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A QUANTITATIVE BASIS FOR THE RELATION BETWEEN VISUAL ACUITY AND ILLUMINATION

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1. The ability of the eye to distinguish details varies with the illumination. Measured as visual acuity—the reciprocal of the angular distance which must separate two contours in order for them to be recognized as discrete—this capacity of the eye has been investigated by numerous workers; but best perhaps by Koenig. Koenig[1] found thirty years ago that visual acuity increases very nearly as the logarithm of the intensity of illumination. His data are given in figure 1.

In spite of the familiarity of this information and the accuracy of the data, there exists no explanation for this curious but consistent dependence of visual acuity on illumination.

2. Visual acuity is an expression of the resolving power of the retina. Variations in visual acuity under comparable conditions of the dioptric mechanism, therefore, demand corresponding variations in the resolving power of the retina. The resolving power of a surface which, like the retina, is composed of sensitive elements of approximately uniform size is a function of the number of elements present per unit area. To account in such terms for the range of variation in visual acuity would suppose that the number of sensitive elements per unit retinal area can and does vary nearly a hundred-fold as the illumination changes. But the number of rods and cones in the retina is fixed anatomically. Therefore, it is necessary to assume that the number of elements in the retina can be varied functionally.

To accomplish this, let it be supposed that the sensibility of the individual rods and of the individual cones is not the same, but is distributed in relation to the intensity in the manner of populations, errors, etc., familiar from the work of statisticians. This distribution is given in

figure 2. The intensity units in the abscissas are in terms of retinal illumination; the ordinates give relative number of retinal elements specifically stimulated by the effects of a given illumination. The rod and cone curves are identical in form, but different in position and in heights of ordinates.

Figure 3 presents the integral distribution curves corresponding to the differential curves of figure 2 and, therefore, gives the *total* number of rods or cones which function at any intensity. The numerical values of the ordinates in figure 3 are arbitrarily chosen to read directly in visual acuity units, because the actual number of elements per unit area depends on the unit area chosen.
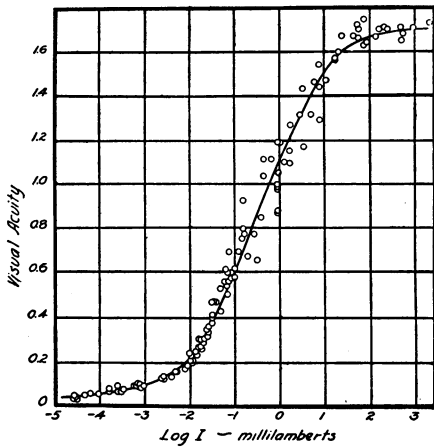

FIGURE 1

Relation between visual acuity and illumination. Koenig's original values of the intensity are multiplied by 0.072 to convert them into millilamberts.
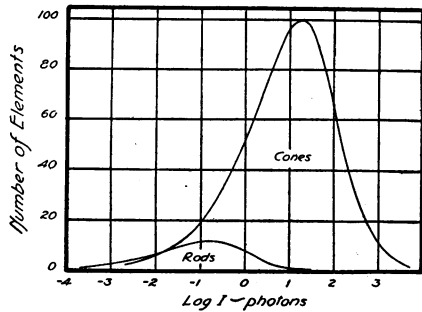

FIGURE 2

Frequency distribution curves of the thresholds of the individual rods and cones of the retina. The intensity unit represents retinal illumination and corresponds to the outside illumination in millilamberts at a standard pupil opening of 1 sq. mm

The explanation of the dependence of acuity on illumination follows from figure 3. At the lowest illuminations, vision is mediated by the rods. The number of rods which function is small, which is equivalent to a resolving surface with the receiving elements sparsely distributed. The retinal distance between two just discriminable contours must be large, and visual acuity is low. As the illumination increases, more and more rods become functional. The average distance between the functional elements becomes smaller, and visual acuity becomes larger.

Presently an intensity is reached at which the cones begin to function. Since the cones come into play nearly ten times as fast as the rods, the

number of functional cones per unit area in the fovea is soon greater than the rods in the periphery. Visual acuity then becomes a function of the foveal cones, and continues to increase steadily until all the cones are active and no further increase is possible.

The composite curve of rods and cones in figure 3 resembles the data of figure 1. In fact the curve drawn through the data of figure 1 is really this theoretical curve corrected for pupil area according to the data of Reeves.[2] The adequacy of the present explanation may thus be judged by the accuracy with which it describes the classical data of Koenig.

