# THE DARK ADAPTATION OF RETINAL FIELDS OF DIFFERENT SIZE AND LOCATION*

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I

## Purpose of Work

The histological structure of the human retina (Rochon-Duvigneaud, 1907; Wolfrum, quoted by Dieter, 1924) is such that a central area whose diameter subtends a visual angle of a little less than 2° is practically free of rods and made up almost entirely of cones, whereas retinal areas outside of this restricted region contain rods in addition to the cones. From the center of the retina to its periphery the number of rods increases while the number of cones decreases, so that the ratio of rods to cones in a retinal area of given size increases as the area is moved from the center to the periphery.

It follows from these facts and from von Kries' theory of the separate functions of rods and cones (von Kries, 1929) that measurements of visual capacities should show an almost pure cone behavior when restricted to the rod-free 2° central area, and a combination of both rod and cone behavior for larger central areas, or for any areas situated outside the fovea. Numerous researches have shown that this is true for visual acuity (Koenig, 1897), for dark adaptation (Hecht, 1921; Kohlrausch, 1922; Takagi and Kawakami, 1924; Dieter, 1929), for color vision (Koenig, 1903; Dieter, 1924), for flicker (Hecht and Verrijp, 1933), and for intensity discrimination (Hecht, 1934).

The existing measurements of dark adaptation have made it clear that cone and rod adaptation possess distinctly different characteris-

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tics.  Cone dark adaptation as ordinarily measured (Hecht, 1921; Kohlrausch, 1922; Dieter, 1929) is (a) limited in extent, covering at most an intensity range of 100 to 1; and (b) rapid in speed, being practically complete in the fovea in 3 minutes.  On the other hand, rod dark adaptation (Piper, 1903; Kohlrausch, 1922) is (a) extensive, covering an intensity range of 10,000 to 1; and (b) slow, being practically complete only in about 30 minutes.

Working with a very small area situated 5° above the fovea, Kohlrausch (1922, 1931) has measured its dark adaptation with differently colored lights and has found that in such a retinal region containing rods and cones, the course of adaptation shows the presence of both functions, and that the relative extent of the two is determined by the color of the light, according to the relative spectral sensibilities of the two types of element.

Because the retina varies so strikingly in rod-cone population at different points, it seemed to us that even with white light alone, we could vary the relative contribution of rods and cones to the course of dark adaptation by properly choosing the size and location of the retinal area used for measurement.  We present here the results of our measurements of dark adaptation, first with centrally located areas of increasing size, and second with peripherally situated areas of different size and location so chosen as to elucidate the behavior of the retina as a whole.

II

*Apparatus and Procedure*

The arrangements for making the measurements are shown diagrammatically in top view in Fig. 1.  The source of light is a 3.8 volt flash-light lamp kept at 0.28 amperes.  It illuminates an opal glass plate which serves as the test-field whose brightness is controlled by neutral decimal filters and by a neutral wedge with a transmission range of 1:1000.  The filters and wedge were calibrated with a Macbeth illuminometer.  The size and position of the test-field are fixed by metal diaphragms next to the opal glass.  A fixation point whose position and brightness can be controlled independently of the test-field, is reflected into the observer's eye by a very thin glass cover-slip.  The field is viewed through the exit pupil 2.85 mm. in diameter, and through the lens $L_2$ which assists the accommodation of the observer's eye, since the distance from exit pupil to the test-field is only 10 cm.  Lens $L_1$ serves practically no function when the opal plate is in place. When high intensities are necessary for use with monochromatic filters, the opal

plate is removed and another lens is placed between $L_1$ and the source. This gives an image of the source at the exit pupil and furnishes about 1000 times as much light as with the arrangement shown in the diagram. The illumination of the field is cut off by a shutter which can be raised and lowered by a knob in the hand of the observer.
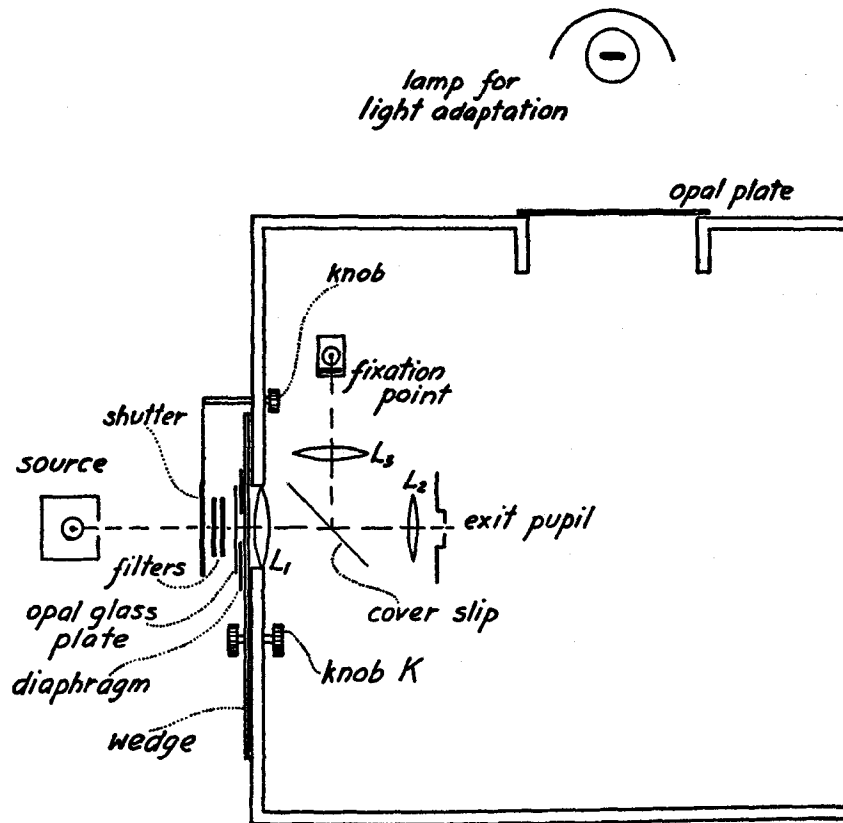


