AREA AND VISUAL THRESHOLD

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I

INTRODUCTION

Increase in the area of a visual field results in orderly decreases in the threshold for light and color, the minimum separable and discriminable, the fusion interval,[1] and the latent period of electrical response in the retina, optic nerve, and cortex. Various of these relations have been observed in the conger eel, frog, rabbit, cat, and man.[2] The variation of each of the properties cited with area may be represented graphically by a smooth curve convex to the origin. In every case the effect of increase in area is an improvement in visual performance.

It is apparent that these phenomena reflect some basic retinal characteristic. Recently this has been assumed to be the reflex interaction of disperse portions of the retinal surface. Various area relations have been attributed to summation, inhibition, and in one significant case to inhibition of summation (Graham and Granit, 1931).

If it were true that just proximal to the layer of rods and cones the impulses from widely separated retinal areas converge on common paths (Granit, 1932), then the exquisite image-forming mecha-

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[1] By this term is meant the reciprocal of the minimum frequency at which an intermittent stimulus produces a "fused" sensation.

[2] Investigations upon the visual threshold are referred to in the course of the paper. Work upon other functions includes: minimum separable (Wertheim, 1894); minimum discriminable (Aubert, 1865, p. 86; Cobb and Moss, 1927); fusion interval (Granit and Harper, 1930); latent period of the electrical response in the retina and optic nerve of the conger eel and frog (Adrian and Matthews, 1927); in the retina of the cat (Granit, 1933); in the cortex of the rabbit (Bartley, 1935).

nisms of the eye; the correspondence of dimensions of retinal receptors with the optimal visual acuity (Helmholtz, 1911); and the relatively intact spatial projection of the retina upon the cerebral cortex (Lashley, 1934) should be alike meaningless. All these relations indicate a mosaic of relatively independent receptor-nerve units. It is the purpose of this paper to show that simple properties of a mosaic retina account qualitatively and quantitatively for the characteristic variation with field area of the visual threshold.

II

Measurements

The threshold-area measurements reported in this paper were obtained in collaboration with Dr. Charles Haig at the close of an investigation of dark adaptation in various retinal areas (Hecht, Haig, and Wald, 1935–36). The same apparatus was used, and indeed the experiments shown in Figs. 1 and 2 formed part of the latter research. I am greatly indebted to Professor Hecht and Dr. Haig for permission to use these data.

TABLE I

(*Effective Distance, Eye to Field, 385 mm.*)

Field diameter	Angular diameter	Area	Relative area
mm.		*sq. mm.*	
1.184	55.25′	30.06	1.00
2.421	1°53′	125.8	4.18
3.633	2°49′	283.2	9.42
4.932	3°50′	521.6	17.35
6.367	4°56′	869.6	28.93

All of the original measurements reported have been performed upon the author's right eye. The dark adaptation procedure has already been described (Hecht, Haig, and Wald, 1935–36). In examining the effect of area on threshold, the subject was first dark adapted for 30 minutes, and then exposed to circular fields of various dimensions, fixated by means of a small bright "star" placed at various distances above the fields. The threshold of each field was determined three times consecutively. Definition of the outlines of the field was not required; the threshold response was the simple liminal light sensation. The field could be exposed at will by raising a blind, and was opened for successive flashes of about 1 second duration in the course of a measurement. At times, at the end of a series of readings, initial measurements were repeated to find whether changes had occurred during the experiment. No significant change was ever detected.

Five fields were used, varying in relative area from 1 to 28.9, and in angular diameter from approximately 1° to 5°. These approximate visual angles are used to characterize the fields throughout the present paper. Their accurate dimensions are shown in Table I.

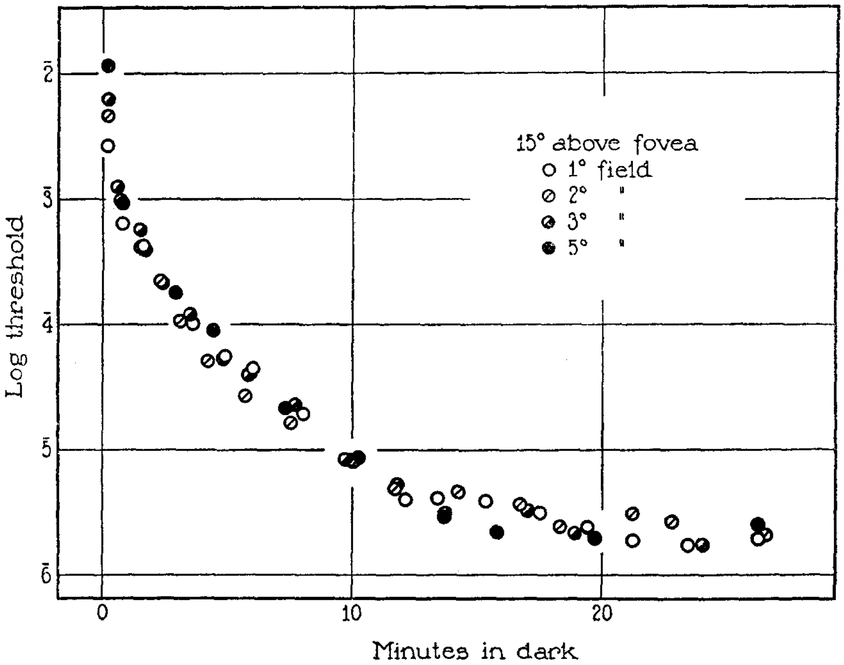

FIG. 1. Dark adaptation in fields fixated 15° above the fovea. The thresholds for the 5° field are in millilamberts. The remaining curves have been uniformly displaced on the *log threshold* axis to emphasize their identity in form.

