INTERMITTENT STIMULATION BY LIGHT

III. The Relation between Intensity and Critical Fusion Frequency for Different Retinal Locations*

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I

Present State of Problem

1. Previous Work.—The critical frequency at which the visual fusion of rhythmically produced illumination takes place depends for its value on a variety of factors. The most effective of these is the intensity of the illumination.

The dependence of critical frequency on illumination was recognized by Plateau a century ago (1829), and is apparent from the later work of Emsmann (1854) and of Nichols (1884); but it was Ferry (1892) who first proposed the formulation that the critical fusion frequency varies directly with the logarithm of the intensity.[1] Ferry's published measurements do not support his generalization. In a plot of critical frequency against log I, his data, though covering little more than one

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[1] Ferry's actual statement is that the "persistence" of vision is inversely proportional to log I. By "persistence" Ferry merely means the necessary duration of the light flash alone, at the critical fusion frequency. The interval is thus equal to one half of the reciprocal of the critical frequency. It was generally believed that this time interval measures "the duration of the retinal impression," and Ferry so construes his data. The term is still used by Allen (1926), though Grünbaum (1898) long ago exposed its absurdities.

logarithmic unit, form a sharply curved line convex to the log *I* axis, and bear no resemblance to the results of later investigators.

Adequate measurements of the relation between intensity and fusion frequency were first made by Porter (1902) who used an intensity range of 1 to 50,000. His data fall on two straight lines intersecting at an illumination of about 0.25 meter candles. Porter's work was corroborated by Kennelly and Whiting (1907), by Ives (1912), and by Luckiesh (1914). Ives measured not only white light but also colored lights and found that the data for different parts of the spectrum show a dual logarithmic relation similar to that for white light. The slope of the lines, however, varies with the wave-length, the upper and lower lines varying independently. For blue light Ives found that the lower line becomes horizontal. All these peculiarities of slope disappear when a small field is used.

Allen (1919, 1926) has in general confirmed the work of Porter and of Ives, but has differed from them by drawing through his measurements about five short straight lines of different slope instead of the usual two. In our estimation, the data presented by Allen do not justify this treatment; the points appear to lie on a continuously curving line. The recent work of Lythgoe and Tansley (1929), distinctly gives no support to Allen's multiplicity of straight lines.

Lythgoe and Tansley's measurements confirm the logarithmic relation of intensity to fusion frequency, but Lythgoe and Tansley attach no importance to its strict formulation as done by Ferry, by Porter, and by Ives, and consider that their data agree only under certain conditions with the linear relation of critical frequency to log *I*. The same may be said about the measurements of Granit and Harper (1930), who found that for a range of about 1 to 1000 in intensity the critical frequency is very nearly directly proportional to the logarithm of the intensity. For higher intensities the relationship does not hold, and the curve of frequency against log *I* tends to become horizontal, as already found by Grünbaum (1898).

Recently Sälzle (1932) has measured this relation for the first time in an animal other than man. He finds for the dragon fly larva that critical frequency is a sigmoid function of log *I*, the curve being nearly horizontal at upper and lower critical frequencies. In a paper just published, Wolf (1933) records precisely similar measurements for the honey bee.

Of the other numerous observations relating to intensity and critical frequency, some cover so small a range (*e.g.* Piéron, 1922; Polikarpoff, 1926) that no certain conclusions can be drawn from them about these variables, while others deal with the influence of various conditions on critical frequency and are not relevant here (*cf.* Parsons, 1924).

2. *Need for the Present Work.*—In spite of all this work the relation between intensity and critical fusion frequency is not adequately known in several important respects. In the first place, none of the measurements cover a range of intensities sufficiently wide to define the relationship over the functional range of the eye, and to include very high and very low illuminations. As a result of this lack, we know almost nothing about fusion frequencies below 10 cycles and above 40 cycles per second.

