INTERMITTENT STIMULATION BY LIGHT

VI. Area and the Relation between Critical Frequency and Intensity*

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I

For a central area approximately 2° in diameter the retina is practically rod-free and contains only cones. Outside of this area, rods appear and increase in number toward the periphery. Judging by this fact and by previous work on flicker (Hecht and Verrijp, 1933), on intensity discrimination (Steinhardt, in press; cf. Hecht, 1934), and on dark adaptation (Hecht, Haig, and Wald, 1935), the relation between critical fusion frequency and intensity as measured with central areas smaller than 2° in diameter should be a continuous function representing cones, whereas with larger areas the relation should show a duplex character illustrative of the predominant working of rods at low intensities, and of cones at high intensities.

We have measured the relation between critical fusion frequency and intensity for white light, using four centrally located areas 0.3°, 2°, 6°, and 19° in diameter, and our measurements confirm these expectations.

II

In making the measurements we used the apparatus described by Hecht, Shlaer, and Verrijp (1933) with the new optical system and procedure described in the immediately preceding paper of this series by Hecht and Shlaer. The four sizes of test field were obtained with four separate photometric cubes having the corresponding openings

* A preliminary report of this work was given to the Optical Society of America in February, 1935 (Hecht and Smith, 1935) and to the XV International Physiological Congress in Leningrad in August, 1935.

in the silvering on the diagonal face. The holes in the silvering are actually ellipses, but in front view they appear circular.

The surround for all the test fields has the same diameter, 35°. This increase in size of surround in comparison with the 10° one used earlier was for the purpose of removing, if possible, the drop in critical frequency which occurs at very high intensities after the critical

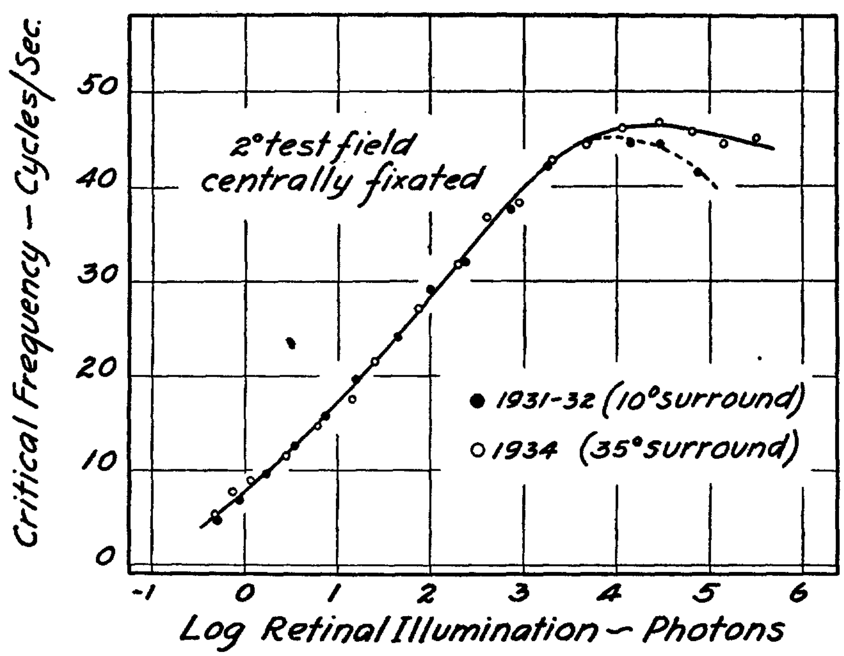

FIG. 1. Relation of critical frequency to retinal illumination. Comparison of previous measurements with a 2° centrally fixated field made in 1931 and 1932 (Hecht and Verrijp, 1933) with a 10° surround, and repeated in 1934 with a 35° surround. Right eye of S.H.

frequency has reached a maximum. Since the drop is prominent in the absence of a surround, it seemed likely that a surround larger than 10° would eliminate most of the comparatively small drop previously found with the 10° surround.

