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VISUAL SENSORY UNITS AND THE MINIMAL ANGLE OF RESOLUTION*

Frank W. Weymouth, Ph.D.

Los Angeles, California

It is now 100 years since Aubert and Förster demonstrated that visual acuity is better centrally than peripherally and that the decline of sensitivity is gradual and orderly. Although this relation is now generally recognized and is known to apply to other capacities of the retina, the details and the underlying mechanism are far from being satisfactorily explored. The importance of this gradient is well recognized. Polyak, in his monumental work on the retina, gives as the seventh reason for undertaking such a task the fact that the "known structures are inadequate to explain the retinal gradient. Even such an apparently elementary problem as to what anatomical factors are responsible for the striking difference between the central and the peripheral acuity . . . remains unsolved. . . ." (Polyak, 1941, p. 186). It is only necessary to point out the relation of the gradient to such clinical problems as the loss of acuity due to central scotomas, small angle squints, and amblyopia, for example, to show the practical importance of a detailed knowledge of the retinal gradient. Despite interest, the difficulties of the experiments have limited the number of attempts and have prevented wholly satisfactory results.

A contributing cause to the difficulty of analysis has been the absence of any simple mathematical characterization of the curve of acuity as a function of distance from the fovea. The curves are often described as a fall of acuity "at first very rapid but later progressively slower" or some similar expression which could apply with equal vagueness to several distinct mathematical curves. Precision is necessary for effective comparison of curves from different individuals or obtained under different conditions.

Gradient in terms of minimal angle of resolution

It is, therefore, of interest that the minimal angle of resolution, the reciprocal of the visual acuity, presents a much simpler picture of the gradient than does the acuity. The eye is unique in that the sensitivity has been used for its rating rather than the threshold, as is customary with other sense organs, but the minimal angle of resolution (MAR), a true threshold, is now coming into general use. In Figure 1 are presented the visual acuity and the minimal angle of

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* From the Los Angeles College of Optometry.

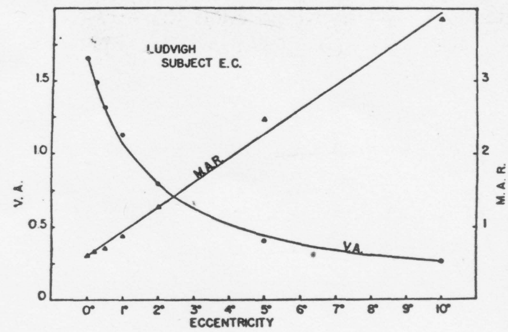

Fig. 1 (Weymouth). Visual acuity and minimal angle of resolution as functions of retinal eccentricity. Data from Ludvigh, subject E. C.

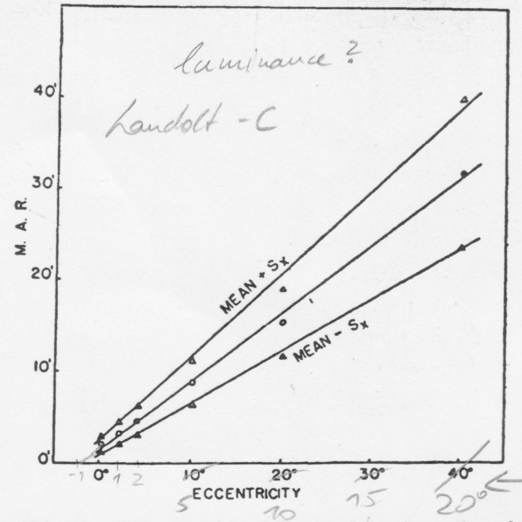

Fig. 2 (Weymouth). Mean minimal angle of resolution and points, one standard deviation above and one standard deviation below, as functions of retinal eccentricity. Data from 20 observers, one eye only.

resolution plotted as functions of the distance from the point of fixation in degrees. These values for the light adapted eye are from Ludvigh (1941). It is obvious that these data are reasonably represented by a straight line.

If this relation is close and general enough, a precise and simple description of the curve is available in the constants of the straight line, the slope and intercept. Since the minimal angle of resolution is the reciprocal of the visual acuity, existing data may readily be transformed.

Before generalizing from this example, several questions must be asked. How satisfactory is the fit of the straight line? Does it apply to data from other workers? Does it apply to the full range of eccentricity that has been explored? To turn farther afield: Does the linear relation apply to other thresholds of the eye, and, if so, which ones?

The first question is not easily answered to the satisfaction of the statistician. Published data of this type are traditionally presented in the form of average acuities for each eccentricity, and without the original observations none of the measures of reliability can be calculated. The means conceal the variability and in consequence the fit always appears better than it really is. In the absence of the original observations for the classical work, data from a course in physiologic optics have been analyzed; the results are presented in Figure 2 and Table 1.