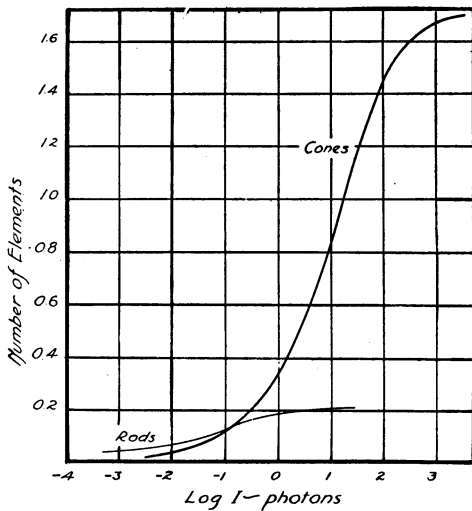3. These data are for the normal eye, and the proposed explanation

FIGURE 3

Integral frequency curves giving the total number of functioning elements per unit area at the different retinal illuminations.
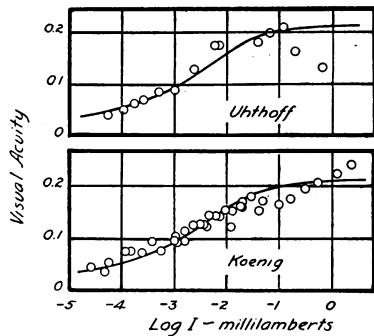

FIGURE 4

Relation between visual acuity and illumination for two completely color-blind individuals, one measured by Uhthoff and the other by Koenig. Uhthoff's original ordinates have been multiplied by 0.75 to make them comparable to Koenig's.

obviously rests on von Kries' theory of the functional separateness of rods and cones corresponding to their anatomical separation by Schultze. Koenig recognized this and attributed the lower limb of the data to the rods, and the remainder to the cones. He also recognized the implications involved, namely that in a completely color-blind individual the cone portion of the curve should disappear and leave only the lower rod limb plus any extensions of it. Figure 4 gives the data for two such individuals, one measured by Uhthoff[3] and the other by Koenig. They bear out Koenig's supposition that the two limbs of the normal eye follow von Kries' "duplicity" theory.

These data are equally significant for our explanation. Figure 3 shows that, for the normal eye, the cones overtake the rods at the middle of their range. It, therefore, follows that in a completely color-blind eye the visual acuity data should extend to a distance beyond the rod-cone intersection point equal to that which has preceded it. Moreover, the entire visual acuity data of such a case should be described by the single rod distribution curve of figure 3. The curves in figure 4 are this rod curve, the pupil correction being included as before. It is apparent that both sets of independent data are reproduced by the rod sensibility distribution curve.

4. In figure 3 the number of elements functional per unit retinal area was arbitrarily chosen to correspond directly to visual acuity units, because the actual number must depend on the size of the unit area specifically selected. It is possible, however, that there is such a thing as a minimal retinal area which carries out all the functions of the retina as a whole, such as seeing the entire range of color perception, of intensity discrimination and of visual acuity. If this were so, then the size of this minimal area, as found from the data of the different visual functions should be comparable.

From the data of intensity discrimination, Koenig computed that the whole range of intensities visible to the eye is made in only 572 discrete steps in intensity recognition. About 30 of these steps are mediated by the rods; the rest, 542, by the cones. In terms of the present notion of the sensibility distribution of rods and cones,[4] this would mean that the recognition of an intensity difference corresponds to a change from n to $n + 1$ or to $n - 1$ elements functioning in a unit area. Therefore, the minimal retinal area must contain 542 cones, or some multiple of that number.

In the same way a minimal retinal area must be able to mediate the whole range of visual acuity. The lowest visual acuity in the data of figure 1 is 0.03 unit. This corresponds to a visual angle of slightly over 44 minutes, and to a distance of 0.2 mm. on the retina. The minimal retinal area would then be 0.04 square mm. There are 13,500 cones per square mm. of fovea, from which it appears that the minimal retinal area of 0.04 sq. mm. contains 540 cones in the fovea. This is a rather striking agreement from two independent sources. A corresponding area in the periphery would then contain about 60 rods (or groups of rods, since unlike the cones, several rods are often connected to a single nerve fiber).