FIG. 1. Diagrammatic top-view of apparatus for measuring dark adaptation. For convenience in drawing, the fixation point has been placed to the right of the observer at the exit pupil; in the set-up as used, it is actually above the observer.

A measurement at any moment of dark adaptation consists in the observer's moving the wedge into such a position that the test-field just becomes visible. Usually this involves two or three exposures of the field by means of the shutter. More exposures are to be avoided because they raise the threshold perceptibly. The wedge is moved by a rack and pinion controlled by the knob $K$.

Each run is preceded by 2 minutes light adaptation to a brightness of 300 millilamberts, obtained by placing the eyes 4 cm. from an externally illuminated opal glass in the wall of the cubicle. Observations can begin almost immediately after light adaptation, because the moment the adapting light is turned off the observer can turn his head and place his eye at the exit pupil.

In the first few minutes of dark adaptation the threshold drops so precipitously that measurements are made as rapidly as possible. After the first three or four points have been determined, measurements are made more leisurely at intervals of 2 to 5 minutes. The position of the wedge is noted by the recorder in the dark room outside the cubicle. Time is measured with a stop-watch.

## III

### *Centrally Fixated Fields*

The measurements were made on the right eye of each of us; we in turn acted as recorders and observers. We have also made occasional runs with various people in the laboratory and with visitors, and are satisfied that our results cover the normal range of variation.

Our first measurements were with centrally located retinal areas 2°, 3°, 5°, 10°, and 20° in diameter. For each area we made at least three runs, frequently five, and occasionally six or seven. Though each individual run is continuous and smooth, its intensity level varies from day to day. Therefore several runs have to be averaged in order that comparisons between the different areas may be made with confidence. We have made some measurements with a 1° centrally fixated field; the results are not much different from a 2° field, but are more irregular, very likely due to the interference of the fixation point (which of course is far from being a point) with the sensitivity and adaptation of so small an area.

The averaged measurements are given in Table I, which is so arranged that comparable times for all areas are on the same horizontal line for each observer. The time in the dark is given in minutes, and the threshold is given as the logarithm of the brightness in micromillilamberts. This unit is one millionth of a millilambert, and was adopted to avoid the fractions and negative logarithms which appear under these conditions with ordinary units like the millilambert. The final threshold of the dark adapted eye for large fields lies between 1 and 10 micromillilamberts.

Inspection of Table I shows that with increasing area the threshold at any moment drops steadily to lower and lower intensity values. However, to gain an adequate idea of the nature and the course of

### TABLE I

*Centrally Fixated Fields of Different Size.   Time in Dark in Minutes.   Intensity in Micromillilamberts*