Hecht, Haig, and Wald have shown that in centrally fixated fields wider than 1°, the fall in threshold of the dark adapted eye with increase in area is due primarily not to the change in area itself, but to variation in the rod-cone composition of the fields. This heterogeneity of the central retina is reflected in an orderly way in large changes in the form of the dark adaptation curves. The latter, therefore, offer a convenient index of variations in the character of the retinal population.

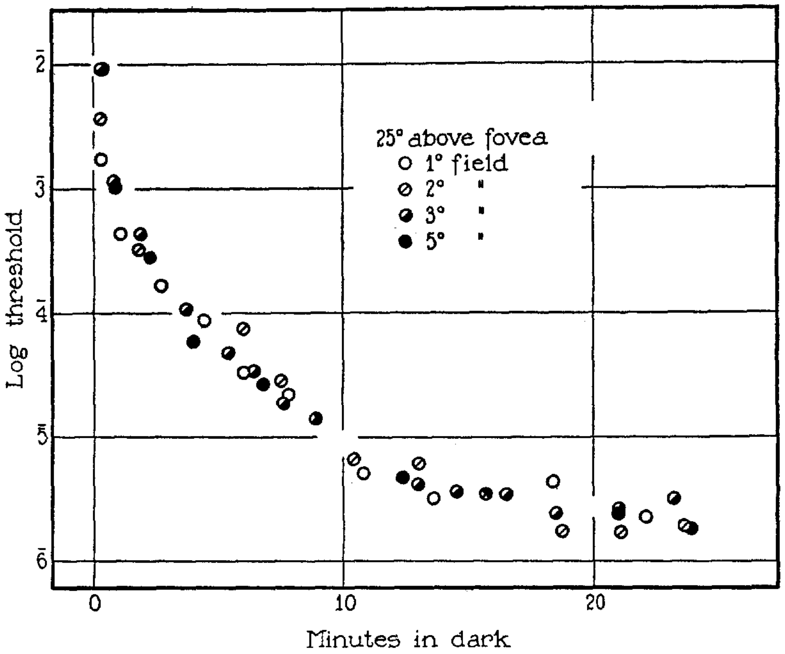

FIG. 2. Dark adaptation in fields fixated 25° above the fovea. Thresholds as in Fig. 1.

TABLE II

(1) Number of measurements	(2) Area	(3) Average log threshold	(4) Computed log threshold
	15° above fovea		
	sq. cm.	*ml.*	*ml.*
9	0.301	$\bar{6}.82$	$\bar{6}.81$
9	1.258	$\bar{6}.24$	$\bar{6}.28$
12	2.832	$\bar{6}.14$	$\bar{6}.14$
9	5.216	$\bar{6}.06$	$\bar{6}.05$
9	8.696	$\bar{7}.97$	$\bar{7}.97$
	25° above fovea		
6	0.301	$\bar{6}.99$	$\bar{6}.98$
8	1.258	$\bar{6}.43$	$\bar{6}.43$
10	2.832	$\bar{6}.16$	$\bar{6}.21$
7	5.216	$\bar{6}.03$	$\bar{6}.06$
7	8.696	$\bar{7}.98$	$\bar{7}.94$

In fields fixated 15° or 25° above the fovea, the shape of the dark adaptation curves remains unaltered as the field diameter is increased from 1° to 5° (Figs. 1 and 2). Apparently within these limits the elementary composition of the fields remains constant.

In these homogeneous regions of the retina pronounced effects of area on threshold are found. At 15° above the fovea, increase in the field diameter from 1° to 5° lowers the threshold sevenfold; at 25° above the fovea, tenfold (Figs. 3 and 4). The figures show the individual measurements. Averages of these data are presented in Table II. No attempt has been made to indicate in the figures several instances in which identical threshold readings were obtained repeatedly; therefore they show the range, but not always the precise weight of the measurements.

III

Analysis

General Considerations.—In any region of the retina the receptor units—rods, cones, or summating clumps of rods or cones—form a population within which retinal properties are distributed in various ways. Obviously the number of elements which possess a specific value of a property increases with the size of the field. If the population is homogeneous throughout the regions examined, this increase is proportional, and curves describing the distribution of the property among the elements are multiples of one another, proportional in height to the field area. This situation is presented schematically in Fig. 5, in which for simplicity a linear form of distribution of a retinal property, x, is shown for a series of areas.