In the second place, none of the measurements except those of Ives describe the real relation between illumination and retinal effect, because they were all made with the natural pupil, and thus contain an additional and uncertain variable. The correction of such data by means of existing measurements of the pupil area (Reeves, 1918), already a dubious procedure since Schroeder's (1926) work, has now become meaningless in terms of the studies on the pupil by Stiles and Crawford (1933).

In order that an adequate theoretical structure may be built for the physiology of intermittent illumination, it is obviously necessary to possess the data in a fairly complete condition. We therefore measured the relation between critical fusion frequency and intensity for different portions of the retina over as large a range of illumination as possible, and under such conditions as to render the data reproducible and definitive.

II

Method and Material

The details of the apparatus and of the procedure which we used for this work have, for editorial convenience, been described separately in the preceding paper of this group.

All the measurements here recorded were made with the right eye of C. D. V. and with the right eye of S. H. When C. D. V. was the observer, S. H. acted as manipulator and recorder. When S. H. was observer, the manipulations and recording were made in the main by Mr.

Morton Schweitzer, and occasionally by Mr. Simon Shlaer. We wish to record here our indebtedness to both these gentlemen for their kindness.

III

Measurements with the Fovea

The data which we secured fall into several groups, depending on the ideas which urged us to make them. The original measurements of Porter, when plotted as critical frequency against log I show two straight lines, one of small slope, and continuing from it, another of greater slope. In conformity with the duplicity theory (von Kries, 1929) it is generally supposed that the lower line represents the functioning of the rods, while the upper, steeper line represents the function of the cones. The transition from the dominance of one system to that of the other then corresponds to the region of intersection of the two straight lines, which in Porter's data comes at a frequency of about 18 cycles per second.

If this separation of rod and cone function is correct, it should be possible to get a more complete cone curve below this critical value by deliberately confining the measurements to the rod-free area of the fovea, and by maintaining the fixation at this place even below the break when the fixation normally would wander to the periphery. Our first measurements were therefore made with strictly central fixation. We used white light, and a flickering area 2° in diameter surrounded as already described by a 10° field continuously illuminated. The measurements thus concern that part of the fovea which according to Wolfrum (Dieter, 1924) is practically rod-free.

The lowest intensity at which readings can be taken in this manner with the fovea is obviously well above the threshold of the rod system. It is even above the thresholds of some of the foveal cones as well, because we had to choose such an intensity that the slowest interruption in the illumination was clearly visible with central fixation. This is very nearly 0.01 photons. Below these intensities the field appears uniformly illuminated with central fixation even when the central test area of 2° is completely extinguished.

The measurements for central fixation were taken over a period of 3 months for C. D. V. and of a year and a half for S. H. Fig. 1 shows the 176 individual measurements made by S. H. Each setting is separately recorded so as to give an idea of the reproducibility of the observations. In this respect, the measurements of C. D. V. are exactly like those of S. H., but about three times as numerous, and thus more difficult to plot similarly in one figure. It is clear that the measurements, though protracted over a long period of time, are concordant and describe a real relationship in the eye. They may therefore be averaged in groups to record this relationship. The data so averaged are given in Table I and in Figs. 2 and 3. The line drawn through the unaveraged, individual measurements in Fig. 1 is the same as the one drawn through the average data of Fig. 2, and shows that the process of averaging has merely served to smooth the data without in the least distorting the relationship which they describe.