| Diameter.. | 2° | | 3° | | 5° | | 10° | | 20° | |
|---|---|---|---|---|---|---|---|---|---|---|
| Observer | Time in dark | Log intensity | Time in dark | Log intensity | Time in dark | Log intensity | Time in dark | Log intensity | Time in dark | Log intensity |
| S. H. | | | | | | | 0.10 | 5.11 | | |
| | 0.20 | 4.37 | 0.22 | 4.25 | 0.22 | 4.36 | 0.20 | 4.52 | 0.15 | 4.34 |
| | 0.55 | 3.98 | 0.79 | 3.70 | 0.81 | 3.78 | 0.59 | 3.88 | 0.65 | 3.75 |
| | | | | | | | 1.30 | 3.57 | | |
| | 2.00 | 3.82 | 2.40 | 3.65 | 2.20 | 3.55 | 2.50 | 3.49 | 1.80 | 3.59 |
| | | | | | | | | | 3.60 | 3.46 |
| | 4.40 | 3.87 | 4.70 | 3.57 | 4.50 | 3.36 | 4.20 | 3.35 | 4.80 | 3.26 |
| | | | | | | | | | 6.70 | 3.00 |
| | 8.30 | 3.88 | 8.10 | 3.54 | 7.60 | 3.16 | 7.20 | 3.00 | 7.90 | 2.57 |
| | | | | | 10.0 | 2.97 | 9.30 | 2.61 | 9.40 | 2.23 |
| | 11.8 | 3.85 | 12.0 | 3.51 | 12.6 | 2.72 | 12.3 | 2.34 | 11.5 | 1.97 |
| | 15.5 | 3.76 | 14.1 | 3.41 | 15.1 | 2.55 | 15.5 | 2.12 | 15.5 | 1.68 |
| | | | 16.3 | 3.32 | 18.2 | 2.45 | 18.2 | 1.91 | | |
| | 20.9 | 3.71 | 20.3 | 3.22 | 21.9 | 2.24 | 21.4 | 1.82 | 20.9 | 1.42 |
| | | | 24.9 | 3.13 | | | 25.1 | 1.71 | | |
| | 27.5 | 3.73 | 30.2 | 3.01 | 28.2 | 2.13 | 29.5 | 1.66 | 28.2 | 1.22 |
| G. W. | 0.20 | 4.38 | 0.30 | 4.33 | 0.14 | 4.34 | 0.23 | 4.27 | 0.19 | 4.34 |
| | 0.68 | 3.96 | 0.71 | 3.97 | 0.54 | 3.82 | 0.60 | 3.76 | 0.60 | 3.79 |
| | | | | | | | 1.50 | 3.49 | 1.40 | 3.54 |
| | 2.10 | 3.85 | 2.50 | 3.64 | 2.00 | 3.58 | 3.00 | 3.24 | 2.50 | 3.23 |
| | 4.20 | 3.95 | 5.20 | 3.64 | 4.30 | 3.47 | 4.60 | 3.11 | 4.70 | 3.01 |
| | | | | | 6.90 | 3.35 | 6.50 | 2.84 | 6.60 | 2.64 |
| | 7.40 | 3.94 | 8.30 | 3.55 | | | 7.90 | 2.62 | 8.40 | 2.21 |
| | | | | | 9.30 | 3.14 | 9.30 | 2.40 | | |
| | 11.8 | 3.83 | 10.7 | 3.45 | 11.5 | 3.00 | 10.7 | 2.28 | 11.0 | 1.88 |
| | | | 13.5 | 3.35 | 13.8 | 2.86 | 12.9 | 2.10 | 13.5 | 1.68 |
| | 17.0 | 3.81 | 16.6 | 3.23 | 17.4 | 2.63 | 16.6 | 1.90 | 16.6 | 1.57 |
| | 21.9 | 3.74 | 20.4 | 3.14 | 21.7 | 2.47 | 20.0 | 1.82 | 19.8 | 1.39 |
| | 27.5 | 3.67 | 26.3 | 3.06 | 25.1 | 2.39 | 24.0 | 1.78 | 26.2 | 1.36 |
| | 35.5 | 3.66 | 29.5 | 3.06 | 31.0 | 2.34 | 30.2 | 1.73 | | |
| C. H. | 0.32 | 4.37 | 0.35 | 4.34 | 0.22 | 4.34 | 0.38 | 4.27 | 0.30 | 4.37 |
| | 0.79 | 3.81 | 0.74 | 3.75 | 0.68 | 3.84 | | | | |
| | | | | | 1.10 | 3.57 | 0.93 | 3.73 | 1.10 | 3.73 |
| | 1.50 | 3.53 | 2.00 | 3.51 | 1.90 | 3.39 | 2.00 | 3.46 | 2.20 | 3.48 |
| | 3.20 | 3.43 | 3.20 | 3.36 | | | 3.20 | 3.21 | | |
| | | | | | 4.50 | 3.16 | 4.60 | 2.92 | 4.30 | 3.01 |

TABLE I—*Concluded*

| Diameter.. | 2° | | 3° | | 5° | | 10° | | 20° | |
|---|---|---|---|---|---|---|---|---|---|---|
| Observer | Time in dark | Log inten- sity | Time in dark | Log inten- sity | Time in dark | Log inten- sity | Time in dark | Log inten- sity | Time in dark | Log inten- sity |
| C. H.— | 5.60 | 3.31 | 5.40 | 3.35 | 6.80 | 2.73 | 6.20 | 2.76 | | |
| *Concl'd* | 8.30 | 3.27 | 7.90 | 3.22 | | | 7.90 | 2.45 | 7.80 | 2.37 |
| | | | | | 9.60 | 2.56 | 10.2 | 2.28 | 9.60 | 2.00 |
| | 12.9 | 3.22 | 12.3 | 3.06 | 12.6 | 2.31 | 12.9 | 2.06 | 13.8 | 1.65 |
| | 17.0 | 3.00 | 17.8 | 2.82 | 15.5 | 2.15 | 16.2 | 1.86 | 18.6 | 1.36 |
| | 22.4 | 2.89 | | | 19.5 | 2.05 | 21.9 | 1.69 | 22.9 | 1.26 |
| | | | 25.7 | 2.58 | 24.6 | 1.94 | 25.1 | 1.60 | | |
| | 28.8 | 2.91 | | | 29.5 | 1.86 | 29.5 | 1.56 | 29.5 | 1.19 |

