visual acuity is 0.03 units. Koenig's unit of visual acuity corresponds to a visual angle of $1' 20''$. Therefore a visual acuity of 0.03 refers to an angular separation of slightly over $44'$, and to a retinal

distance of 0.2 mm. The resulting square area is 0.04 sq. mm. The fovea contains 13,500 cones per sq. mm. (Helmholtz, 1896⁶). The minimal area derived directly from visual acuity data therefore contains 540 cones, which is the same number as that derived from intensity discrimination.

From Figs. 4 and 6, it is apparent that in the normal eyes the cones take over the mediation of visual acuity from the rods when only half of the rods are functional. There must therefore be about 60 rods per unit area in the retinal periphery in order to account for intensity discrimination. This is a ratio of 1:9 of rods to cones. Note the same relationship in visual acuity. The maximum cone visual acuity is 1.71, the maximum rod visual acuity is 0.21. This is a ratio of 1:8+ of rods to cones.

This does not necessarily mean that the number of rods is actually only about 60 per unit area. Whereas the cones in the fovea are connected in a 1:1 ratio with optic nerve fibers, the rods in the periphery are connected in a much larger ratio to nerve fibers. Such a group of connected rods can have but a single local sign, and act as a unit in visual acuity. There are probably many more than 60 rods per unit area, the exact number depending on the ratio of rods to nerve fibers.

It should be pointed out that the ratio of rods to cones in a unit retinal area corresponds with the findings in the photochemical system suggested as a basis for the sensibility distribution of the retinal elements. For a minimal intensity discrimination it was found (Hecht, 1924-25) that in the cones this means an increase of 0.20 units of photochemical decomposition, whereas in the rods the increase is 1.6 units. Since there are 100 units in each photochemical system, there are possible 500 photochemical steps for the cones, and 60 for the rods; again a ratio of 1:8+ of rods to cones.

3. *Relation to Color Vision.*—It must be obvious that the assumption of statistical variations in the threshold sensibility of the rod and cone populations of the retina is capable of wide application in the physiology of vision. This relates particularly to color vision.

It has been frequently suggested (*e.g.* Troland, 1917) that the three "fibers" of Young's original color theory may be considered as three

⁶ Helmholtz (1896), p. 260.

species of cones. Such a three cone hypothesis incorporates the three fiber idea of Young and the three substance idea of Helmholtz. Each type of cone contains its own photosensitive substance whose absorption spectrum can be derived from the *Grundempfindungen* of Koenig and Dieterici (1892); and at the same time it is connected with an optic nerve fiber, stimulation of which produces in the brain the corresponding sensation.

This supposition of separate cones for the three different *Grundempfindungen* is valuable because it enables one to extend to color vision the all-or-none law with all its realistic and clarifying consequences. Formally, however, it is only slightly better than the original fiber theory of Young, which also rests on Müller's doctrine of specific energies. In order to convert the three cone idea into a useful tool for the analysis of color vision there must be added to it the concept which has helped us in our present study of visual acuity. It must be assumed that the individuals of each of the three species of foveal cone are distributed with regard to their threshold sensibility in a manner comparable to that which we have postulated for the cones as a whole. In other words one must suppose that the cone curve of Figs. 3 and 4 is a composite curve consisting of three identical curves, each relating to one species of cone, and comprising about one-third of the cone population per unit area. The number of cones of a given species which is functional per unit area depends on the relation given by Fig. 4, where the intensity is determined by the amount of light absorbed by the corresponding sensitive substance at any wave-length. This depends on the absorption spectrum of the photosensitive substance in each cone species and may be derived from the three *Grundempfindungen* curves of Koenig and Dieterici.

The implications of such an idea can be shown by a few examples. Consider for the moment only the matter of the number of cones. Brightness depends on the total number of cones functioning in a unit area; and brightness discrimination corresponds to the addition or subtraction of one functional cone per unit area. Similarly color or hue depends on the relative number of the three kinds of cones which are functional in a unit area; and hue discrimination at constant brightness corresponds to the addition or subtraction of one functional cone of a specific type per unit area.