Fig. 1 shows the data of S. H. with the 2° test field, using the new surround of 35° and the old one of 10°. The two sets of data are practically identical except at high intensities where the new observations show only a slight decrease in critical frequency beyond the maximum. Even this decrease is frequently absent; again and again in these and in the preceding measurements with color, we have made runs in which the top of the curve is entirely flat.

The importance of a large surround in this type of measurement is also evidenced by its subjective effects. The glare and discomfort, and even subsequent headaches, characteristic of working at very high intensities with a small field minus a surround, are much mitigated even with a 10° surround, and are almost completely absent with the 35° surround.

III

The data are given in two tables. Each datum represents the average of three complete runs; in each run two observations were usually made at each intensity, though on the infrequent occasions when these did not agree closely, three and four measurements were included. The tables show that as the field size increases, measurements of critical frequency can be made at lower and lower intensities.

The meaning of the data is apparent from Fig. 2, where the measurements of E. L. S. are plotted in the usual manner of critical frequency against log I. As expected, the measurements for 6° and 19° break into two sections which from previous work must be identified with rod function at low intensities and with cone function at high intensities. Note that the rod part is less extensive, and its plateau lower for the 6° field than for the 19° field. For the 2° and 0.3° fields the rod part is definitely missing.

For E. L. S. the maximum critical frequency at high intensities increases with field size. The data for S. H. show only slight differences in maximum for the different areas; in fact, the 6° field is actually slightly higher than the 19° field. No great reliance is to be placed on this because of the comparatively large variation in maximum shown by S. H. in the course of the measurements.[1]

The behavior of the low intensity rod section of the data with

[1] The slope of the curve relating frequency to log I undergoes similar variations since the slope is determined by the maximum (or the reverse), and depends to a large extent on the criterion adopted for the critical frequency as well as on unexplained daily and long time variations (*cf.* Hecht and Verrijp, 1933, footnote).

increasing area resembles its behavior with a 2° test field placed in different retinal locations. The farther in the periphery the 2° field is measured, the lower is the position of the rod section on the in-

TABLE I

Brightness and Critical Fusion Frequency for Circular Areas of Different Diameter, Centrally Fixated. Data for S. H.

Intensity in photons	Cycles per second			
	0.3°	2°	6°	19°
0.00120				3.48
0.00182				4.61
0.00275				5.42
0.00407				6.71
0.00933				8.07
0.0174			2.94	9.29
0.0398			4.91	10.5
0.0891			6.41	10.9
0.200			7.40	11.8
0.468		5.33	8.52	11.8
0.724		7.69		
1.12	6.38	8.84	9.46	11.6
1.82	9.03			
2.75	9.87	11.6	11.2	11.6
6.17	13.1	14.7	14.1	13.6
14.1	16.9	17.6	17.5	15.9
31.6	20.4	21.4	21.4	23.0
75.9	27.1	27.2	26.4	27.5
191.	27.7	31.7	32.2	33.2
398.	33.1	36.7	36.9	36.3
891.	36.8	38.2	41.4	39.7
2000.	41.3	42.8	47.5	42.5
4680.	44.1	44.4	49.3	42.9
11200.	48.0	46.2	51.6	43.3
27500.	49.6	46.7	52.3	46.8
61700.	49.0	45.7	52.3	47.1
141000.	47.4	44.7	53.4	48.1
316000.		45.0	53.7	49.7

tensity axis (Hecht and Verrijp, 1933). The same is true in the present data when the centrally fixated area is increased. It is as if the effect of increasing the area is mainly concerned with bringing the measurements into the periphery. A similar situation exists in rod dark adaptation where the increasing adaptation range associated with increasing test fields is duplicated by a small test field placed in increasingly more peripheral locations (Hecht, Haig, and Wald, 1935).

TABLE II

Brightness and Critical Fusion Frequency for Circular Areas of Different Diameter, Centrally Fixated. Data for E. L. S.