dark adaptation under these conditions, it is necessary to examine the data graphically. As an example, the measurements of S. H. are reproduced in Fig. 2. This shows that for the 2° field, dark adaptation is rapid and shallow. After 2 minutes, the threshold remains practically constant for about 15 minutes, when there appears a slight additional drop. This second drop is variable in the data of S. H., showing up on some days and not on others; it is more regularly present with G. W.; and always shows up in the data of C. H. This secondary drop is always present for all observers with the 3° field, and occurs earlier at about 11 minutes. The significance of the secondary drop becomes clear in the larger fields where, as Fig. 2 shows, it appears sooner and goes lower as the field increases in size. For the 5° field the secondary burst of dark adaptation contributes as much to the total range of adaptation as the initially rapid drop in threshold, whereas for the 20° field it contributes about $2\frac{1}{2}$ times as much.

The transition between the primary, comparatively rapid adaptation, and the secondary, more leisurely adaptation is fairly abrupt except for the 20° field where it is more gradual. This is true for S. H., for G. W., and for all other people whose adaptation we have measured. For C. H. the transition is gradual even for the 10° field, this being due to the fact that the primary decrease in threshold for C. H. is slower than for the rest of us. The abrupt transition appears in some of the older measurements of Piper (1903), but the

recognition of its presence and its significance is due to Kohlrausch (1922), who showed definitely that the rapid primary adaptation is due to the cones, and the slower secondary adaptation to rods.
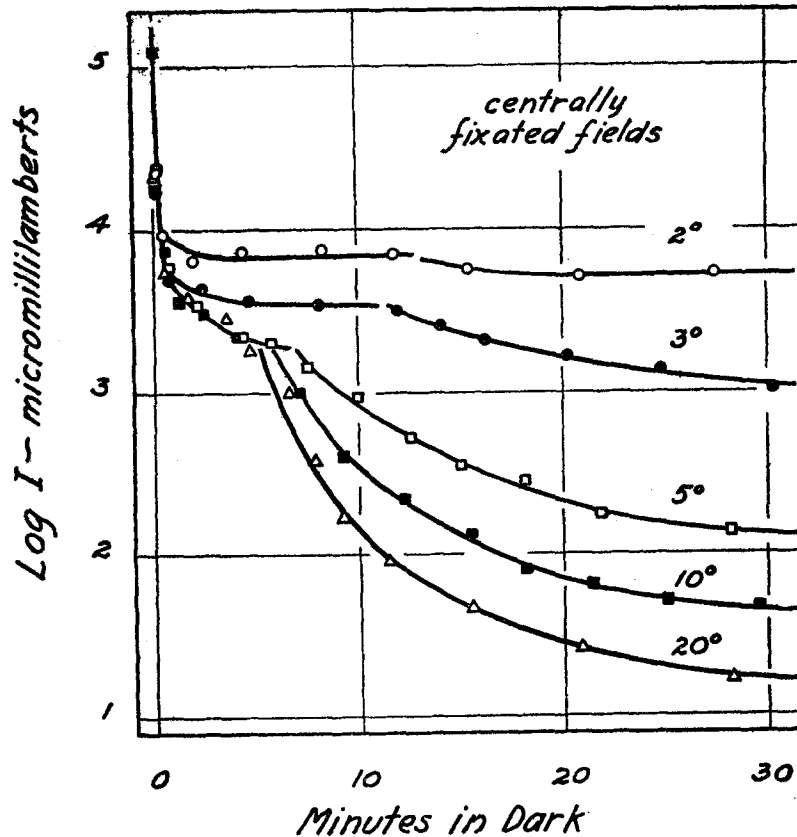


Fig. 2. The threshold during dark adaptation for centrally fixated areas of different size. The primary and secondary portions of the dark adaptation curves have been separated by a slight gap since it is uncertain whether the transition between them is sharp or rounded; most likely it is rounded.

Our measurements confirm this conclusion. In the $2°$ field there are practically no rods, and dark adaptation is therefore mainly a foveal cone function. In a $3°$ area enough rods are present to show themselves when their threshold has fallen below that of the cones. In a $5°$ field the number of rods is of course much greater still; their

lower thresholds appear sooner, and adaptation goes lower. The same is true with the increasingly greater number of rods in the 10° and 20° fields.