A shutter was used to limit the time of exposure of a Landolt C at the given eccentricity; this reduced but did not completely eliminate inexact fixation and too high acuities are often obtained, particularly at low eccentricities. On this account and because some observers failed to obtain an acuity within the range of the apparatus at the maximum eccentricity of 20 degrees, a few

TABLE 1

MINIMAL ANGLE OF RESOLUTION BASED ON STUDENT RECORDS

Eccentricity	0°	1°	2°	5°	10°	20°
Number of observations	20	40	40	40	40	40
Minimal angle of resolution (mean)	2.06	3.26	4.58	8.77	15.50	32.08
Standard deviation	0.82	1.17	1.54	2.38	3.71	8.16
Mean + standard deviation	2.88	4.43	6.11	11.15	19.21	40.24
Mean − standard deviation	1.24	2.08	3.04	6.38	11.78	23.93
Standard error of mean	0.18	0.18	0.24	0.38	0.59	1.29

records were discarded. Because of the short exposure and the low illuminance involved in projecting, the acuities as a whole are low.

The data are for 20 eyes of 20 students, none experienced observers and all doing this experiment for the first time. These conditions would promise maximum variability. Since no systematic difference was found between the nasal and temporal fields, the corresponding eccentricities were combined, giving a fixation value based on 20, and five peripheral values based on 40 observations each, a total of 220. All visual acuities were transformed to minimal angles of resolution and the regression line determined by least squares.

The standard deviations for the various eccentricities are obviously not equal, being closely proportional to the angle of resolution, and since the standard error of estimate is not valid for heteroscedastic data, it was not calculated. The graph shows the means with their standard deviations and the fitted regression line. This gives a clear idea of the variability in highly variable data and indicates the validity of the fit of the straight line for this range of eccentricities.

Generality of linear relations

The question of generality is important. The eccentricities explored in the various studies have ranged from about one to 70 degrees; the most common are those from 10 to 20 degrees. The minimal angle of resolution, which we are now considering, shows a satisfactory linear relation in the limited range of Ludvigh (10 degrees) or in the very restricted study of Weymouth, et al. (1928), in which only a little over one degree was explored (fig. 3). One the other hand, as may be seen in the graph of Wertheim's data (fig. 5), at eccentricities greater than 20 or 30 degrees there is a variable but undoubted tendency for the minimal angle of resolution as a function of eccentricity to become greater than expected from lesser eccentricities so that the curve is concave upward.

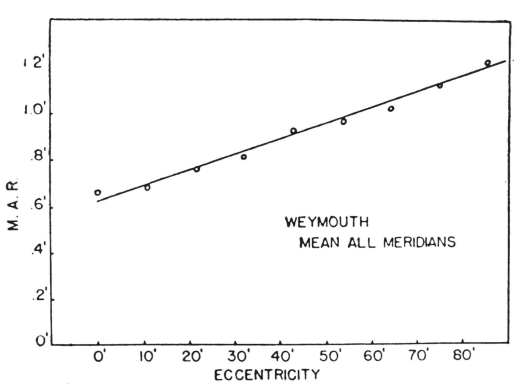

Fig. 3 (Weymouth). Minimal angle of resolution (mean of four meridians) as function of retinal eccentricity. Subject F. F. W.

Several elements may be operative here. The increasingly greater difficulty of the more peripheral observations is notorious; this would result in greater variability but not necessarily in higher values. The true angle of eccentricity presents a problem, since large external (field) angles progressively exceed the corresponding internal angles. Although this error is present and tends to cause the deviation noted, there are no adequate studies permitting correction and the usual field angles have been used.

Light incident from the periphery of the visual field encounters increased reflection and obliquity of the pupil is reduced in intensity (Weale, 1956, p. 393). Accurate values are lacking, but any marked reduction of intensity would require greater angular separation of resolvable detail and would lead to an undue peripheral rise of the minimal angle of resolution.

There are cortical, histologic (Polyak), and perimetric indications (Traquair, 1949, p. 6) of a significant distinction between "central" and "peripheral" with the boundary falling in the neighborhood of 20 or 30 degrees which perhaps would justify treating the two regions separately. In conclusion we may say that for the more important and better known central region the minimal angle of resolution as a function of eccentricity is satisfactorily linear.

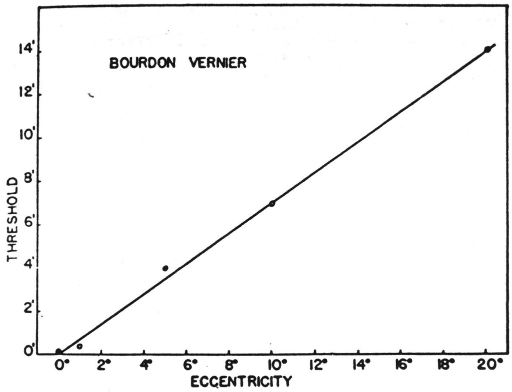

Fig. 4 (Weymouth). Vernier threshold as function of retinal eccentricity. Data from Bourdon.

TYPES OF THRESHOLDS SHOWING LINEAR RELATIONS

To what types of threshold does the linear relation apply? The minimal angle of resolution of the light adapted eye has been considered; to this may be added the vernier threshold, and several horopteral values. The light threshold of either the light- or the dark-adapted eye is not linear, nor is the critical fusion frequency. Does this incomplete list present any logical basis for classification?