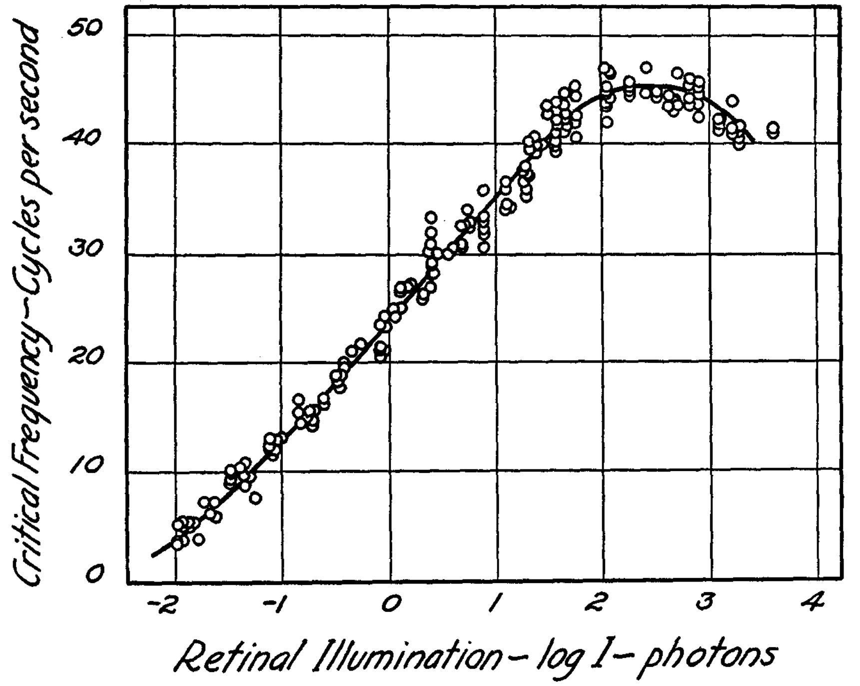

FIG. 1. Critical frequency function of the rod-free fovea as influenced by the illumination. Data for S. H. recording the 176 separate measurements. The curve is the same one as drawn through the average data in Fig. 2.

The data indicate that the direct logarithmic relation between intensity and critical frequency holds for the middle region of intensities, but that the complete relationship is more nearly sigmoid, the S shape being quite drawn out. Two aspects of the data require special consideration: first, the slope of the middle portion and second, the levelling-off and decrease of the critical frequency at the highest illuminations.

TABLE I

Critical fusion frequency (cycles per second) for white light at various retinal illuminations (photons). Test field 2° in center of fovea. Surround 10°.

	Right eye S.H.			Right eye C.D.V.		
Criterion	No. of readings	Retinal illumination	Critical frequency	No. of readings	Retinal illumination	Critical frequency
Normal	10	0.0131	4.59	30	0.0105	3.95
	4	0.0219	6.75	22	0.0207	6.14
	10	0.0424	9.59	21	0.0328	8.51
	8	0.0834	12.55	35	0.0635	11.70
	10	0.184	15.55	25	0.161	15.00
	8	0.391	19.63	23	0.440	19.86
	12	1.02	24.39	32	1.34	25.82
	14	2.43	29.18	33	7.18	33.98
	15	5.79	32.15	29	19.8	38.64
	20	18.0	37.64	40	56.8	44.13
	20	42.7	42.43	48	129.	47.38
	13	124.	44.96	35	334.	50.40
	10	321.	44.70	35	698.	52.87
	9	638.	44.68	22	1803.	52.00
	13	1832.	41.66	25	3556.	52.15
				28	6039.	51.03
No flicker on slight shift	10	490.	50.3			
	5	1585.	51.3			
	12	4571.	48.0			
Rapid readings	5	120.	41.7			
	3	331.	40.7			
	2	1000.	39.4			
	3	1950.	37.5			

In the range of intensities between about 0.1 photons and 100 photons, the data, when plotted as in Figs. 2 and 3, lie with extra-