It is seen in Fig. 2 that the primary cone portions of the curves for areas larger than 2° are not the same as for the 2° field. This becomes understandable when it is remembered that as the area increases, there come into play not only rods but also cones outside the fovea. It is hardly to be expected that the thresholds and rates of adaptation of these peripheral cones are the same as those of the central cones.

TABLE II

*Centrally Fixated 10° Field. Right Eye of C. H. Time in Dark in Minutes. Intensity in Micromillilamberts*

| Time in dark | Log intensity |
|---|---|
| 0.10 | 5.05 |
| 0.70 | 4.09 |
| 1.70 | 3.66 |
| 3.10 | 3.20 |
| 6.30 | 2.71 |
| 9.30 | 2.20 |
| 12.0 | 2.02 |
| 15.1 | 1.74 |
| 20.9 | 1.52 |
| 30.2 | 1.52 |
| 42.7 | 1.50 |
| 57.5 | 1.51 |
| 109.6 | 1.49 |
| 151.4 | 1.56 |
| 169.8 | 1.51 |

However, it is not improbable that near the transition point, especially with the larger fields the rods exert an influence on the primary threshold before they dominate in function in the secondary drop.

The data of Table I and of Fig. 2 stop at about half hour of dark adaptation. The changes which take place after this time are so slight in comparison, that we have usually not continued measurements beyond 30 minutes. However, for the record, we show in Table II the average of two runs made by C. H. with a centrally fixated area of 10° diameter, the measurements going out to 3 hours.

It is apparent that between half hour and 3 hours in the dark the threshold does not decrease significantly.

In this we can confirm Achmatov (1926) whose data show practically no threshold change in this period, and in some cases for periods lasting even 5 hours. For much more prolonged adaptation up to 24 hours Achmatov found curious, sudden additional drops in threshold separated by levels lasting several hours. The significance of these changes is hard to evaluate; it would not be surprising if they were complicated by central factors induced by lack of sleep and the prolonged stay in the dark.

TABLE III

*Threshold in Log Micromillilamberts after 30 Minutes Dark Adaptation*

| Centrally fixated fields of different size | | | | 2° field at different distances from center | | | |
|---|---|---|---|---|---|---|---|
| Diameter | S.H. | G.W. | C.H. | Distance from center | S.H. | G.W. | C.H. |
| *degrees* | | | | *degrees* | | | |
| 1 | | 4.03 | 3.45 | | | | |
| 2 | 3.72 | 3.67 | 2.88 | 0 | 3.67 | 3.67 | 2.88 |
| 3 | 3.03 | 3.05 | 2.57 | | | | |
| 5 | 2.10 | 2.35 | 1.85 | 2½ | 2.13 | | |
| 10 | 1.64 | 1.73 | 1.55 | 5 | 1.70 | 1.88 | 1.48 |
| 20 | 1.20 | 1.30 | 1.20 | 10 | 1.44 | 1.65 | 1.35 |
| | | | | 15 | | 1.56 | 1.32 |

Our data and those of Achmatov for the threshold between half hour and 3 hours dark adaptation fail to confirm the findings reported by Kravkov and Semenovskaja (1933) and by Semenovskaja (1934). These authors find that after preliminary light adaptation to as little as 5 millilamberts and to as much as 100 millilamberts (their recorded maximum), the threshold drops as usual for about an hour but that after this it increases again. The measurements in Table II were preceded as usual by a 2 minute light adaptation to 300 millilamberts, and they show no rise in threshold during 3 hours of stay in the dark.

The most striking thing about the data for centrally located areas, presented in Table I and Fig. 2, is that as the area increases in size the intensity range covered during dark adaptation increases tremendously. The range of the 2° field between 0.2 and 30 minutes is

about 0.5 log unit whereas that for the 20° field is 3.5 log units, an increase of 1000 times.  Another way of looking at this is in terms of the final threshold at about 30 minutes, which fixes the range, because the initially measured threshold immediately after light adaptation is very nearly the same for all the fields, it being probably determined by the foveal cones.

The relation between test-field diameter and final threshold is shown in Table III and in the left half of Fig. 3.  The values are
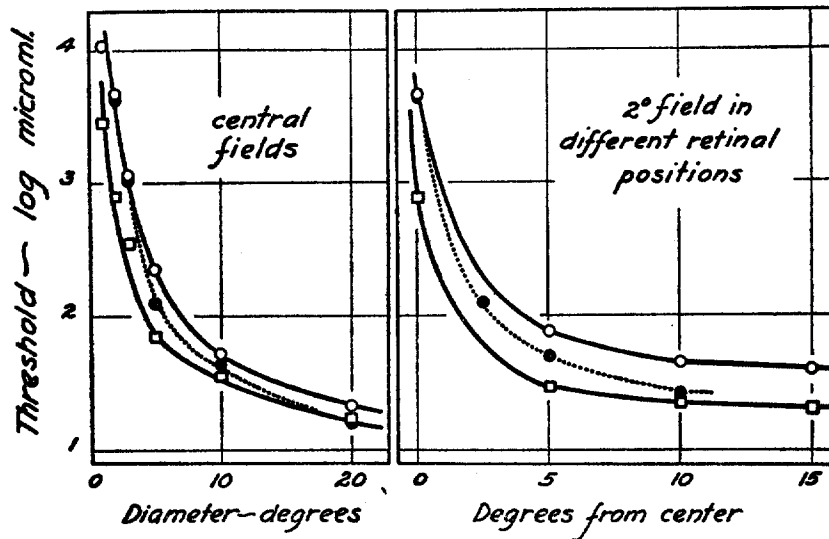