Spatial and intensity thresholds are at once suggested. The visual acuity or the minimal angle of resolution is expressed in spatial terms of angular size, although this is not the only factor involved; this is equally true of the vernier threshold (fig. 4), the perception of motion (fig. 6), and the values involved in the horopter such as the width of the haplopic zone (Panum areas, fig. 7),

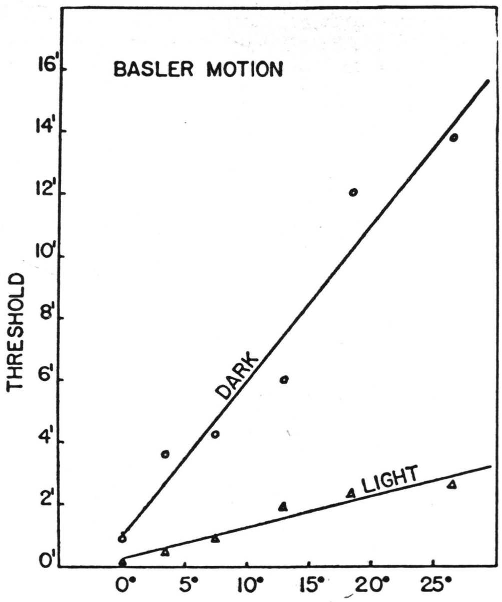

Fig. 6 (Weymouth). Threshold of motion measured in light and in dark as functions of retinal eccentricity. Data from Basler.

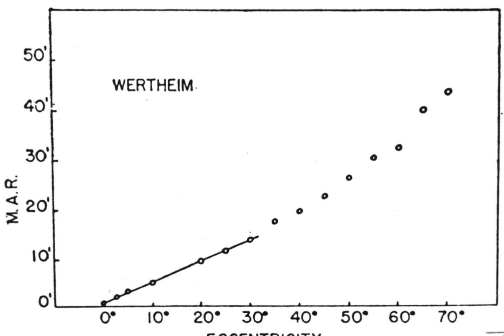

Fig. 5 (Weymouth). Minimal angle of resolution for temporal field as function of retinal eccentricity. Least square line fitted to values for 0 to 30 degrees inclusive. Data from Wertheim.

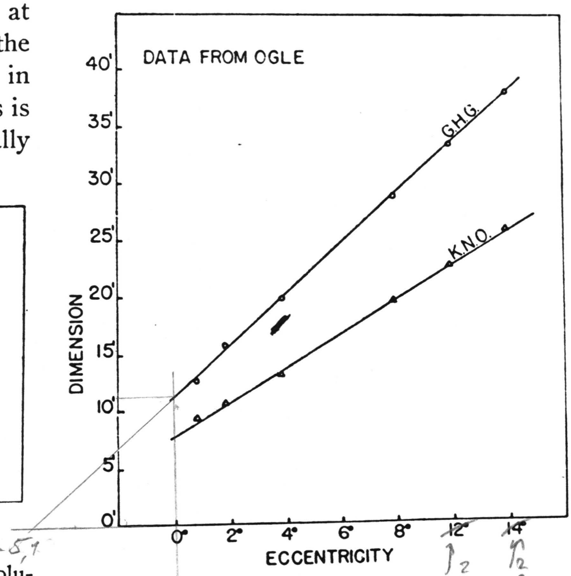

Fig. 7 (Weymouth). Diameter of Panum area for two subjects as functions of retinal eccentricity. Data from Ogle.

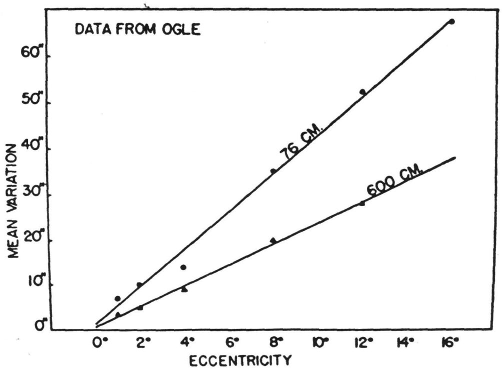

Fig. 8 (Weymouth). Mean variation of the settings of the horopter rods for fixation distances of 76 and 600 cm. as functions of retinal eccentricity; these values closely parallel the stereothreshold. Data from Ogle.

and the mean variation in the setting of the rods which is proportional to the stereoscopic threshold (fig. 8).

All these thresholds may be stated in terms of visual angle either as distances on the retina or in comparisOn between the two retinas. It should again be noted that the linear type of spatial threshold is characteristic of the light-adapted eye only, as may be seen from Figure 9 in which the values of Fick for both the light- and dark-adapted eye are plotted. Incidentally it may be pointed out that beyond 30 degrees adaptation has little effect.