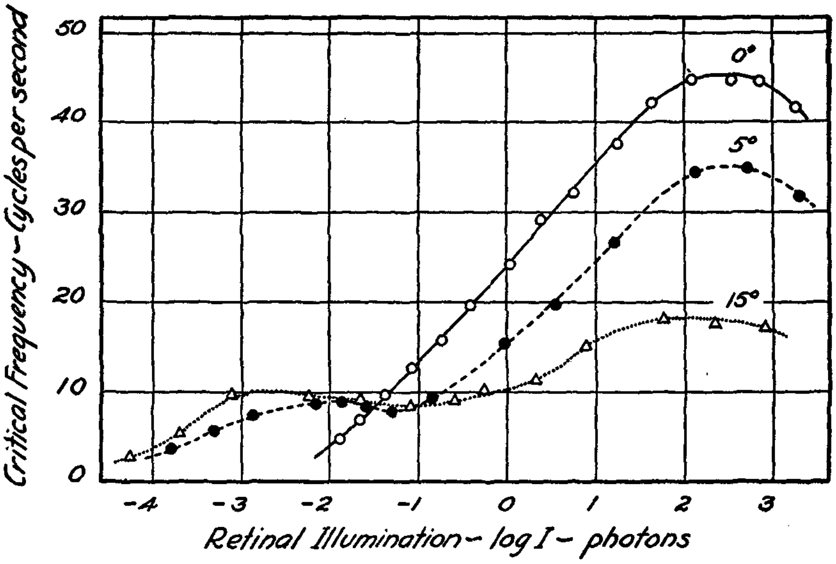

FIG. 2. Data for S. H. showing relation between critical frequency and log *I* for white light for three different retinal locations: at the fovea, and at 5° and 15° above the fovea.

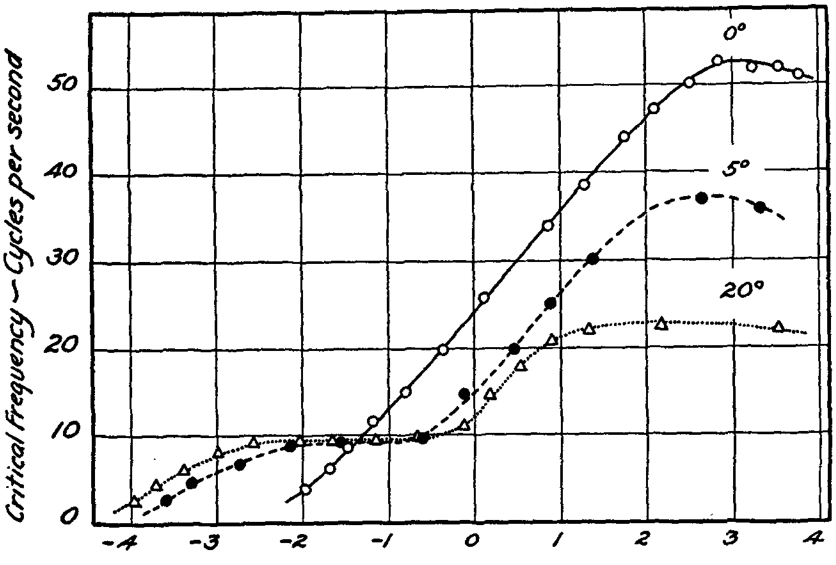

FIG. 3. Data for C. D. V. showing relation between critical frequency and log *I* for white light for three retinal locations: at the fovea, and at 5° and 20° above the fovea.

ordinary precision on a straight line. In this respect we can confirm Porter, Ives, and the other workers. The slope of this line is 11.1 for C. D. V., and 11.0 for S. H.

We may strictly compare our measurements with those of Ives (1912 and 1922), the only previous worker who used a pupil of fixed dimensions. The slope of Ives' 1912 data is 11.2, whereas for his 1922 data it is 10.0. The slope of the upper portion of Porter's data is 12.4. Kennelly and Whiting's slope is 11.0. Luckiesh's slope as published is 5.6, which is an extraordinarily low value. Most sectored wheels are constructed to give 4 cycles per revolution, and it is quite possible that Luckiesh erred in multiplying his motor frequencies by 2 and not by 4 to give cycles per second. His published slope, when multiplied by 2 gives 11.2. The same holds for Granit and Harper whose slope appears to be 5.5, but whose values must clearly be multiplied by 2 to record cycles per second and not motor frequencies. Their slope is therefore 11.0. Lythgoe and Tansley's data for the fovea contain 3 or 4 points in this region of the curve. For their only observer who was trained in visual work (R. L.) these points are regular and show a slope of 11.0. For their two untrained observers the points are irregular; but they seem to show a slope of about 9.0. Allen's (1926) measurements give a slope of 8.6 for yellow light of 570 mμ, which on the basis of general experience, may be considered the same as for white light. Thus most observers record values between 9 and 12, with a preponderance of 11. These variations do not seem to be connected with any obvious experimental conditions like pupil area, binocular observation, or size of field.[2]