FIG. 3. A comparison of the 30 minute threshold for different sizes of central fields with the 30 minute threshold of a 2° field placed at different distances from the center of the retina.

those for 30 minutes dark adaptation and have been determined graphically from the data of Table I.  The final values for the 1° central field are included here.  Fig. 3 shows that the decrease in threshold with area is regular, and that no great changes are to be expected for areas beyond 20°.  The basis for this regular change in threshold brings to light an important property of the retinal mosaic in relation to dark adaptation.

IV

*Peripheral Fields*

There exists a well established body of data describing the relation between the area of a field and the minimum intensity required to make it visible (for a summary, see Parsons, 1914). It might therefore seem that the present data of dark adaptation are merely another manifestation of this area-threshold relationship, especially since the final threshold data in Table III can be approximately represented by Riccò's law (Riccò, 1877) that threshold is inversely proportional to retinal area. However, it is simple to show that the major factor involved in these data of dark adaptation and final threshold has almost nothing to do with area as area, but rather with the fact that the retina is not a uniformly sensitive surface. Coupled with its histological structure already referred to, it possesses a permanently graded sensitivity. Experiments show that the characteristics of this gradation are the main basis for such data as shown in Figs. 2 and 3.

Assume for the moment that the elements in the fovea are the least sensitive ones, and that in progressing toward the periphery there appear elements which have a permanently greater and greater sensitivity to light. If this were true, then the decrease in threshold with the larger, centrally fixated, retinal areas would be due to the inclusion in these fields of the permanently more sensitive elements located farther and farther away from the center.

We made several sets of measurements to test this supposition. The most extreme change in threshold occurs with the 20° field. If the final threshold and the dark adaptation of a centrally located 20° field represent the sensitivity and behavior not of all the elements covered by this field but mainly of those elements situated most peripherally, then it should be possible to duplicate the essentials of the data by measuring the dark adaptation of the retina by means of an annulus of light covering only this peripheral region.

The measurements were with a test-object composed of 1° circles situated on the circumference of a circle 20° in diameter; the appearance of the field near the threshold is that of a continuous narrow annulus of light on an unilluminated background. The fixation point is in the center.

The average data for three such runs with the eye of S. H. are given in Table IV and in Fig. 4. Included in Fig. 4 are the data for the 20° central field from Fig. 2, and the essential, quantitative similarity of the two sets of data is obvious at a glance. The total range of the two is the same, and the final threshold is the same. The rod-cone transition is not the same in the two cases, but this is hardly to be expected since the 20° central field contains the fovea and its cones, whereas the annulus contains only peripheral cones. Moreover, the method of observation is different in the two cases: with the full field one watches for the appearance of a disc of light thus per-

TABLE IV

*Annulus of 1° Circles on Circumference of a Circle of 10° Radius. Right Eye of S. H. Time in Dark in Minutes. Intensity in Micromillilamberts*

| Time in dark | Log intensity |
|:---:|:---:|
| 0.20 | 4.40 |
| 0.74 | 3.85 |
| 2.00 | 3.53 |
| 3.40 | 3.16 |
| 4.80 | 3.00 |
| 7.20 | 2.55 |
| 10.2 | 2.15 |
| 12.9 | 1.89 |
| 15.9 | 1.68 |
| 19.1 | 1.53 |
| 22.4 | 1.42 |
| 26.9 | 1.40 |

mitting the central elements considerable influence, whereas with the annulus field one is on the lookout only for the edge. As a result, in the annulus field it almost seems as if at the transition the rods and cones function together in some way to reduce the threshold,—a fact already evident even in the central field. Aside from this, however, it is plain that the main characteristics of dark adaptation as revealed by measurements with a 20°, centrally fixated field are determined by the behavior of the most sensitive elements situated in the periphery of the retinal area corresponding to the 20° field, and the size of the area as such is of secondary importance.