Most types of visual measurement appear to involve not the entire population of the retinal field, but a comparatively small number of units which are peculiarly susceptible to the stimulus. Tentatively one may assume that a threshold response involves the activity of a fixed number of retinal elements. Such an assumption appears in Fig. 5 as a line drawn parallel to the abscissae. It cuts the distribution curves for increasing areas in decreasing values of the retinal variable, x. When values of x and area obtained from such a diagram are plotted graphically, they assume precisely the general form of all the area relations.

Several arbitrary steps which have appeared in this procedure are not essential. Any type of distribution of x among the elements does as well qualitatively as the linear form used in the diagram. Moreover, the distributions may vary in form or increase disproportionately with area. Even the assumption of the participation of a constant number of elements in the measurements is unnecessary. The qualitative decrease in x with increase in area follows from any law included between this one and the assumption that the number of elements entering the measurements is proportional to the area of the field, which would appear in the diagram as a line parallel to the ordinates. It is shown below that actually the threshold number of active elements, if it increases at all, does so much more slowly than the field area.

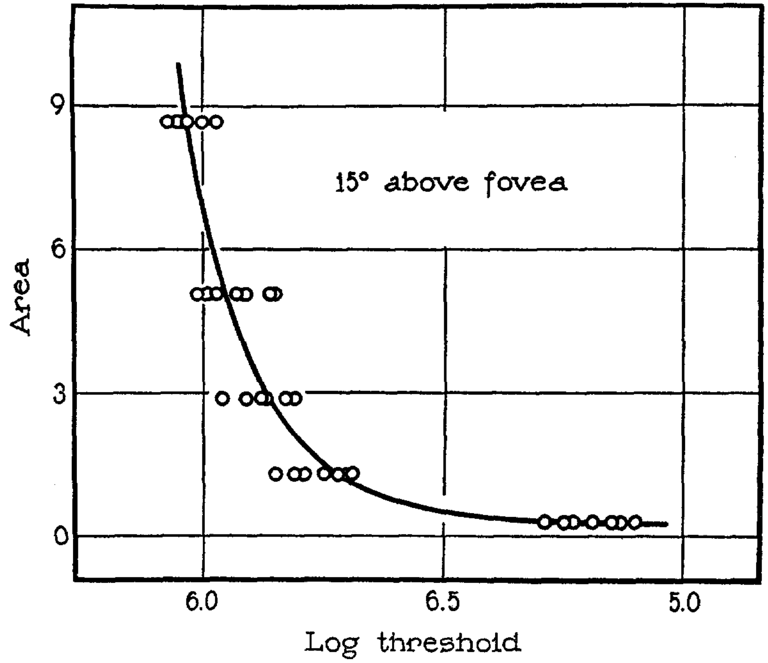

FIG. 3. The area-threshold relation in fields fixated 15° above the fovea. Field areas in square centimeters, thresholds in millilamberts. The points are individual measurements taken from three experiments. The curve is theoretical; its equation is $0.33 \log (A - 0.275) + \log I = -5.72$.

Ultimately, only the basic concept of the retina as a population of relatively independent units is indispensable to the analysis. With this accepted, the characteristic type of dependence of all retinal properties upon area follows inevitably.

Area and Threshold.—Applied specifically to the area-threshold problem, these considerations reduce to two propositions, the first implicit in the homogeneity of the retinal areas examined, the second a reasonable assumption concerning the threshold.

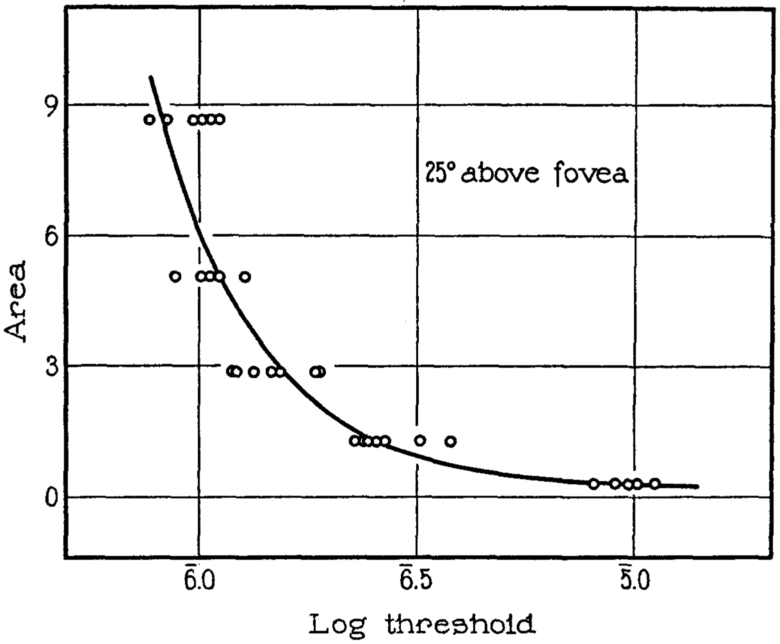

FIG. 4. The threshold-area relation in fields 25° above the fovea. Units as in Fig. 3. The points are from two experiments. The curve is theoretical; its equation is $0.54 \log (A - 0.20) + \log I = -5.56$.