Little need be said about the data below 0.1 photons. The critical frequency continues to decrease as log I decreases forming a gentle curve convex to the axis of abscissas, and stopping fairly abruptly

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[2] The measurements with white light here recorded were terminated for C. D. V. in 1930 and for S. H. early in 1932. Recently, *i.e.* about a year after the series was terminated, measurements with white light, with foveal fixation, and with the identical apparatus have been made by S. H. with the startling result that the slope of the data is now nearly 10.0 instead of 11.0. It is significant also that Ives in later publications (Ives, 1922) shows a similar change in slope from 11.2 to 10.0 for white light. Obviously there are unknown factors which seem to influence the value of the slope.

when with central fixation the field appears uniform even when the test area is extinguished.

At the highest intensities the relation between critical frequency and log *I* rapidly ceases to be linear. As the intensity is raised a maximum critical frequency is soon reached, beyond which a further increase in intensity results in no further increase in critical frequency; rather it results in a decrease. The maximum critical frequency comes at about 500 photons for S. H. and at about 1000 photons for C. D. V. The value of the critical frequency at this maximum is 53 cycles per second for C. D. V. and 45 cycles per second for S. H. With a further increase in the intensity, the critical frequency distinctly decreases. At first we were skeptical about this, and therefore made many measurements in order to be certain of it.

In the course of these observations at the higher intensities we tried two variations in the technic for securing the data already given. In the first, the procedure was like that heretofore used, except that the end-point for the extinction of flicker was considered reached on prolonged observation only when no flicker was apparent even on a slight shift in fixation. The data, shown in Table I, indicate that by this rather undesirable criterion the critical frequency is raised considerably. In the second procedure, rigid fixation was maintained as usual, but the readings were made as rapidly as possible, say in about 30 seconds, thus preventing the complete adaptation of the eye to the experimental intensity. The data, also given in Table I, show clearly that inadequate light-adaptation decreases the critical frequency, a fact already evident from the work of Lythgoe and Tansley. The significant thing about these data, is that in common with the procedure normally used, they show a maximum critical frequency and a decline at the highest intensities.

Considered as a whole, the foveal measurements definitely bear out the general notion advanced to account for the abrupt change in slope in the original data of Porter and in the subsequent measurements of Ives. This is that the steeper part of the data represents the function of the cones, and the less steep part represents the participation of the rods. When, as has been done by us, the measurements are confined to the fovea, in an area which is practically rod-free, only one continuous relationship appears between critical frequency and intensity over the whole range, and it is to this relationship that the cone portion of previous investigators clearly corresponds.

IV

Measurements with the Periphery

The correctness of this conclusion becomes even more apparent when the measurements are made with regions of the retina outside the fovea centralis. We measured the critical frequency for white light with the same set-up as before but with fixation at 5° above the center, 15° above the center, and 20° above the center. The data thus concern a retinal test area of 2° diameter having a surround of 10°, and situated at 5°, 15°, and 20° above the center of the eye.

TABLE II

Critical fusion frequency (cycles per second) for white light at various retinal illuminations (photons). Test field 2° placed 5° above center of fovea. Surround 10°.

Right eye S.H.			Right eye C.D.V.		
No. of readings	Retinal illumination	Critical frequency	No. of readings	Retinal illumination	Critical frequency
4	0.000166	3.50	11	0.000258	2.53
2	0.000491	5.64	9	0.000518	4.59
4	0.00134	7.31	7	0.00185	6.80
4	0.00710	8.51	5	0.00698	8.90
2	0.0138	8.97	12	0.0276	9.21
5	0.0264	8.25	12	0.239	9.67
4	0.0514	7.70	12	0.764	14.80
6	0.146	9.41	7	2.98	19.90
6	0.968	15.32	10	7.93	25.20
6	3.66	19.70	13	24.2	30.16
7	16.5	26.66	11	448.	37.10
4	138.	34.70	8	2118.	36.00
5	514.	34.96			
5	1954.	31.70			

The data for 5° above the center are given in Table II and Fig. 2 for S. H. and in Table II and Fig. 3 for C. D. V. In all essentials the two sets of measurements agree. At the lowest illumination the critical frequency rises very distinctly with log I. As the intensity reaches about 0.01 photons, the critical frequency ceases to increase, and remains approximately constant over a range of 1.25 logarithmic units.