Intensity in photons	Cycles per second			
	0.3°	2°	6°	19°
0.00120				2.95
0.00182				4.13
0.00275				5.87
0.00407				7.18
0.00933				9.11
0.0174			4.86	11.7
0.0398			5.90	12.9
0.0891			7.38	14.3
0.200		2.45	9.18	15.7
0.302		3.68		
0.468		5.56	9.69	16.0
0.724		7.10		
1.12	6.18	10.2	10.3	15.8
1.82	8.58			
2.75	10.2	13.8	12.8	16.0
6.17	13.4	16.0	15.5	20.3
14.1	15.3	19.1	19.2	25.0
31.6	17.6	22.4	24.5	30.1
75.9	19.9	26.9	29.1	33.6
191.	22.2	31.1	33.7	37.1
398.	26.9	34.6	38.0	42.5
891.	30.8	38.2	40.8	45.8
2000.	33.7	42.0	43.2	50.4
4680.	37.1	43.9	44.6	55.3
11200.	39.6	44.3		56.6
13800.			45.6	
27500.	41.6	44.9		58.1
32400.			45.3	
61700.	39.2	44.4	44.2	55.4
141000.	39.2	44.1		55.0
182000.			46.3	
316000.	39.4	43.6		56.8

The position of the cone sections of the present data seems to be the same regardless of the area of the centrally fixated test field. The cones in the center of the eye, being the most sensitive, come into play at about the same intensity regardless of whether or not they are surrounded by other, less sensitive cones in the periphery. This is borne out by the measurements of a 2° field placed in different retinal locations (Hecht and Verrijp, 1933) in which the cone section appears at higher intensities the farther the test field is placed in the periphery. Thus the rod section and the cone section of the data behave differently with area and retinal location, depending on the fact that the sensitivity and number of rods increase as one goes toward the periphery

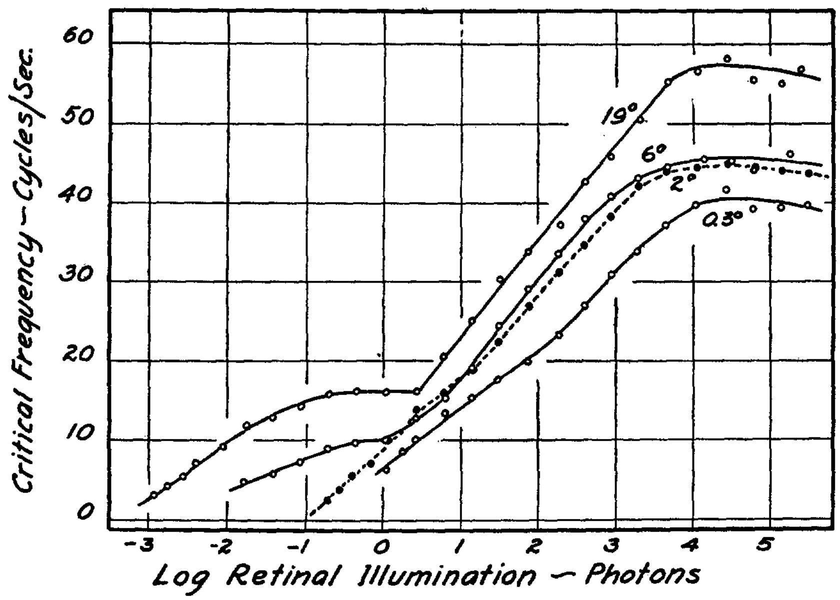

FIG. 2. Influence of area of centrally fixated test field on the relation between critical frequency and log I. Data of E.L.S.

while the sensitivity and number of cones decrease under the same conditions.

The data for the 6° and 2° fields are of pointed interest in the problem of flicker and area. Except for the absence of the rod piece in the smaller field, the two sets of data are almost identical. Under the circumstances of possessing the same surround, a ninefold increase in area of the test field hardly changes the relation of critical frequency to intensity so far as cone function is concerned (cf. Granit and Harper, 1930).