1. Throughout all portions of a homogeneous retinal region the percentage of elements which possess a specific intensity threshold is the same. In a series of fields of various sizes located within such a region, the number of elements of fixed threshold is directly proportional to the field area. The integral distribution curves for such fields are therefore simple multiples of one another. This is the situation shown in Fig. 5 and obtaining in the present experiments.

2. A clue to the significance of the threshold was furnished by a subjective observation noted consistently throughout these experiments. Thresholds were always measured to the liminal light sensation, regardless of definition of the field. Nevertheless, when this limen is attained in a 1° field, its boundaries are sharply defined. At the threshold of a 2° field, its boundaries have become hazy. This dissipation of the sensation increases rapidly with further increase in area. Finally, in 5° fields no spatial impression at all remains, but merely a formless sensation of light flashing on and off as the blind is raised and let fall.

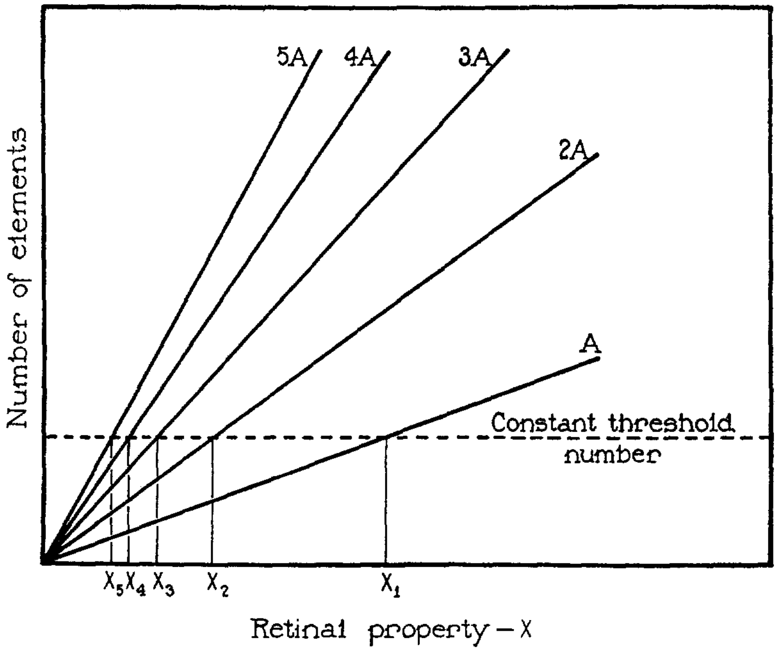

FIG. 5. The mechanism of variation of a retinal property, x, with field area. The heavy lines are hypothetical integral distributions of the property in a series of areas, A to $5A$. As the area increases, a constant threshold number of elements respond at decreasing values of the property, x_1 to x_5.

If the threshold corresponded with the excitation of a constant *density* of retinal elements, all fields should have been equally well defined. The actual responses are as though at the threshold a number of elements is active, sufficient to define a small field but too small to resolve a large one. This number, if it increases at all, does so much more slowly than the area. We shall assume that it remains constant for all the fields: *that the threshold corresponds to the stimulation of a constant number of elements.*

This assumption does not imply reflex interaction among the threshold elements. The formal conditions of the analysis are fulfilled if the threshold number is taken to be 1. Since in the present experiments the form of the smallest field is resolved, more than a single element must respond at these thresholds. But this very observation demonstrates that this is not a case of spatial summation, of convergence upon a final common path. For a summating group of elements must behave as a unit, and therefore cannot resolve an image.[3] Certainly some integration of responses from the individual elements which enter the threshold is implied. That this is probably central is shown by experiments upon the binocular threshold, which most investigators have found to be lower than the monocular (Piper, 1903 *a*; Roelofs and Zeeman, 1914; Shaad, 1934). In forming the binocular threshold, impulses from the single retinas must reach the centres, yet fail to elicit a sensation. It seems reasonable to suppose that these subliminal reactions consist of impulses from fewer than the constant threshold number of elements.[4]

Derivation of the Threshold Distribution.—Though any type of function for the distribution of thresholds yields the correct qualitative area-threshold relation, for a quantitative description of the phenomenon a "true" distribution is needed. With the use of the constant threshold number assumption the requisite portions of this may be derived directly from the data.

The following procedure yields the threshold distribution in the 1°

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[3] König (1897) has shown that at the threshold of a large unfixated field, the human eye can resolve a minimum separable of about 25 minutes; *i.e.*, that active elements are about 0.11 mm. apart on the retinal surface.

[4] I believe Beitel's experiments (1934) to provide another example of this phenomenon. Beitel found that two adjacent subliminal test-patches may evoke the liminal response when applied simultaneously. He concluded this to be an example of spatial summation. I should prefer to assume that each patch stimulated fewer than the threshold number of elements, both together just this number.

field, 25° above the fovea. At $log\ I = \bar{6}.99$, the constant threshold number of elements, n_t, is active in this field of relative area, *1.00*. At $log\ I = \bar{6}.43$, n_t elements operate in the 2° field of relative area, *4.18*; therefore at this intensity $n_t/4.18$ elements are active in the 1° field. At $log\ I = \bar{6}.16$, n_t elements are stimulated in the 3° field of relative area, *9.42*; therefore at the same intensity $n_t/9.42$ elements are active in the 1° field. By completing this process five points are obtained on the distribution curve which relates the illumination to the relative number of active elements in the 1° field. The distributions in the larger fields are simple multiples of this, proportional to area.