For C. D. V. this plateau is horizontal within the accuracy of the measurements; for S. H. the plateau has a slight, but distinct undulation. The undulation is not a product of averaging the data. It appears in every set of measurements made by S. H., and occasionally in those of C. D. V. Examination of the data of Ives shows the presence of such an undulation in the measurements for blue light at lower intensities, where Ives supposes the relation between critical frequency and log *I* to be horizontal; it is also apparent in some of the data of Lythgoe and Tansley.

The plateau in our data continues till about 0.2 photons, after which the critical frequency rises with log *I*. It continues to rise until it reaches a maximum at about 400 photons, after which it decreases as the intensity increases.

Figs. 2 and 3 show that the data for 5° off-center clearly fall into two parts. The first is at low intensities, where the critical frequency first rises with log *I* and then reaches a maximum which is approximately maintained. The intensity range covered by this rise and plateau is about 3.25 logarithmic units. The second part also begins with a rise in critical frequency as log *I* increases, and also terminates when the critical frequency reaches a maximum, and then declines. The intensity range covered by the second part is about 4 logarithmic units.

For the low intensity rise of critical frequency, the slope of the data is 5.0 for C. D. V., and 4.5 for S. H. There are only three points each available for these determinations, but the points are well established. For the high intensity rise in critical frequency the slope of the data is 10.5 for C. D. V. and 8.5 for S. H. The slope for C. D. V. is thus only slightly less than for the fovea, whereas for S. H. it is distinctly less for the 5° fixation than for central fixation.

The only measurements with which we can compare ours are those by Lythgoe and Tansley, who made a special point of determining the slope of their data at the higher illuminations for a 1° field placed 10° peripherally. Their two observers give slopes of 14.4 and 11.7 respectively. Lythgoe and Tansley state that the slope remains the same for all parts of the retina, and indeed give the slope for one observer at 50° off-center as 11.7. Their other data (*cf.* especially their Fig. 12) distinctly do not bear out this conclusion, but indicate instead a higher slope for the periphery than for the fovea. This difference between their and our data may be due to the difference in size of surround: ours covered 10° whereas theirs covered the whole eye. This may account also for the rather high values of the critical frequency found by them for the periphery.

TABLE III

Critical fusion frequency (cycles per second) for white light at various retinal illuminations (photons). Test field 2° placed 15° above center of fovea for S. H. and 20° above center for C. D. V. Surround 10°.

Right eye S.H. 15° above center			Right eye C.D.V. 20° above center		
No. of readings	Retinal illumination	Critical frequency	No. of readings	Retinal illumination	Critical frequency
2	0.0000551	2.62	9	0.000109	2.65
3	0.000205	5.33	9	0.000194	4.44
2	0.000760	9.61	9	0.000402	6.08
2	0.00577	9.31	9	0.00104	8.10
2	0.0214	9.14	8	0.00258	9.04
2	0.0796	8.43	8	0.00887	9.26
2	0.551	10.15	7	0.0209	9.44
2	2.05	11.45	9	0.0678	9.63
2	7.60	15.05	9	0.218	9.81
2	57.7	18.05	9	0.726	11.30
3	214.	17.63	9	1.52	14.83
2	796.	17.05	9	3.24	18.00
			5	7.78	21.00
			15	21.1	22.06
			13	144.	22.60
			9	3319.	22.10

The new element contained in our measurements of the periphery is the existence of two separate parts to the relationship between critical frequency and intensity. The measurements with the test field farther out in the periphery confirm and extend these findings. The data for a retinal test area of 2° with a 10° surround placed at 15° above the center are given in Table III and Fig. 2. The data for a similar area placed at 20° above the center are given in Table III and

Fig. 3. The data show the same division into two parts, each with a rise of critical frequency versus log I and subsequent plateau as do the data already given for a 5° peripheral displacement.