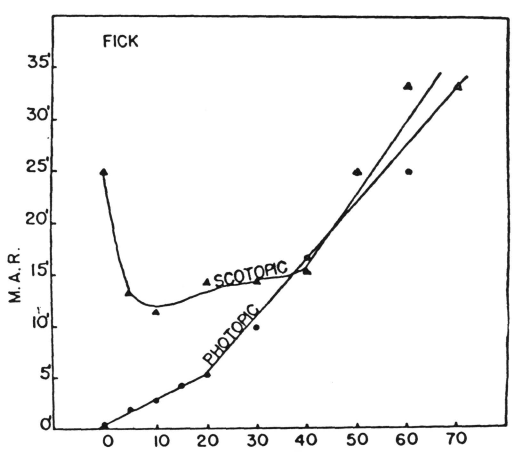

Fig. 9 (Weymouth). Minimal angle of resolution of the light and of the dark adapted eye as functions of retinal eccentricity. Data from Fick.

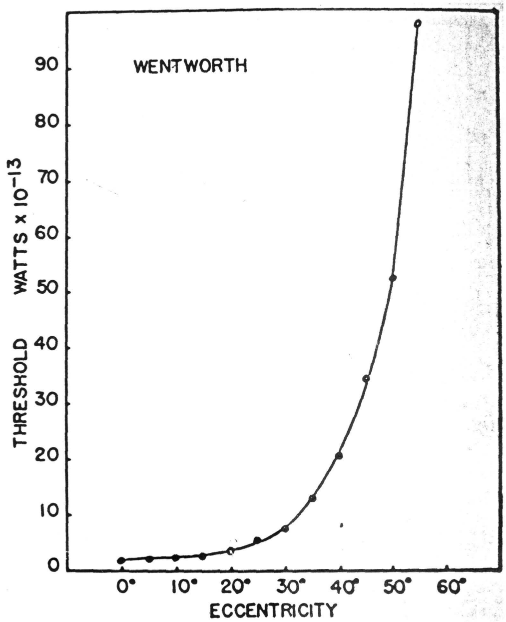

Fig. 10 (Weymouth). Light threshold (mean of four principal meridians) as a function of retinal eccentricity. Data from Wentworth.

Contrasted to these spatial thresholds linearly related to eccentricity is another group of thresholds such as that for light, the closely related pupillomotor threshold and the critical fusion frequency, which cannot be expressed in angular terms but may conveniently be considered intensity thresholds. These may be illustrated by the light thresholds of Wentworth (fig. 10). She found that progressively more energy was required to stimulate as the point of application is more peripheral, but the curve is far from a linear function of eccentricity.

Anatomic basis of visual spatial sensory units

If we are justified in saying that the common feature of those visual capacities showing linear thresholds is that these thresholds are spatial, we must seek as their anatomic basis some spatial feature of the retina. The spatial feature most often considered is cone density, for which are available the excellent data of Østerberg (1935) and Polyak

(1941). Thus, among others, Ludvigh and Polyak have plotted together visual acuity and cone density. Both decrease toward the periphery, if comparable scales are used; their relation will later be considered in more detail. Here it is sufficient to point out that physiologists accept some definition similar to the following, "the number of receptors connected by a single fiber to the brain . . . defines the extent of unitary field." (Piéron, 1952, p. 209.) If the optic nerve fiber or its cell of origin is taken as defining the retinal receptive unit, it is the density of the ganglion cell, not that of the cone, which should be related to the minimal angle of resolution or other thresholds which we are considering.

Ganglion-cell density

Unfortunately information on the density of the ganglion cells, although its logical importance is obvious, is far inferior to that for the rods or cones. The importance of ganglion cell density was recognized by Lashley in his study of vision in the rat (1932) and an analysis was attempted; but this aspect has usually been neglected. For man the work of Polyak (1941) is the best source of information, although no direct study was made and the data on ganglion-cell density are incidental. An analysis of this material was attempted. Drawings of retinal sections of the various regions are presented, and in these it was possible to make approximate counts of the ganglion cells and from the indicated magnifications to reduce these to distances between adjacent cells. The drawings were not made with this use in mind and the exact locations of the sections within the regions are not specified. Other uncertainties such as the amount of displacement of cells from the foveal to the parafoveal regions make the attempt merely an approximation.

Figure 11 is an attempt to present the data thus obtained. The calculated separation of the ganglion cells in minutes is plotted in the regions to which have been assigned the

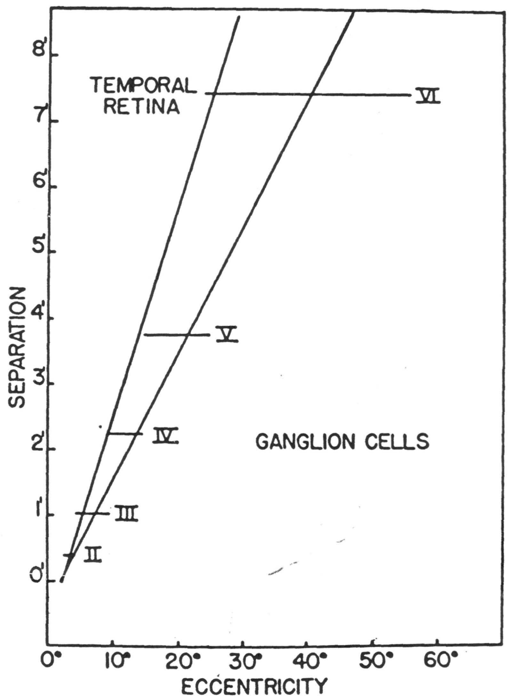

Fig. 11 (Weymouth). Ganglion cell separation as a function of retinal eccentricity; the two lines represent the two assumptions that the cell counts are characteristic of the inner margins or of the centers of the regions the width of which are represented by the horizontal lines.