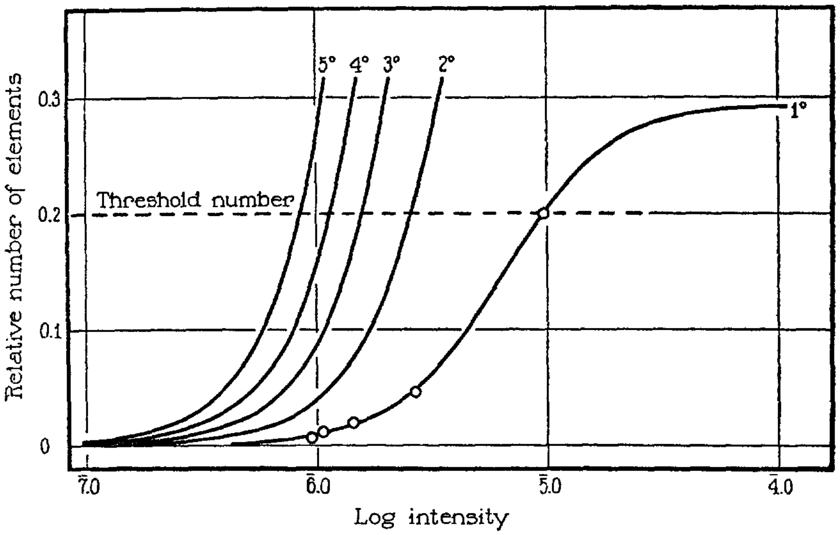

FIG. 6. Graphic analysis of the threshold-area relation, 25° above the fovea. The open circles were calculated from the averaged data of Table II as described in the text. The distribution curves conform to the equation, $0.54\ log\left(\frac{A}{n} - 1\right) + log\ I = -5.20$. The constant threshold number line cuts them in theoretical thresholds for the various areas.

The points obtained in this way for the 1° field, 25° above the fovea, are plotted in Fig. 6. The curve drawn through them is theoretical, and is described below. The data for fields 15° above the fovea yield similar results. It is apparent that the points themselves adequately complete a quantitative analysis. This may be recapitulated: (1) Using the constant threshold number assumption, the relevant portion of the threshold distribution in one area is obtained from the area-threshold data. (2) The distributions for other areas are simple multiples of this. (3) The intercepts of these distributions with the constant threshold number line at n_t regenerate the original data.

Derivation of an Area Equation.—A general equation for the type of distribution derived in the preceding section would be very useful, since from it a rational formula for the area-threshold relation might be obtained. The points derived in the previous section describe correctly the beginnings of the distribution function. Obviously it must end by becoming parallel to the abscissa, when the total number of elements in the area becomes active. The complete function is, therefore, sigmoid in form, when threshold is plotted logarithmically. Hecht (1928–29) has concluded from quite independent evidence that the distribution of log threshold intensity is sigmoid.

A number of formulae for sigmoid curves have been applied in the present analysis with varying degrees of success. All of them yield roughly the right type of answer. This is inevitable, for even so naive a diagram as Fig. 5 does so. The equation of the lines in Fig. 5 is $n = kAI$, in which n is the number of active elements; A, area; $I = x =$ intensity; and k is a proportionality constant. If n is held constant to the threshold value n_t, the equation becomes $AI = n_t/k =$ *constant.* This relation is familiar as "Riccò's law" (1877); it is inexact but encouragingly close to a correct solution.

One expression has been peculiarly successful in describing the present and related data. I shall derive this by two methods with quite different, though not mutually exclusive, implications:

1. Hecht (1928–29) has based the form of the threshold distribution upon the photochemical steady state. The equation for this may be written (Hecht, 1934–35):

$$KI = \frac{x^p}{(a - x)^q}$$

in which I = intensity, x = concentration of photoproducts, a = maximum value of x, and K, p, and q are constants. Rewritten in the form of a threshold distribution this becomes

$$KI = \frac{n^p}{(A - n)^q}, \text{ or}$$

$$(A - n)^q I = n^p/K,$$

in which A, n, and I are respectively the field area, number of active elements (really the "active area"), and intensity. If n is held constant to the threshold value n_t, this reduces to

$$(A - n_t)^q I = n_t^p/K = \text{constant}, \tag{1}$$

the desired area-threshold relation.

