INTERMITTENT STIMULATION BY LIGHT

V. THE RELATION BETWEEN INTENSITY AND CRITICAL FREQUENCY FOR DIFFERENT PARTS OF THE SPECTRUM*

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(Accepted for publication, October 14, 1935)

I

Expected Results

Our previous studies of the relation between light intensity and critical fusion frequency (Hecht and Verrijp, 1933 *b*) have shown that the differences which the measurements exhibit when they are made in different retinal locations are an expression of the duplex structure of the retina (Schultze, 1866; Parinaud, 1885; von Kries, 1929). With a centrally located 2° field the data are continuous over the whole intensity scale, and may be described by a simple sigmoid curve, whereas with a peripherally located 2° field the data divide sharply into a low intensity section and a high intensity section each of which may be described by a single curve. Since the central, 2° field falls within the rod-free area of the retina, the continuous nature of the data indicates that they are a function of the cones alone. The double nature of the peripheral measurements very likely represents rod function for the low intensity section and cone function for the high intensity section. This is borne out by the increasing separation of the two sections as measurements are made farther and farther from the center: the cone section shifts to higher intensities and the rod section to lower intensities, as would be expected from the increasing ratio of rods to cones in these regions.

In order to confirm the identification of the two sections with rod

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* A preliminary report of these measurements was made to the Optical Society of America in February, 1935 (Hecht and Shlaer, 1935) and to the XV International Physiological Congress in Leningrad, in August, 1935.

and cone function, we have now used different parts of the spectrum to study the relation of critical frequency to intensity. For this purpose we employed a central retinal area 19° in diameter, containing both rods and cones.

Fig. 1 gives the relative spectral sensibilities of the cones and rods, and shows what may be expected of the measurements. Spectral energy can produce no visual effect until it reaches the relative intensity indicated by the rod curve. Above that, rod function dominates until the cone threshold is reached. The intensity distance over which the rods dominate in visual function changes throughout the spectrum: between 670 and 630 mμ it is small and alters only slowly; beginning at about 600 mμ and going toward the blue the dis-

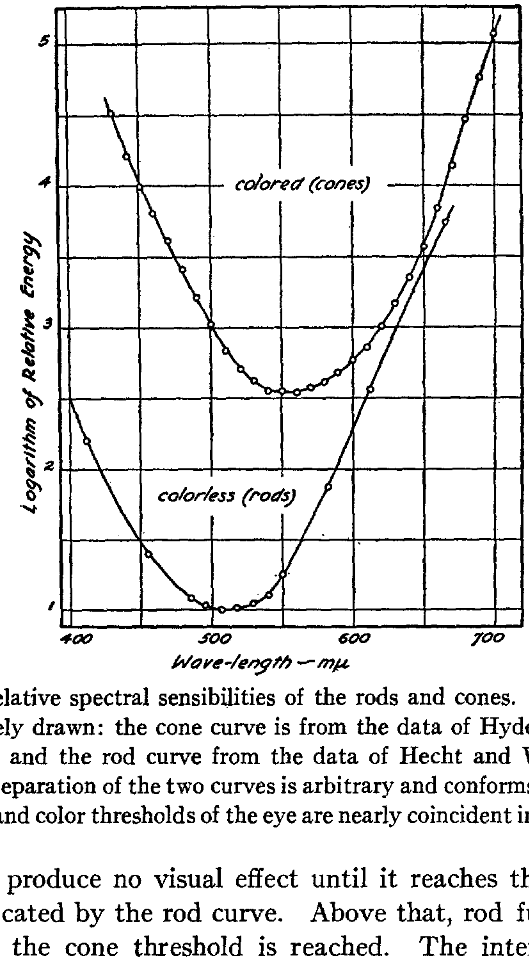

FIG. 1. Relative spectral sensibilities of the rods and cones. The curves are each accurately drawn: the cone curve is from the data of Hyde, Forsythe, and Cady (1918), and the rod curve from the data of Hecht and Williams (1922). The vertical separation of the two curves is arbitrary and conforms to the fact that the colorless and color thresholds of the eye are nearly coincident in the red.

tance becomes rapidly larger, while below 500 mμ it remains practically constant.

Preliminary investigation (Hecht and Verrijp, 1933*a*) confirmed these expectations. Critical frequency measurements with a small peripheral field showed that whereas the high intensity portions are much the same for all colors, the low intensity section is very short with red light and becomes longer as the light moves down the spectrum toward the blue. The monochromatic filters used by Hecht and Verrijp reduce the brightness to about 1 per cent of the incident light. With the optical system in the apparatus (Hecht, Shlaer, and Verrijp, 1933), this reduction limited the measurements to only a part of the high intensity cone curve. We have therefore redesigned the optical system so as to furnish about 100 times as much light as in the previous research. At the same time we have increased the total field size to a diameter of 35° which may be used in various configurations of non-flickering surround and flickering test area.