If a given portion of the spectrum brings into play n_r , n_g and n_b number of cones of these types per minimal retinal area, then a portion of the spectrum which will cause a change from n to $n + 1$ or to $n - 1$ in one of these three types of cone will be discriminated by the eye as different in hue from the first portion of the spectrum. Moreover, since the three *Grundempfindungen* extend practically over the whole extent of the spectrum, the change from n to $n + 1$ in one cone species must mean an associated change in the other two species as well. And since the brightness of the monochromatic patches are usually held constant in such determinations, thus making the total number of functional cones constant, a minimal change in hue will *on the average* involve the simultaneous change of three cones, one of each species. We found that a minimal retinal area contains 540 cones. Granting three cone species of approximately equal numbers we get about 180 cones per species per unit area. If, now, a spectral hue discrimination involves *on the average* one of each species of cone, then the number of monochromatic patches obtainable with a spectrum is about 180. It is significant that Koenig (1894-95) obtained 160 such patches; Nutting (1920) between 130 and 180; Laurens and Hamilton (1923), 161 and 207 respectively.

Another example of the application of the statistical distribution of thresholds to color vision concerns the matter of complementary colors. Suppose that the sensation of white results in the brain when in a unit area there is functional a definite ratio (perhaps 1:1:1) of cones of the three types. A spectrum color cannot of course produce this ratio, but must involve a preponderance of that species of cone whose absorption maximum lies nearest this particular wave-length. Then the complementary of this spectrum color must be the one which will cause to function such a number of cones of the different types that the total number of functional cones of the three types will be in the ratio required to make white in the brain.

These bare essentials have been mentioned here, because they follow almost obviously from the original assumption applied to visual acuity, namely, that the thresholds of the cones and of the rods are distributed in relation to the intensity in a statistical manner similar to that of other populations. The quantitative details of these applications to color vision will be presented in future communications.

VI.

SUMMARY.

1. Visual acuity varies in a definite manner with the illumination. At low intensities visual acuity increases slowly in proportion to $\log I$; at higher intensities it increases nearly ten times more rapidly in relation to $\log I$; at the highest illuminations it remains constant regardless of the changes in $\log I$.

2. These variations in visual acuity measure the variations in the resolving power of the retina. The retina is a surface composed of discrete rods and cones. Therefore its resolving power depends on the number of elements present in a unit area. The changes in visual acuity then presuppose that the number of elements in the retina is variable. This cannot be true anatomically; therefore it must be assumed functionally.

3. To explain on such a basis the variations of visual acuity, it is postulated that the thresholds of the cones and of the rods are distributed in relation to the illumination in a statistical manner similar to that of other populations. In addition the rods as a whole have thresholds lower than the cones. Then at low intensities the increase in visual acuity depends on the augmentation of the functional rod population which accompanies intensity increase; and at higher intensities the increase in visual acuity depends on the augmentation of the functional cone population. The number of cones per unit foveal area is much greater than the number of rods per unit peripheral area, which accounts for the relative rates of increase of rod and cone visual acuity with intensity. At the highest illuminations all the cones are functional and no increase in visual acuity is possible.

4. If this division into rod visual acuity and cone visual acuity is correct, a completely color-blind person should have only rod visual acuity. It is shown by a study of the data of two such individuals that this is true.

5. The rod and cone threshold distribution has been presented as a purely statistical assumption. It can be shown, however, that it is really a necessary consequence of a photochemical system which has already been used to describe other properties of vision. This system consists of a photosensitive material in reversible relation with its precursors which are its products of decomposition as well.

6. On the basis of these and other data it is shown that a minimal retinal area in the fovea, which can mediate all the steps in such functions as visual acuity, intensity discrimination, and color vision, contains about 540 cones. Certain suggestions with regard to a quantitative mechanism for color vision are then correlated with these findings, and are shown to be in harmony with accurately known phenomena in related fields of physiology.

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