2. The second derivation assumes no mechanism, and possesses the advantage of being sufficiently general to be applied to other area phenomena in addition to the threshold. It is based upon Verhulst's so called logistic formula (1838), a symmetrical sigmoid function. This is of the form

$$y = \frac{K}{1 + Ce^{-mx}}$$

in which y and x are variables, K is the maximal value of y, and C and m are constants. As a threshold distribution this may be written

$$(a) \qquad n = \frac{A}{1 + Ce^{-m \log I}}$$

This is exactly equivalent to Hecht's photochemical steady state equation for the case $p = q = 1/0.4343m$.

$$(b) \qquad nCe^{-m \log I} = A - n$$

$$(c) \qquad \log nC - 0.4343m \log I = \log (A - n)$$

If $1/0.4343m$ is set equal to a new constant, k, this becomes

$$k \log (A - n) + \log I = k \log nC \tag{2}$$

When n is held constant to the threshold value n_t,

$$k \log (A - n_t) + \log I = k \log n_t C = \text{constant}, \tag{3}$$

or, removing the logarithmic notation,

$$(A - n_t)^k I = \text{constant.} \tag{4}$$

This is an area-threshold equation identical with (1). Written as in (3) it is the equation of a straight line of slope k and intercept $k \log n_t C$. In this form it may readily be tested with the data.

With A expressed in square centimeters, if n_t is set equal to *0.275* for fields 15°, and *0.20* for those 25° above the fovea, the straight lines of Fig. 7 result. Their slopes and intercepts, substituted in equations (3) and (4), yield the following completed area-threshold equations:

$$\begin{array}{ll} 15^\circ \text{ above fovea} & \left\{ \begin{array}{c} 0.33 \log (A - 0.275) + \log I = -5.72 \\ \text{or} \\ (A - 0.275)^{0.33} I = 1.9 \times 10^{-6} \end{array} \right. \\ 25^\circ \text{ above fovea} & \left\{ \begin{array}{c} 0.54 \log (A - 0.20) + \log I = -5.56 \\ \text{or} \\ (A - 0.20)^{0.54} I = 2.75 \times 10^{-6} \end{array} \right. \end{array} \tag{5}$$

From these equations the curves of Figs. 3 and 4 have been computed. It is clear that they describe correctly the course of the individual measurements. The equations have been used also to compute theoretical values of *log threshold* for the areas investigated. These are shown in column 4 of Table II; they agree very closely with the experimental averages.

By substituting the appropriate values of k and C into equation (2), and allowing n to vary while A is held constant, the theoretical threshold distributions may be computed. In this way the distribution curves of Fig. 6 were obtained. The curve for the 1° field fits the points derived by direct analysis of the data. The series of curves is cut by the appropriate constant threshold number line in theoretical values of *log threshold*, corresponding with those computed arithmetically from the equations and shown in Table II.

Piper (1903 *b*) first proposed for peripheral fields the empirical expression, $\sqrt{A}\ I = constant$. Henius (1909) and Fujita (1909), working in the same laboratory, showed this to hold roughly in fields 1° to 10° in diameter, and beyond these limits not at all. An equivalent expression, proposing reciprocity of field diameter and threshold, has been shown by Piéron (1920 *a*, *b*) to hold in neither small peripheral nor foveal fields.

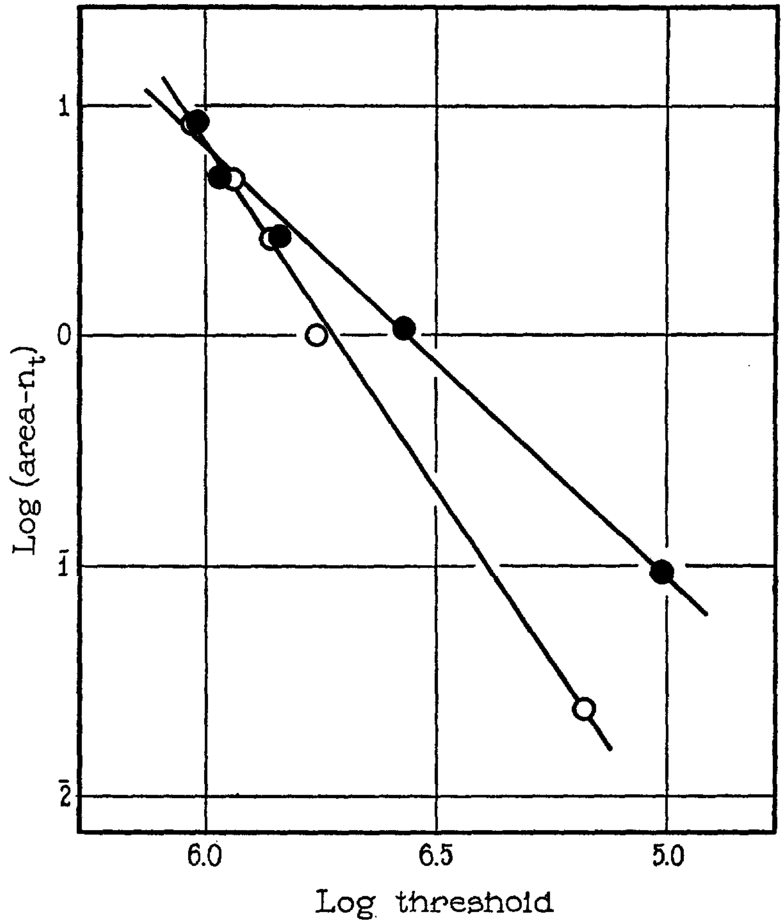

FIG. 7. Linear graph of the threshold-area relation, 15° (open circles) and 25° (closed circles) above the fovea. Areas in square centimeters, thresholds in millilamberts.