II

Apparatus and Procedure

Fig. 2 shows the new arrangements. An image of the incandescent ball of a 2 ampere Osram Punktlicht is focussed by lens $L1$ on the plane of the sector disc. The diverging light is then converged by $L2$ through the unsilvered portion of the photometer cube to fill the field lens $L3$. This forms the flickering central field. Another image of the same source is made to fill the silvered section of the photometer cube in an analogous way by lenses $L1'$ and $L2'$. This constitutes the non-flickering surround. The surround is made equal in brightness to the flickering field (above the critical fusion frequency) by the movement of lens $L2'$, which controls the divergence of the beam in filling $L3$. $L3$ then focusses the two images of S_1 and S'_1 on the field lens $L4$ of the viewing telescope, which in turn forms an image of the photometer cube in the focal plane of the ocular of the telescope. Finally, the ocular focusses images S_3 and S'_3 of the source on the pupil of the eye. The size of the final combined image of the source, as it appears in front of the ocular and falls on the pupil of the eye, is 1.5 × 1.3 mm. There is thus no necessity for an artificial pupil in this system, since the image size remains constant and well below the smallest pupil at the highest brightnesses.

Before it enters the telescope objective the light passes through the circular unsilvered portion of a small photometer cube C, the silvered portion of which reflects a fixation point into the field. The fixation point consists of a pin hole P, strongly illuminated by the image of a flashlight lamp filament projected by a microscope objective. The pin hole is at such a distance from the telescope as to be in focus at the same time as the image of the large photometer cube. The fixation point is mounted as a unit with its lamp and objective, and is movable in all directions within the optical field. The brightness of the fixation point is controlled by a potentiometer available to the observer.

Between the field lens *L*3 and the telescope objective *L*4, there are neutral and monochromatic filters and a neutral wedge and balancer for intensity and color control. We used two neutral filters transmitting approximately 1/100 and 1/10,000. The wedge and neutral filters were calibrated separately for each of the color filters with a Martens polarization photometer as already described in paper II of this series (Hecht, Shlaer, and Verrijp, 1933).

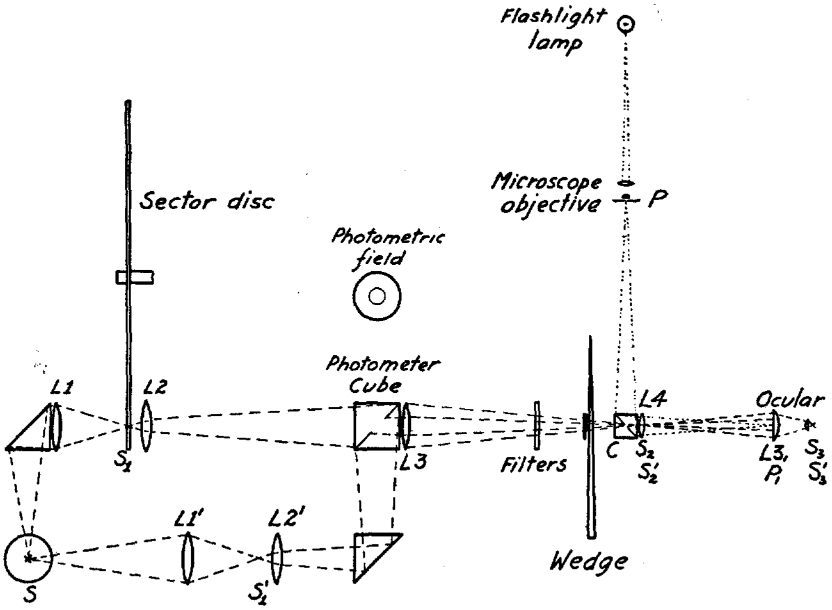

FIG. 2. Diagram of the new optical arrangements for flicker measurements.

For isolating portions of the spectrum, we used Wratten monochromatic filters 70, 71A, 72, 73, 74, 75, and 76, obtained from the Eastman Kodak Company. With filters 75 and 76 we used Corning filter 428 to exclude the slight amount of red which these two filters transmit. In the data the wave-lengths given correspond to the center of gravity of the measured transmission of the filter multiplied by the energy distribution of the source and by the high intensity visibility curve. The brightness of the lights transmitted by the filters was determined by heterochromic matching of contiguous filters, one against the other,—the yellow (73) being matched against white.

Because of the ocular, the absolute brightness had to be determined by a binocular match between the test field as viewed with the right eye, and a fixed brightness viewed through a 2 mm. diameter pupil with the left eye. After measuring with a Macbeth illuminometer the brightness of the surface viewed through the left eye, and taking the artificial pupil size of the left eye into consideration, the brightness as seen with the right eye may be described in terms of photons.[1]

The procedure for making the measurements was almost the same as described in the second paper of this series, with two changes added as a result of our experience. In all cases now, the intensity was set and the frequency varied by a slide rheostat until flicker disappeared. Two readings at each intensity were usually adequate; if they did not agree closely we made a third, and rarely a fourth. As before, care was taken to secure complete adaptation to each intensity, but now we allowed no rests in the dark between intensities. We found the rests in the dark neither necessary nor beneficial, and without them we could maintain a continuous state of light adaptation which easily changed its level with increasing intensities. By this procedure we were able in 2 hours to span the whole visible intensity range, making from 16 steps in the red to 24 steps in the blue.