There is a curious bend in the 0.3° data and to a less extent in the 2° data which we find persistently present in both our measurements. The obvious possibility that this bend represents a rod admixture is excluded on three grounds. First, the bend is more evident in the smaller, central field than in the larger; rods would be more likely to appear in the larger field. Second, the location of the bend is at a different critical frequency (and intensity) from the rod sections of the other data. Third, measurements of a small central field with

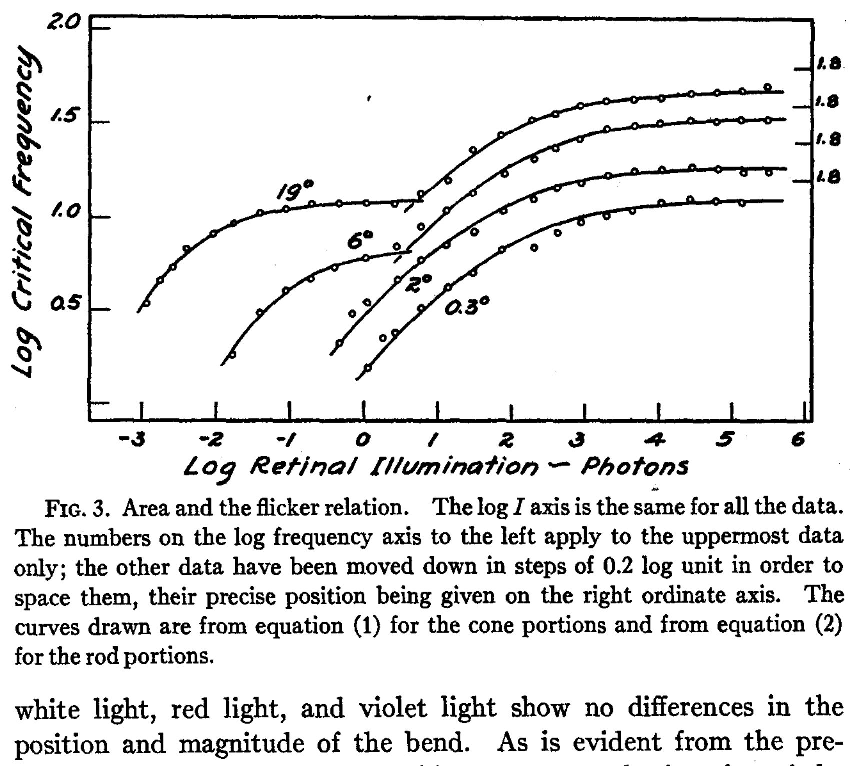

FIG. 3. Area and the flicker relation. The log I axis is the same for all the data. The numbers on the log frequency axis to the left apply to the uppermost data only; the other data have been moved down in steps of 0.2 log unit in order to space them, their precise position being given on the right ordinate axis. The curves drawn are from equation (1) for the cone portions and from equation (2) for the rod portions.

white light, red light, and violet light show no differences in the position and magnitude of the bend. As is evident from the preceding paper, this procedure would separate out the function of the rods if they were present. We hope to investigate the nature of the bend later in more detail.

Fig. 3 presents the data of S. H. as the logarithm of the critical frequency (f) against the logarithm of the intensity (I). This type of plot shows more clearly the phenomena already described. In spite of the irregularity in the 0.3° data, a single curve describes the measurements fairly well. The single curve is even more expressive of the 2° data. The curve drawn is the one used for the cones in the preceding measurements on color, and is also drawn through the cone portions of the 19° and 6° data. Its equation is

$$KI = f^2/(f_{max} - f)^2 \tag{1}$$

where K is the constant which determines the position of the curve on the intensity axis, just as the value of f_{max} determines its position on the critical frequency axis.

The rod sections of 19° and 6° require a slightly different curve which is the same for the two fields. Its equation is

$$KI = f/(f_{max} - f)^2 \tag{2}$$

where the terms have the same meaning as before.