In order to investigate this situation in more detail, we measured dark adaptation with a 2° field placed in different positions on the retina. The data are in Table V. With G. W. and C. H. the measurements for the differently placed fields were made in separate runs. With S. H. all the retinal positions were tested successively in the course of one run. The measurements are the averages of two or more runs. We made similar measurements with a 1° field placed in
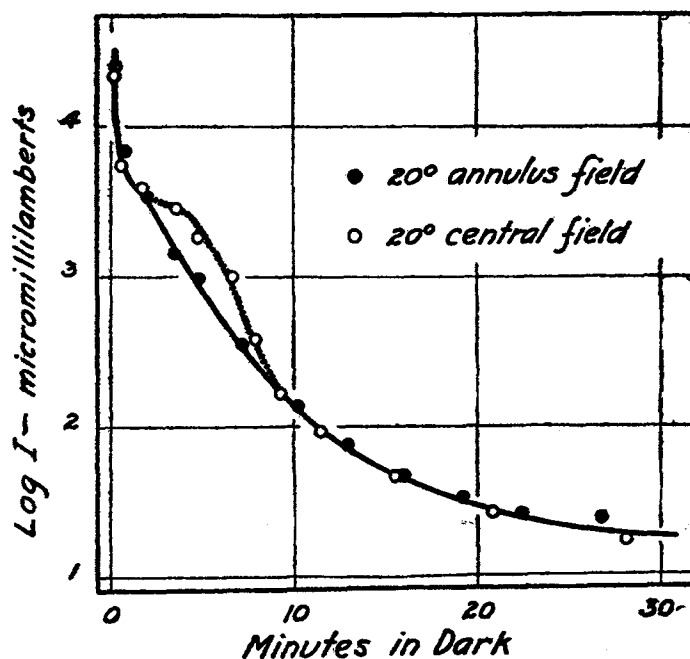


FIG. 4. Comparison between the dark adaptation of a centrally placed 20° field, and that of a narrow (1°) annulus 20° in diameter.

various off-center positions; the data are so similar to those in Table V that it would serve no useful purpose to print them.

The data for S. H. (three runs) are shown graphically in Fig. 5, which is to be compared with Fig. 2. The 2° field centrally placed is about the same in the two cases. Placed $2\frac{1}{2}$° from the center, a 2° field yields data which correspond approximately to the behavior of a 5° whole field fixated centrally. Placed 5° from the center, it

TABLE V

2° *Field Different Distances from Center. Time in Dark in Minutes. Intensity in Micromillilamberts*

| Observer | 0° Time in dark | 0° Log intensity | 2½° Time in dark | 2½° Log intensity | 5° Time in dark | 5° Log intensity | 10° Time in dark | 10° Log intensity | 15° Time in dark | 15° Log intensity |
|---|---|---|---|---|---|---|---|---|---|---|
| S. H. | 0.22 | 4.40 | | | | | | | | |
| | 0.78 | 3.87 | | | | | | | | |
| | 1.70 | 3.66 | | | | | | | | |
| | | | 5.40 | 3.72 | 4.90 | 3.41 | | | | |
| | | | | | 8.50 | 3.27 | 8.30 | 2.80 | | |
| | | | 11.8 | 3.10 | 13.5 | 2.40 | 14.5 | 2.04 | | |
| | | | 17.8 | 2.64 | 20.0 | 2.09 | 20.9 | 1.65 | | |
| | | | 25.1 | 2.23 | 26.9 | 1.76 | 28.8 | 1.45 | | |
| | 30.9 | 3.67 | 33.1 | 2.09 | 34.7 | 1.63 | 35.5 | 1.41 | | |
| | 38.9 | 4.55 | 41.7 | 2.15 | 43.7 | 1.54 | 45.7 | 1.32 | | |
| | 52.5 | 4.56 | 55.0 | 1.93 | 55.0 | 1.50 | 56.2 | 1.38 | | |
| G. W. | | | | | 0.26 | 4.37 | 0.30 | 4.40 | 0.55 | 4.42 |
| | | | | | 0.63 | 3.98 | 1.00 | 3.87 | | |
| | | | | | 1.20 | 3.84 | | | 1.20 | 4.03 |
| | | | | | 1.80 | 3.77 | 1.90 | 3.60 | | |
| | | | | | 2.90 | 3.39 | 2.90 | 3.41 | 2.20 | 3.74 |
| | | | | | 4.00 | 3.21 | 4.40 | 3.18 | 3.70 | 3.31 |
| | | | | | 4.90 | 3.11 | 5.40 | 3.01 | 5.00 | 3.14 |
| | | | | | 6.80 | 2.83 | 6.60 | 2.78 | 6.30 | 2.84 |
| | | | | | 8.70 | 2.57 | 8.10 | 2.59 | 8.10 | 2.67 |
| | | | | | 10.7 | 2.34 | 10.2 | 2.24 | 11.2 | 2.31 |
| | | | | | 13.5 | 2.20 | 12.3 | 2.05 | 13.2 | 2.09 |
| | | | | | | | 14.1 | 1.97 | 14.8 | 1.99 |
| | | | | | 16.6 | 2.01 | 16.2 | 1.91 | 18.5 | 1.80 |
| | | | | | 20.4 | 1.94 | 20.3 | 1.76 | 21.4 | 1.64 |
| | | | | | 24.0 | 1.93 | 24.0 | 1.71 | | |
| | | | | | 27.5 | 1.89 | 28.9 | 1.65 | 26.1 | 1.61 |
| C. H. | | | | | 0.60 | 4.36 | 0.28 | 4.40 | 0.30 | 3.76 |
| | | | | | 1.20 | 3.71 | 1.80 | 3.39 | | |
| | | | | | 2.30 | 3.34 | | | 2.10 | 3.23 |
| | | | | | 4.10 | 3.19 | 3.60 | 2.97 | 4.20 | 2.52 |
| | | | | | 5.60 | 3.12 | | | | |
| | | | | | 7.20 | 2.69 | 6.90 | 2.64 | 7.40 | 2.17 |
| | | | | | 9.10 | 2.50 | 10.0 | 2.07 | | |
| | | | | | 12.0 | 2.09 | | | 11.5 | 1.85 |
| | | | | | 15.9 | 1.80 | 14.5 | 1.75 | 17.0 | 1.65 |
| | | | | | 20.9 | 1.60 | 19.1 | 1.55 | 23.4 | 1.40 |
| | | | | | 28.2 | 1.49 | 25.1 | 1.39 | | |