The slope of the rise at low intensities is 6.1 for C. D. V. and 6.0 for S. H. The slope for the rise at the higher intensities is 9.6 for C. D. V. and 7.0 for S. H. Again the value for C. D. V. is not very much below that for the fovea, whereas that for S. H. is distinctly less.

The plateau for the 15° and 20° off-center measurements is about 0.75 log units longer than for the 5° off-center data. This is because at 15° and 20° the low values of the critical frequency occur at lower intensities and the high values occur at higher intensities than at 5° off-center. We are quite certain of this broadening out of the curve at low and high intensities for the more peripheral positions because we made special measurements to test this point. We do not record these special measurements here because they merely corroborate those already given in the tables and figures.

V

Various Quadrants

The results we secured with peripheral stimulation seemed so striking, and yet so clear in their significance that we wished to be certain of their general validity over the retina. The peripheral data so far reported deal with regions above the fovea. We therefore measured the relation between critical frequency and illumination for the same test area and surround as before, but placed 5° peripherally in the four principal directions: up, down, nasal, temporal.

The data for C. D. V. are given in Table IV and in Fig. 4. Each group represents only one set of measurements made in a day. Each point is thus the average of two or three concordant readings. It is apparent that the essential phenomenon recorded is a general one, since the data all show the same division into two parts, with a rise and a plateau for each part.

Certain details are to be noted in which the four directions differ. The height of the low intensity plateau seems to increase in the following order: temporal, nasal, down, and up. The two horizontal positions have the same slope for the high intensity rise; its value is 8.7, and it is therefore less than the up position which as before is 10.4.

TABLE IV

Critical fusion frequency (cycles per second) for white light at various retinal illuminations (photons). Test field 2° placed 5° away from center in four different directions. Right eye of C. D. V. Surround 10°.

Nasal		Temporal		Down		Up	
Retinal illumination	Critical frequency	Retinal illumination	Critical frequency	Retinal illumination	Critical frequency	Retinal illumination	Critical frequency
0.000372	2.20	0.000372	2.24	0.000438	1.93	0.000310	2.50
0.000873	4.24	0.00163	4.84	0.000693	4.08	0.000647	4.24
0.00381	6.88	0.00604	5.76	0.00145	5.80	0.00214	6.32
0.00980	6.96	0.0219	6.68	0.00418	7.40	0.0163	8.92
0.0276	7.48	0.0662	6.88	0.0142	7.84	0.0235	8.28
0.0662	7.40	0.200	8.68	0.0428	7.96	0.289	10.4
0.103	7.40	0.317	10.7	0.129	8.28	0.491	12.4
0.159	9.08	0.873	14.8	0.390	10.5	1.38	16.8
1.05	15.2	3.99	19.9	0.693	15.2	6.18	24.2
4.80	20.3	15.5	25.0	1.59	19.7	19.5	29.4
38.1	29.6	56.4	30.3	5.02	23.8	28.3	29.8
276.	35.1	276.	36.2	15.2	30.3	1589.	34.8
				41.8	36.4		
				276.	37.7		
				1026.	37.4		
				4375.	36.0		