5. The assumption at the basis of the present explanation of visual acuity is that the rod and cone populations of the retina are like most other biological populations in the way in which their special sensory characteristic is distributed among their constituent individuals. This apparently statistical distribution of rod and cone thresholds is a funda-

mental, even if novel, point for an understanding of the visual process. Obviously, it describes the data of visual acuity. It also describes the data of intensity discrimination and of intensity recognition.[4]

In addition it can be applied to a basis for color vision. The three groups of color-sensitive fibers of Young's original color-vision theory may be considered as corresponding to three groups of color-sensitive cones. If it is then supposed that within each group of cones there exists a sensibility distribution comparable to that given here for the cones as a whole, a great many properties of color vision and of color blindness automatically follow, and are expressible in quantitative form. This supposition is here presented because it follows from the idea developed for visual acuity. The details of its application will be presented in future communications.

6. The quantitative basis here given for visual acuity is proposed independently of any mechanism to account for the statistical distribution of the sensory thresholds of the retinal elements. Nevertheless, it is necessary to point out that the form of the frequency curves of figures 2 and 3 is neither empirical nor arbitrary, but is derived from certain considerations of the photochemical properties of the retina. Studies of such visual phenomena as dark adaptation have shown that in the rods and cones there very likely exists a reversible photochemical system which may be written

$$S \underset{\text{``dark''}}{\overset{\text{light}}{\rightleftharpoons}} P + A$$
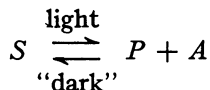
where S is a photosensitive substance, and P and A are its two principal precursors. The substances are probably different for the rods and the cones; but their dynamics may be considered as similar. Under continuous illumination by the intensity I the system comes into a stationary state described by the equation

$$KI = \frac{x^2}{a - x}$$

when a is the initial concentration of S, $a - x$ the concentration at the stationary state, x the concentration of its decomposition products P and A, and K is a constant.

In such a system the sensibility of a given retinal element depends on the concentration x of decomposition products P and A necessary to discharge an impulse to the nerve fiber. To derive the integral frequency curves of figure 3 from the equation of the stationary state it is supposed that the retinal elements are uniformly distributed in relation to the concentration x necessary to discharge an element. This amounts to making the total number of active elements a linear function of the concentration x. In relation to log I the number of functional elements

becomes identical with the stationary state curve relating x and log I, and it is this curve which is used in figure 3. Its first differential is given by the curves in figure 2.

Further details of this photosensory system are to be found elsewhere.[4] It is presented in its bare essentials here, so as to show that the frequency curves forming the basis of the present theoretical treatment of visual acuity are derived from it; and, therefore, that this phenomenon is not isolated, but explainable in terms of a mechanism which has been used for the study of other properties of vision. The complete details of this work will appear in the *Journal of General Physiology*.

[1] A. Koenig, *Gesammelte Abhandlungen zur physiologischen Optik*, Leipsic, 1903.

[2] P. Reeves, *Psychological Review*, 25, 1918.

[3] W. Uhthoff, *Archiv Opthalmalogie*, 32 (1), 1886.

[4] S. Hecht, *J. General Physiology*, 7, 1924.

THE FLORA OF THE HERMIT SHALE IN THE GRAND CANYON, ARIZONA

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The upper part, including nearly 300 feet, of the great series of red beds found in the walls of the Grand Canyon, is known as the Hermit shale. The base of this formation lies on the sandstone forming the "Esplanade," the topmost member of the Supai formation, also red, and the lowest of its beds occupy a shallow stream erosion network cut in the top of the "Esplanade." The Hermit shale consists of scattered thin sandstones and sandy shale, of a slightly warm brick red. The sediments are fresh-water laid, mainly rather fine, more or less distinctly angular sand grains, thinly coated with red oxide of iron. The shales are stream ripple-bedded and wavy. Occasional thin beds of sand evidently were rapidly deposited. Erect plants rose through and above them. Argillaceous or mud layers are largely confined to very thin slimy silt deposits that settled to form films or thin coverings on the sandy bottoms and sloping shores of quiescent pools after the run off of water.

The lower part, at least, of the formation was laid down by streams, first gradually filling the old drainage system and later building up a flood-plain over the "Esplanade" sandstone. The streams were more or less intermittent, with dry intervals in which the water in some of the shallow channels was largely or wholly evaporated. Steepness of the banks of the old waterways suggests arroyo systems cutting a great flood-plain of red sand.