eccentricity in degrees. Two lines have been drawn, one on the assumption that the slides were characteristic of the inner margin of the regions, a second on the assumption that they came from the middle of the regions. The peripheral regions are wide and poorly represented by sections; VII was omitted for lack of drawings and VI is used with hesitation. The reasonableness of the results was checked by transforming the separations into densities and multiplying by the areas of the regions to give the total number of ganglion cells. The value obtained, of approximately a million cells, was considered satisfactory. It will be noted that both lines indicate no ganglion cells in the fovea. This, of course, is true, an area 0.3 or 0.4 mm. in diameter is without cones. The ganglion cells for the sensory units of this area are found in the parafoveal region. For the center of the fovea there is independent evidence that each cone is a sensory unit, but data are lacking by which the size or number of units in the parafoveal region can be determined.

In spite of the obvious shortcomings of the data, certain general features justify the labor involved. First, the separation of the cones (number of cones per minute of arc) as a function of eccentricity is linear. Second, the slope of the line lies between +0.2 and +0.3 or within the range of slopes shown for the minimal angle of resolution and other thresholds. The parallelism between the anatomic and the functional evidence that the diameter of the sensory unit is a linear function of eccentricity is the first reasonable, if sketchy, quantitative picture of the basis of spatial discrimination. It is to be hoped that an adequate histologic study of ganglion-cell density will in time give a firm anatomic basis for the spatial gradient.

Cone density and visual acuity

Let us return to the comparison of cone density and visual acuity. Polyak says, "Represented diagrammatically Fig 12A (fig. 99) the above figures of the size and separation of the cones form a curve similar to the visual-acuity curve of Wertheim and others, with a rapid fall close to the center and a slower decline toward the periphery of the field of view. The falling-off in the curve representing the cone gradient is, however, somewhat less steep than in the functional curve, suggesting a greater increase in the size of the functional cone units in the extra-foveal regions than indicated by the numerical distribution of the cones" (p. 436).

Although there is some confusion in the scales of the figure, the description is essentially correct. On another page he throws doubt on his own interpretation: "The belief of physiologists that the lesser peripheral visual acuity is due to several photoreceptors forming here a single physiological unit is still an assumption based at best only on computation. . . ." In the following analysis the logic of "computation" is rated rather higher.

For significant comparison, comparable scales are necessary. The visual acuity scale is based on an assumed "normal" angle of resolution of one minute of arc. The Snellen fractions are ratios representing the number of resolvable thresholds per minute; the Snellen decimal of 0.5 indicates that there is only half of a threshold per minute; that is, that the threshold is two minutes. The comparable scale for the cones would be the number of cones (better, the number of center-to-center cone separation) per minute. This is the reciprocal of the "separation" of cones as given by Polyak. Plotted on these scales as functions of eccentricity the comparison is shown in Figure 12A. The data of Fick have been used because the better known values of Wertheim are given only in the relative form, with foveal acuity set at 1.00. It will be seen that the foveal values differ little, but that as the periphery is

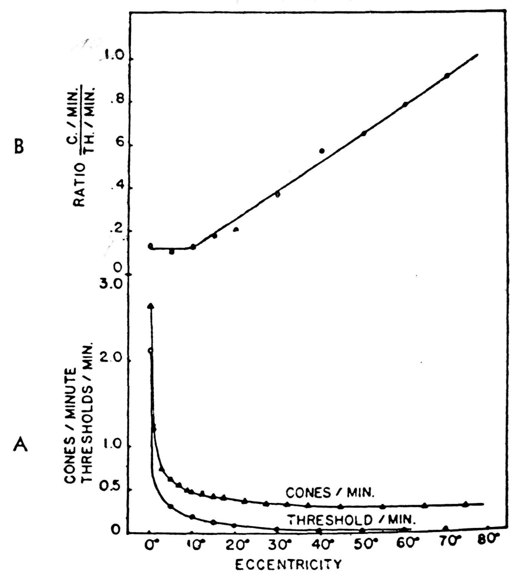

Fig. 12 (Weymouth). (A) Visual acuity (threshold/minute of arc) and linear cone separation (cones/minute of arc) as functions of retinal eccentricity. Visual acuity data from Fick; cone data from Polyak. (B) Ratio (cones per minute of arc/thresholds per minute of arc) as a function of retinal eccentricity.

invaded the "linear cone density," as the scale may be called, lies at a higher level than visual acuity. It is clear by "computation" that the sensory units, except at the fovea, must include more than one cone.