It is worth emphasizing that the rod sections of the 19° and 6° fields have the same curve drawn through them. While this is not clearly seen in an ordinary plot of critical fusion frequency against log I, it becomes plain in the log f-log I plot of Fig. 3. The identity of the curves shows that the difference between the 19° and 6° rod data is not basic, but merely represents a displacement on the axes in the log plot corresponding to a change in the scale of plotting on the ordinary plot. Exactly the same is true for any systematic differences which the cone data show. Fundamentally the systems in the rods and cones which determine the relation between critical frequency and intensity remain the same regardless of area. Only the dimensional constants are changed by changing the area.

IV

Equations (1) and (2) whose curves have been drawn in Fig. 3 are varieties of the stationary state equation

$$KI = x^n/(a - x)^m \tag{3}$$

in which frequency f is made proportional to concentration of photoproducts x, and m and n are the reaction orders of the photochemical and dark reactions respectively. The four varieties of equation (3) corresponding to values of m and n as 1 or 2, are shown in Fig. 4.

Examination of the data in Fig. 3 (and of the data in Fig. 4 of the preceding paper on color) shows that the rod curve always has twice the slope of the cone curve. This determines the value of n in the two cases; $n = 1$ for the rods, and $n = 2$ for the cones. The best curve to fit the cone data always has $n = 2$, and $m = 2$, as was found also for intensity discrimination (Hecht, 1934). The rods, however, are somewhat variable with regard to the value of m. This is illus-

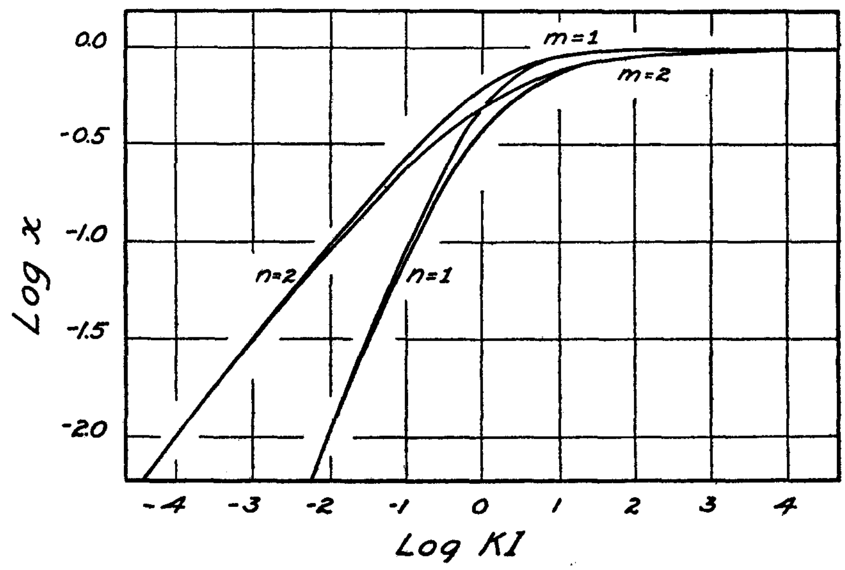

FIG. 4. The stationary state equation (3) plotted when m and n are each 1 and 2. Because of the log plot the shape of the curves remains constant regardless of the values of K and a which merely locate the position of the curves on the axes.

trated by Fig. 5 which contains our individual measurements with the 19° field. Besides showing the adequacy and reproducibility of the data, especially in relation to the curves, Fig. 5 indicates this systematic variability of the rod measurements. Of the six runs, the rod data of four are described adequately by equation (3) only when $m = 2$, while the two others are better fitted when $m = 1$. Fig. 4 shows that when $m = 2$, $n = 1$, the curvature is more gradual, whereas when $m = 1$, $n = 1$, the transition between the rising limb and the plateau is sharper. Also, the plateau itself continues to rise gently in the 2,1 curve, whereas it flattens off quite rapidly in the 1,1 curve.