corresponds to the 10° area centrally fixated; similarly the 10° off-center field corresponds to the 20° field centrally fixated. The thresholds at 30 minutes for these 2° off-center measurements are shown in the right half of Fig. 3 for comparison with the data for centrally fixated fields. Clearly the threshold alters with retinal position much as it alters with centrally fixated areas of different size.
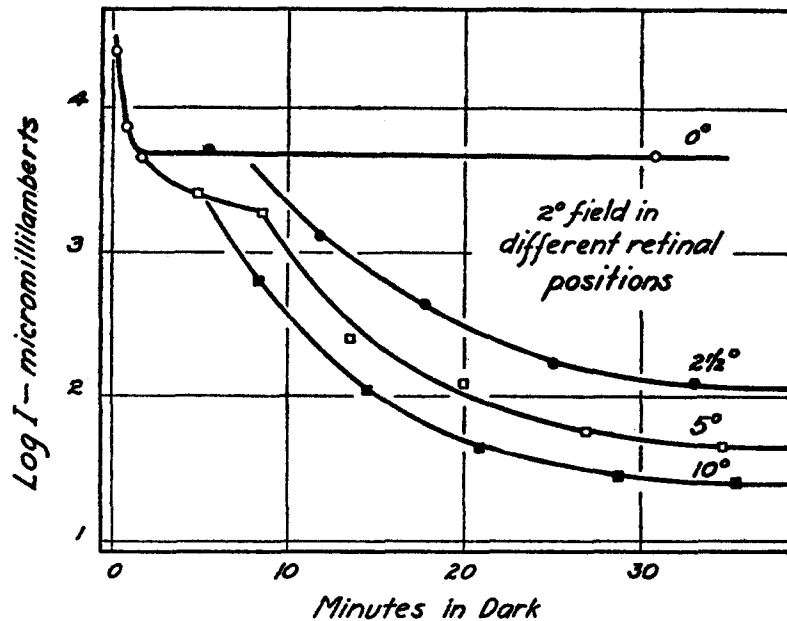


FIG. 5. Dark adaptation as measured with a 2° field placed at different distances from the center. Compare this with Fig. 2 for centrally fixated fields of different size.

From all this we must conclude that in centrally fixated fields of different size the general character of the dark adaptation and the value of the final threshold are determined essentially not by the area as area, but by the fact that as the areas increase in size their edges reach into regions of increasingly greater sensibility of the retina. This conclusion naturally applies only to centrally fixated areas. To study the influence on dark adaptation of area specifically as area, it will be necessary to confine the measurements to a peripheral region of the retina which is essentially homogeneous in its sensibility.

SUMMARY

The decrease in threshold shown by the eye during dark adaptation proceeds in two steps. The first is rapid, short in duration, and small in extent. The second is slow, prolonged, and large. The first is probably due to cone function; the second to rod function.

In centrally located fields the two parts of adaptation change differently with area. With small, foveal fields the first part dominates and only traces of the second part appear. As the area increases the first part changes a little, while the second part covers an increasing range of intensities and appears sooner in time.

Measurements with an annulus field covering only the circumference of a 20° circle show most of the characteristics of a 20° whole field centrally located. Similarly a 2° field located at different distances from the center shows dark adaptation characteristics essentially like those of large centrally located fields whose edges correspond to the position of the central field.

Evidently the behavior in dark adaptation of centrally located fields of different size is determined in the main not by area as area, but by the fact that the retina gradually changes in sensitivity from center to periphery, and therefore the larger the field the farther it reaches into peripheral regions of permanently greater sensibility.

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