The ratio, cones per minute divided by thresholds per minute, should then give the number of cones in the diameter of a sensory unit; these ratios are given in Table 3 and are plotted in Figure 12B. It will be noted that in the fovea there is one threshold to one cone but that in the periphery the number of cones per sensory unit increases, as has often been repeated, as a linear function of the eccentricity to reach a value of over nine at 70 degrees, the limit of Fick's data.

The average of the ratios, weighted to take into account the areas involved, should be the ratio of the total number of cones divided by the total number of ganglion cells. The data, extrapolated to 80 degrees, give a weighted mean of 7.5; the number of cones by Østerberg's count is 6,550,000, the number of optic nerve fibers is 852,500 (Bruesch and Arey, quoted by Polyak); this gives a total ratio of 7.7.

Considering the wide range of published counts and the sources of error in comparing the acuity of one author with the cone density of a second, this strikingly confirms the previous analysis that the ganglion cells are the anatomic representatives of the sensory units and their regional distribution the basis of the linear relation of the threshold to eccentricity.

Earlier work

Has the linear relation of threshold to eccentricity been noted by earlier workers in this field? In Ogle's plots of the Panum areas on eccentricity (1950, p. 65, fig. 33) the lines connecting the points form linear regressions in some, in others there is a small concavity upward. He comments, "The relative proportion of Panum's areas to the peripheral angle is important. Figure 34 shows the curve which described the relationship. . . . The abscissa is the peripheral visual angle eccentricity and the ordinate is the ratio, expressed in percent, of the horizontal dimension of Panum's area to the visual angle. The curve decreases rapidly from the macula to a visual angle of four degrees, and then reaches a nearly constant value of about three percent for visual angles beyond five to six degrees."

Again on page 228 in Table 18 he gives as simple fractions the relative visual acuities as functions of eccentricity from Wertheim, Fick, and Ludvigh. In Figures 138 and 139 are plotted values derived from the table and mean deviations of the rod settings of the horopter for several workers for comparison with percentage magnification of images. Although a number of these approximate straight lines, this feature is not commented upon.

Ogle is impressed with the apparent constancy of the Panum areas as percentages of the eccentricity. If the threshold as a function of eccentricity were a straight line passing through the origin (this does not occur and would require an infinite foveal sensitivity) the threshold would be a constant percentage of the eccentricity. It is here claimed that these curves approximate a straight line, but with a finite and positive intercept; this would lead to a decreasing percentage, falling, at first, rapidly but changing more and more slowly in the periphery. The "constant" percentage relation noted by Ogle is therefore a consequence of the straight line relationship here discussed and is secondary and less useful mathematically. Although Ogle must have observed this linear relationship, he does not seem to have developed its consequences as is here done.

Interrelation of constants

In discussing the anatomic basis of spatial discrimination only the minimal angle of resolution has been considered, partly because of the more satisfactory data available. How do the other linear thresholds correlate

TABLE 2

CONSTANTS OF LINES FITTED TO SETS OF DATA FOR VARIOUS TYPES OF THRESHOLDS

No.	Fig.	Author	Date	Type of Threshold	No. Obs.	Ecc.	Slope	Intercept
1	—	Aubert & Förster	1857	(Data too scattered for fitting)				
2	5	Wertheim	1894	MAR temporal[1]	1	0°–30°	0.425	1.046[2]
3	9	Fick	1898	MAR horizontal	1	0°–20°	0.241	0.472
4	4	Bourdon	1902	Vernier	1	0°–20°	0.696	0.443
5	6	Basler	1906	Motion—light[3]	1	0°–26.5°	0.106	0.195
6	6	Basler	1908	Motion—dark[4]	1	0°–26.5°	0.502	0.988
7	3	Weymouth et al.	1928	MAR—ave. 4 meridians	1	0′–85′	0.406	0.614
8	1	Ludvigh	1941	MAR—horizontal (E.C.)	1	0°–10°	0.334	0.598
9	—	Ludvigh	1941	MAR—horizontal (ave.)	3	0°–10°	0.331	0.568
10	7	Ogle	1950	Panum area[5]	4	1°–12°	1.519	7.457
11	—	Ogle	1950	Panum radius[6]	4	1°–12°	0.759	3.729
12	7	Ogle	1950	Panum area (G.H.G.)	1	1°–12°	2.272	10.672
13	8	Ogle	1950	Mean variation—6 m.[7]	1	1°–12°	0.038	0.010
14	8	Ogle	1950	Mean variation—76 cm.	1	1°–16°	0.069	0.019
15	2	Original	—	MAR—students	20	0°–20°	1.504	1.469
16	—	Original	—	MAR—students (stand. dev.)	20	0°–20°	0.359	0.692
17	—	Original	—	MAR (St. error mean)	20	0°–20°	0.056	0.123
18	—	Original	—	MAR (Subject K.)	1	0°–20°	1.731	4.633
19	—	Original	—	MAR (Subject M.)	1	0°–20°	1.816	3.285