Whether these differences really represent daily variations in the state of the rod photoreceptor system, it is hard to say. The con-

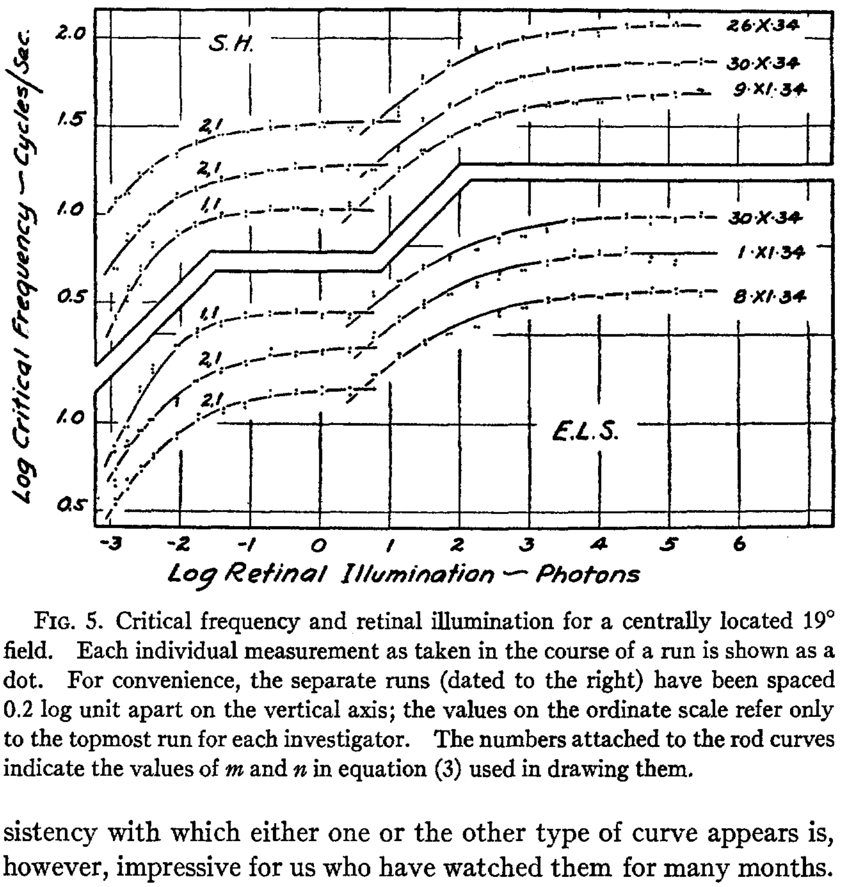

FIG. 5. Critical frequency and retinal illumination for a centrally located 19° field. Each individual measurement as taken in the course of a run is shown as a dot. For convenience, the separate runs (dated to the right) have been spaced 0.2 log unit apart on the vertical axis; the values on the ordinate scale refer only to the topmost run for each investigator. The numbers attached to the rod curves indicate the values of m and n in equation (3) used in drawing them.

sistency with which either one or the other type of curve appears is, however, impressive for us who have watched them for many months.

SUMMARY

1. In the retina, central areas whose diameter is less than 2° possess only cones, while larger areas have rods and cones. In conformity with this, the relation of critical fusion frequency to intensity is a single function for centrally fixated areas below 2°, and a double function for similarly fixated, larger areas. The two sections of such

data are easily identified with rod activity at low intensities and with cone activity at high intensities.

2. The curves describing the rod data are the same for all areas, differing only in the values of the associated dimensional constants which control the location of the curves on the coordinate axes. Similarly, the curves for the cone data are the same for all areas; the tendency for an increase in maximal frequency with area is the expression merely of the value of a constant which determines the position of the data on the frequency axis. Area, therefore, does not influence the fundamental nature of the flicker relation through each receptor system, but merely alters the extraneous constants of the relation.

3. The curves which describe the measurements are represented by two equations, one for rods and one for cones; both equations are derived from the stationary state descriptive of the initial event in the photoreceptor process.

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