The present analysis has led to the general expression $(A - n_t)^k$ $I = constant$. When the threshold number of elements, n_t, is a small fraction of the total number in the visual field, A, the term $(A - n_t)$ approaches A as its limiting value. This condition is fulfilled in quite small foveal fields, in which the concentration of receptor units—presumably individual cones—is very high. It should obtain only in much larger peripheral fields, since in the periphery the retinal elements are comparatively large summating clumps of rods. In both cases the threshold-area equation reduces to the simple form, $A^k I = constant$.[5]

If, with n_t a small fraction of A, k chance to take the value *0.5*, the equation becomes $\sqrt{A}\ I = constant$, or Piper's rule. This is a rough approximation to the present solution, in which k is found to equal 0.33 and 0.54 in two peripheral regions.

IV

Foveal (Cone) Thresholds

A number of investigators have measured the area-threshold relation in small fields, centrally fixated. When the diameters of the fields do not exceed 1.5°, they may be assumed to fall wholly within the fovea and to stimulate a relatively homogeneous population of cones. The analysis proposed here should be directly applicable to such data.

Experiments of Abney (1897) and Piéron (1920 *b*) have been examined. In both cases the direct plot of *log area* against *log threshold* yields straight lines. This relation was discovered empirically by Abney. Apparently the threshold number of elements, n_t, is a negligible fraction of the total populations of these fields.

The data of Abney obtained with test illuminations of wave length 527 mμ are shown in Fig. 8. Their equation is $0.85 \log A + \log I = 0.49$. Data obtained at other wave lengths are described by similar expressions, differing only in the terminal constant. Piéron's data agree reasonably well with the equation, $0.88 \log A + \log I = -4.37$. The variation in terminal constants here is due to the use of different units of area and intensity. The slope constants are independent

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[5] This expression was discovered empirically by Abney (1897). Its limitations in small fields (under 1°8′ diameter) have been defined by Abney and Watson (1916): within the fovea, or in monochromatic red light—both conditions for stimulating cones—the rule holds; in fields of other colors outside the fovea it fails. These restrictions agree sensibly with our theoretical expectations.

of these units and agree well with each other. Both equations may be combined in the form $A^{0.85-0.88}I$ = *constant.*

Riccò (1877) and again Charpentier (1882) proposed for foveal fields the empirical rule, AI = *constant.* This expression states that the liminal foveal response is evoked by a constant flux of light, regardless of its spatial dispersion. The simplicity of this rule has preserved it in spite of repeated demonstrations of its failure to describe accurate data (Aubert, 1865; Abney, 1897; Abney and Watson, 1916; Piéron, 1920 *b*). "Riccò's law" is still widely accepted as a basis for theoretical discussion.

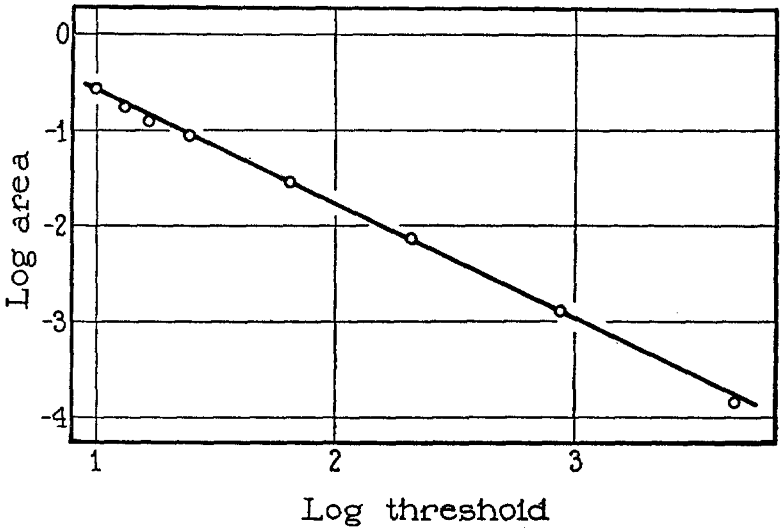

FIG. 8. Foveal thresholds to light of wave length 527 mμ, as a function of field area. Data of Abney (1897).

With n_t a small fraction of A, if k chance to assume the value 1, the general expression $(A - n_t)^k I$ = *constant* reduces to AI = *constant*, or Riccò's law. The accurate values of k in the two sets of data we have analyzed are 0.85 and 0.88. In other cases they may fall below 0.5 (data of Watson, in Abney and Watson, 1916). No basis exists, therefore, for the acceptance either of Riccò's rule or of its implication of perfect spatial summation in the fovea (Creed, 1931; Houstoun, 1932).

DISCUSSION

The quantitative development of the present area-threshold analysis rests upon the assumption that at the threshold a constant number of elements respond. This is probably approximately true for a wide range of areas. It may be expected to fail both in very small and very large fields.