No. Obs. = number of observers.
Ecc. = range of eccentricity fitted—in some cases the original data covered a wider range.
Slope is in minutes of arc per degree.
Intercept is in minutes of arc.
[1] In all cases the MAR has been transformed from the original visual acuity.
[2] This value is relative and cannot be compared with other intercepts.
[3,4] Observations were made in the light and in the dark primarily to provide and to exclude comparison objects for the moving test object.
[5] The horizontal angular diameter of Panum areas as measured by the horopter method.
[6] The radius is half the horizontal diameter.
[7] Ogle has given the mean variation of the settings of the rods of the horopter apparatus instead of the standard deviation, the values do not differ much from the stereothresholds of the horopter.

with the retinal organization described above?

The slopes and intercepts of all the sets of data fitted are gathered together for comparson in Table 2. It will be noted that there is a tendency for both to increase or decrease together. The great heterogeneity of the data collected by many methods from many subjects over nearly 100 years precludes any close agreement. Three sets of data seem particularly aberrent.

Bourdon's data on the vernier threshold show a low intercept, corresponding to its great sensitivity, but a large slope; no cause for this is apparent, although it is stated that other workers have obtained a less rapid change in sensitivity with eccentricity.

In the second place, the student data on the minimal angle of resolution appear out of line (fig. 2 and table 1). Both slope and intercept are within the general range shown in Table 2, but the intercept is low for the slope. The high value of both is associated with the difficulty of the task (low illuminance and short exposure) but the discrepancy between them is perhaps related to the mass nature of the data since some individual records (K. and M., table 2) show a more usual relation of these constants. It is interesting that the variability of the student observations (standard deviation, table 2) shows a linear relation to eccentricity and the constants show the usual relations to each other.

The third case, that of the Panum areas, is of particular interest. The horizontal angular disparity of the haplopic or single vision zone of the horopter, which gives the diameter of the Panum areas, ranges from just short of uncrossed to just short of crossed diplopia, and is therefore equivalent approximately to two thresholds of the min-

TABLE 3

RATIO CONES PER MINUTE OF ARC AS A FUNCTION OF ECCENTRICITY THRESHOLDS PER MINUTE

Eccentricity (degrees)	Ratio (cones/thresholds)
0	1.000*
5	1.010
10	1.204
15	1.721
20	1.995
30	3.641
40	5.656
50	6.440
60	7.775
70	9.109

* This value of the ratio in the center of the fovea was not used in fitting the line of Fig. 12B.

imal angle of resolution type. It is clear that half of the horizontal diameter of the Panum "area" or the Panum "radius" should be used for comparison with thresholds.

The correlation of slope and intercept is +0.826. The data are 12 sets from Table 2, omitting the vernier threshold and some duplications, but including six sets of minimal angle of resolution, one standard deviation of minimal angle of resolution, two of motion, two of mean settings of horopter rods, and one Panum radius. This correlation is highly significant, it might be expected by chance from an uncorrelated population less than once in 1,000 times.

What is the origin of this correlation?

Although the slopes and intercepts vary widely, the relation between them tends to be consistent; they increase or decrease together, maintaining a constant ratio. Apparently the ratio is a function of the retinal organization, the absolute values, a function of the difficulty of the particular test. This assumption may be illustrated by an imaginary example.

Consider tests A and B depending upon the spatial organization of the retina; the threshold of A is a linear function of the eccentricity. Suppose that B proves easier than A so that at all eccentricities its threshold is only half that of A. B will then have a slope and an intercept both of which are half those of A.

An actual example is furnished by Basler's thresholds for motion. Tested in the dark without reference points with which the moving object might be compared, it proved about five times more difficult than in the light; the slope in the light is 21.2 percent of that in the dark, the intercept 19.7 percent, a discrepancy of only 1.5 percent from exact proportionality. Tests varying in difficulty or in the aspect of structure on which they depend will vary in this fashion, giving a highly correlated set of constants. If this analysis is correct it is plain that the arguments advanced for a structural basis of the minimal angle of resolution will apply with equal cogency to any other of the spatial thresholds considered in this paper.

USE OF CONSTANTS IN COMPARISONS

Having pointed out that a simple linear relation exists between a group of spatial visual thresholds and retinal eccentricity and that this relation has an anatomic basis, it may be well to illustrate the usefulness of this concept as an analytic tool. In Figure 13 are presented for comparison the plots of four types of visual thresholds and in Table 2, already cited, may be found the constants for the fitted straight lines. The minimal angles of resolution of Ludvigh and the vernier thresholds need no comment, the motion thresholds of Basler are in terms of extent of motion rather than rate, the values here plotted are those taken in the light and in the presence of reference points. Of the mean variation data Ogle says, "The setting of threads or rods of the horopter apparatus by the criterion of the apparent frontoparallel plane is essentially a task of stereoscopic depth discrimination" (p. 48). The conventional stereoscopic thresholds are larger than the values here given but undoubtedly parallel them. For near fixation points, for example, 30 or 40 cm., the mean variation is relatively large and as a function of eccentricity the curves are concave upward; for 76 cm. and 6.0 m. the thresh-