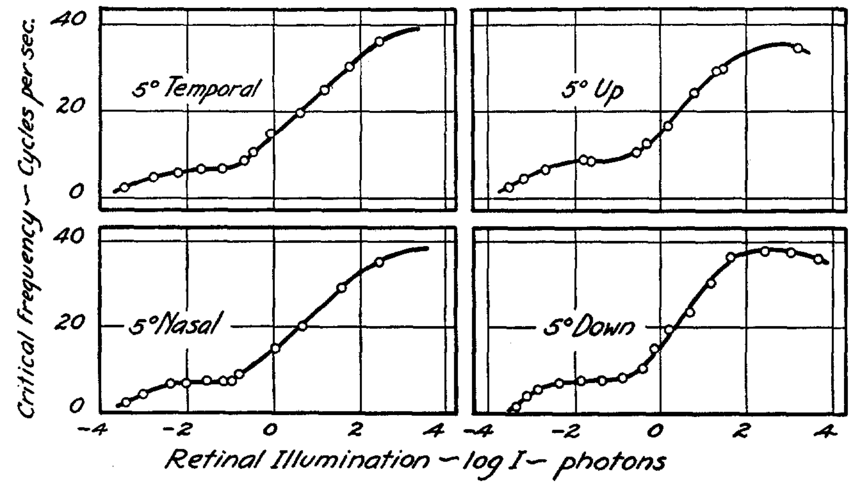

FIG. 4. Data for C. D. V. showing relation between critical frequency and log *I* for white light for 5° off-center in the four principal retinal directions.

Moreover the down position data show a slope of 12.0 which is distinctly greater than that of the up position and of the fovea. Very likely these variations in detail represent variations in structure at which we can only guess in our present knowledge. Possibly they are related to the population density of the elements in various parts of the retina.

VI

Structural Interpretation

The general relations among the data are apparent when they are considered all together as in Figs. 2 and 3. Their interpretation in terms of the well known histological composition of the retina is immediately obvious.

The data for the fovea are represented by a single relationship between critical frequency and illumination. Since there are almost no rods in the foveal area used for the measurements, the central fixation data must surely record the behavior of the cones of the fovea.

The data for the periphery are represented by two separate relationships between critical frequency and illumination. The part at the higher illuminations resembles the foveal curve in appearance, and for the 5° eccentric field, has practically the same slope. Clearly this portion also represents the behavior of the cones. Moreover, the portion of the peripheral data at low illumination is apparently a distinct and complete relationship, and does not appear in the foveal curves. The obvious conclusion here is that the rise and the plateau at low illuminations represent the function of the rods.

These conclusions are strengthened by the fact that as the measurements are made farther in the periphery, the low intensity plateau becomes longer, and therefore the separation between the rise at low intensities and the rise at high intensities becomes greater. Thus the rod system becomes more sensitive and the cone system less sensitive as the measuring area moves from the center farther into the periphery. This is in keeping with the anatomical increase in number of rods and the converse decrease in cones as one proceeds along the retina toward the periphery.

All our data and their structural interpretation are thus strictly in line with the knowledge and ideas embodied in the duplicity theory (von Kries, 1929) which functionally separates the anatomically distinct rods and cones, and places the dominance of the rod system at low illuminations and the dominance of the cone system at higher illuminations. It will be shown in a later paper of this series how this description of the data is further borne out by work with colored lights (*cf.* Hecht and Verrijp, 1933).

VII

SUMMARY

When measurements of the critical fusion frequency for white light over a large range of intensities are made with the rod-free area of the fovea, the relation between critical frequency and log I is given by a single sigmoid curve, the middle portion of which approximates a straight line whose slope is 11.0. This single relation must be a function of the foveal cones.

When the measurements are made with a retinal area placed 5° from the fovea, and therefore containing both rods and cones, the relation between critical frequency and log I shows two clearly separated sections. At the lower intensities the relation is sigmoid and reaches an upper level at about 10 cycles per second, which is maintained for 1.25 log units, and is followed by another sigmoid relationship at the higher intensities similar to the one given by the rod-free area alone.

These two parts of the data are obviously separate functions of the rods at low intensities and of the cones at high intensities. This is further borne out by similar measurements made with retinal areas 15° and 20° from the fovea where the ratio of rods to cones is anatomically greater than at 5°. The two sections of the data come out farther apart on the intensity scale, the rod portion being at lower intensities and the cone portion at higher intensities than at 5°.

The general form of the relation between critical frequency and intensity is therefore determined by the relative predominance of the cones and the rods in the retinal area used for the measurements.

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