Very small fields require fairly intense light to stimulate them. This probably excites certain of their elements to respond at well above their liminal frequencies. The threshold in such cases is likely to correspond more nearly to a constant over-all *frequency* of response than to a constant *number* of active elements. The threshold number of elements may be expected to decrease, as the frequency of response of individual elements rises. In the extreme case, it is likely that any single element, responding at sufficiently high frequencies, may excite the liminal sensation.

A more fundamental consideration, however, is the fact that the present analysis as a whole applies only to populations of elements sufficiently large to permit statistical treatment. It states nothing, therefore, about the behavior either of single elements or of very small fields.

In very large fields the threshold number of elements may be expected eventually to rise, due to the difficulty of distinguishing a very low density of active elements against the persistent background of visual "*Eigenlicht.*"

The quantitative treatment, therefore, rests admittedly upon a reasonable approximation. It yields the threshold-area equation, $(A - n_t)^k I = constant$, which describes the available data accurately, and is the general form of previous empirical formulae for this function. Whether the quantitative theory is finally to be regarded as entirely rational, or as a rational approach to a correct empirical solution, is of little present importance.

Throughout this investigation area phenomena have been assumed to originate in peripheral structures. Since the mosaic character of the retina appears to be transmitted relatively intact as far as the occipital cortex (Lashley, 1934), this point of view is unimportant. It is probable that area relations amenable to the present type of analysis occur at all levels of the visual pathways.

SUMMARY

1. The variation of threshold with field area was measured in fields homogeneous in rod-cone composition. At 15° above the fovea, an increase in field diameter from 1° to 5° reduces the threshold sevenfold, at 25° above the fovea tenfold.

2. These changes are shown to follow qualitatively from simple statistical properties of the retinal mosaic. Analytic treatment leads to the expression, $(A - n_t)^k I = C$, in which A = area, n_t = constant threshold number of elements, I = threshold intensity, and k and C are constants. This equation describes the available data accurately, and is the general form of previous empirical area-threshold formulae.

REFERENCES

Abney, W. de W., *Phil. Tr. Roy. Soc. London, Series A*, 1897, **190**, 155.
Abney, W. de W., and Watson, W., *Phil. Tr. Roy. Soc. London, Series A*, 1916, **216**, 91.
Adrian, E. D., and Matthews, R., *J. Physiol.*, 1927, **63**, 378; 1928, **65**, 273.
Aubert, H., Physiologie der Netzhaut, Breslau, E. Morgenstern, 1865.
Bartley, S. H., *Am. J. Physiol.*, 1935, **110**, 666.
Beitel, R. J., Jr., *J. Gen. Psychol.*, 1934, **10**, 311.
Charpentier, A., *Arch. opht.*, Paris, 1882, **2**, 487.
Cobb, P. W., and Moss, F. K., *J. Exp. Psychol.*, 1927, **10**, 350.
Creed, R. S., *Brain*, 1931, **54**, 29.
Fujita, T., *Z. Sinnesphysiol.*, 1909, **43**, 243.
Graham, C. H., and Granit, R., *Am. J. Physiol.*, 1931, **98**, 664.
Granit, R., *Arch. Ophth.*, New York, 1931, **6**, 104.
Granit, R., Physical and Optical Societies report of a joint discussion on vision, London, The Physical Society, 1932, 263.
Granit, R., *J. Physiol.*, 1933, **77**, 207.
Granit, R., and Harper, P., *Am. J. Physiol.*, 1930, **95**, 211.
Hecht, S., *J. Gen. Physiol.*, 1928–29, **11**, 255; 1934–35, **18**, 767.
Hecht, S., *Physiol. Rev.*, 1937, **17**, 239.
Hecht, S., Haig, C., and Wald, G., *J. Gen. Physiol.*, 1935–36, **19**, 321.
von Helmholtz, H., in Southall, J. P. C., Treatise on physiological optics, translated from 3rd German edition, 1911, Optical Society of America, 1924, **2**, 32.
Henius, K., *Z. Sinnesphysiol.*, 1909, **43**, 99.
Houstoun, R. A., Vision and colour vision, London, Longmans, Green and Co., 1932.
König, A., *Sitzungsber. Akad. Wissensch. Berlin*, 1897, 559.
Lashley, K. S., *J. Comp. Neurol.*, 1934, **60**, 57.

Piéron, H., *Compt. rend. Soc. biol.*, 1920 *a*, **83,** 753; 1920 *b*, **83,** 1072.
Piper, H., *Z. Psychol. u. Physiol. Sinnesorgane*, 1903 *a*, **31,** 161; 1903 *b*, **32,** 98.
Riccò, *Ann. ottal.*, Pavia, 1877, **3** A, VI, 373.
Roelofs, C. O., and Zeeman, W. P. C., *Arch. Ophth.*, Leipsic, 1914, **88,** 1.
Shaad, D. J., *Arch. Ophth.*, New York, 1934, **12,** 705.
Verhulst, P.-F., *Correspondance mathématique et physique*, Ghent and Brussels, 1838, **10,** 113.
Wertheim, T., *Z. Psychol.*, 1894, **7,** 172.