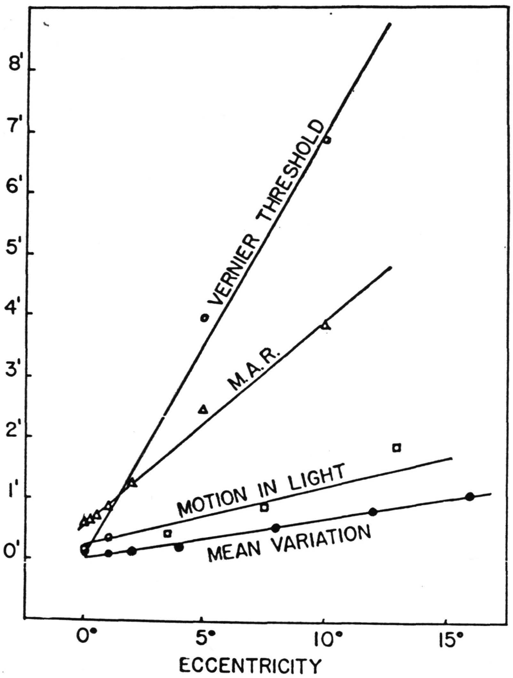

Fig. 13 (Weymouth). Comparison of vernier threshold, minimal angle of resolution, motion threshold, and mean variation of the settings of horopter rods; all are plotted as functions of retinal eccentricity. Data: vernier threshold, Bourdon; minimal angle of resolution, Ludvigh; motion threshold, Basler; mean variation, Ogle.

olds are much smaller and the curves are linear.

In spite of the heterogeneous nature of the data, certain important features are brought out by comparison of these curves. The vernier thresholds start lower than the minimal angle of resolution but increase more rapidly and by five degrees have crossed over to become the larger. Motion and the mean variation (or the stereothreshold) starting at about the same low foveal threshold as the vernier, on the other hand, increase the slowest of all (low slope) and so show in the periphery the lowest thresholds or the greatest sensitivity. The minimal angle of resolution is more often compared with movement and it is sometimes said that the preception of motion is better in the periphery than in the fovea. This is obviously not the case. The threshold of motion is smaller than the minimal angle of resolution in all parts of the retina. Owing to its lesser slope, however, its superiority markedly increases with eccentricity. This relative advantage over resolution in the periphery has apparently led to the idea that motion is more readily perceived in the periphery than in the fovea. The advantages of the linear representation of the visual thresholds, when it can be applied, are obvious in this example.

Summary

As is well known the retina of the light-adapted eye presents a field of graded sensitivity with its peak at the fovea. This has great theoretic and practical importance but accurate description and comparison have been hampered by the absence of a simple mathematical expression for the shape of the gradient. The minimal angle of resolution or threshold in minutes (the reciprocal of the visual acuity) plotted as a function of the eccentricity is a staight line rising from the lowest threshold in the fovea to high thresholds in the periphery. This is true, at least, for the central retina out to 20 or 30 degrees in all the data examined; beyond this it rises rather more rapidly.

The visual capacities may be divided into two groups:

First, spatial thresholds including the minimal angle of resolution, the vernier thresholds, the Panum fusional areas, the mean variation of the settings of the horopter rods (a function of the stereothreshold), the threshold of motion, and perhaps others. Second, intensity thresholds, including the light threshold, the critical fusional frequency, and probably others. The spatial thresholds of the photopic eye are linear functions of retinal eccentricity, the minimal angle of resolution of the dark-adapted eye and the intensity thresholds of both high and low levels of adaptation are nonlinear.

The linear relations of the spatial thresholds to eccentricity must have an anatomic basis in the spatial arrangement of the

retinal structures. If we accept the usual definition of a sensory unit that it includes a group of receptors communicating by a single nerve fiber with the brain, the optic nerve fibers or their cells of origin, the ganglion cells, rather than the cones, should be the anatomic basis of the spatial thresholds. From approximate densities of the ganglion cells in different regions of the retina it is found that the linear separation of the ganglion cells, and hence the diameter of the senory units, is a straight line function of the retinal eccentricity with a slope within the range of those of the spatial thresholds. If the ratio, cones per minute divided by thresholds per minute (derived from visual acuity), is compared for different regions of the retina it is found that peripheral to the fovea (in which the ratio is unity) the ratio is an increasing linear function of the eccentricity. These ratios, weighted by the areas of the retinal regions, give a mean ratio closely corresponding to the ratio of the total number of cones divided by the total number of optic nerve fibers. These relations are taken to prove that the anatomic basis of the linear arrangement of the group of spatial thresholds is a similar distribution of the ganglion cells, representing sensory units consisting of increasing numbers of cones with increasing eccentricity.

The usefulness of the linear relation to eccentricity of the spatial thresholds as a means of describing and comparing gradients is illustrated.

950 West Jefferson Boulevard (7).

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