In all the measurements to be reported in this paper, we used a circular test field, 19° in diameter; it was always surrounded by a non-flickering circular area 35° in diameter, of the same brightness as the test field when it is interrupted at rates beyond the critical fusion frequency. The intensities given are for the non-flickering central test field, and therefore are twice the brightness of the surround.

III

RESULTS

The results are given in Table I. Each datum is the average of the measurements made in three separate runs with the right eye of each

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[1] The photon as a unit of retinal illumination was suggested by Troland (1916). Intensities measured in millilamberts are converted into photons by multiplying with the factor $10a/\pi$, where a is the effective area of the pupil. In Paper II of this series (Hecht, Shlaer, and Verrijp, 1933), we misinterpreted Troland's definition of photon, and made an error in this conversion factor. Because of this and of another minor error, it is necessary to multiply by 40 the numbers given as photons in the three preceding papers of this series (Hecht, Shlaer, and Verrijp, 1933; Hecht and Verrijp, 1933*b* and *c*) in order to make them comparable with the intensities in this and in the following paper by Hecht and Smith.

As an expression of actual retinal brightness, the photon is obviously superior to the millilambert which gives intensities external to the pupil. Nevertheless, photons for different pupil openings record identical retinal brightness only when the pupil areas are small, say below 2.5 mm. in diameter (cf. Stiles and Crawford, 1933).

TABLE I

Brightness and Critical Fusion Frequency for Different Wave-Lengths. Central Fixation; 19° Test Field

450 mμ (Filters 76 and 428)			490 mμ (Filters 75 and 428)			535 mμ (Filter 74)			575 mμ (Filter 73)			605 mμ (Filter 72)			625 mμ (Filter 71A)			670 mμ (Filter 70)		
Intensity in photons	Cycles per second		Intensity in photons	Cycles per second		Intensity in photons	Cycles per second		Intensity in photons	Cycles per second		Intensity in photons	Cycles per second		Intensity in photons	Cycles per second		Intensity in photons	Cycles per second	
	S.H.	S.S.		S.H.	S.S.		S.H.	S.S.		S.H.	S.S.		S.H.	S.S.		S.H.	S.S.		S.H.	S.S.
0.000295	4.09	4.70	0.000234		3.40	0.000977		3.55	0.00324		3.48	0.0162		3.06	0.0422		2.74	0.211	3.94	
0.000447	5.11	5.62	0.000355		4.14	0.00148		4.20	0.00479	4.68	4.27	0.0234	3.02		0.0668		3.61	0.335	4.90	4.12
0.000676	6.12		0.000537	5.27		0.00219	4.32		0.00708	5.88		0.0257		4.10	0.104	3.57	4.79	0.531	5.82	5.09
0.00102	7.38	6.81	0.000776	6.28	6.21	0.00324	6.00	6.10	0.0107	6.97	6.56	0.0347	4.59		0.168	4.91	5.31	0.841	6.75	5.89
0.00246	9.48	9.06	0.00186	8.47	7.30	0.00724	8.22	7.98	0.0246	9.44	8.41	0.0537	6.00	6.35	0.272	6.38		1.36	8.28	7.08
0.00589	11.6	10.2	0.00437	10.6	8.91	0.0166	10.4	10.1	0.0589	11.7	9.98	0.126	8.65	8.04	0.452	7.64	7.28	2.16	10.5	8.51
0.0141	13.4	11.5	0.0100	11.5	10.3	0.0380	12.4	11.4	0.145	13.1	10.8	0.295	10.4	9.02	0.733	9.02		5.31	13.7	11.9
0.0316	14.4	12.7	0.0234	13.5	11.4	0.0891	14.3	13.2	0.295	14.3	12.2	0.724	11.6	10.1	1.25	10.6	11.4	12.2	16.6	16.4
0.0724	14.9	12.8	0.0646	14.9	11.8	0.240	15.7	14.2	0.646	15.3	13.1	1.86	13.3	10.9	2.11	12.4		27.9	20.4	20.6
0.170	16.2	12.3	0.148	15.0	11.8	0.537	15.9	14.5	1.48	16.3	13.4	4.79	15.6	12.2	2.48		12.7	70.0	26.2	25.7
0.417	15.5	12.5	0.339	15.6	12.4	1.20	15.9	14.3	3.47	16.5	14.6	7.59	15.8	15.6	5.96	15.6	15.9	197.	32.5	30.9
0.933	15.7	13.6	0.759	15.2	13.1	2.75	14.4	14.3	8.32	17.5	17.3	17.8	18.3	18.8	14.6	18.3	18.3	484.	39.4	36.1
2.04	15.4	14.6	1.82	14.4	14.1	6.31	15.0	15.3	20.4	23.4	21.0	41.7	22.5	23.6	38.5	24.0	22.4	1110.	44.4	39.8
4.68	16.6	16.1	5.37	16.2	15.6	14.8	16.6	18.2	38.9	26.6	24.1	105.	28.6	27.4	104.	30.8	28.2	2480.	48.1	45.0
10.7	19.9	18.3	12.3	18.9	19.7	40.7	22.8	24.6	87.1	32.2	28.4	269.	35.9	32.5	299.	37.3	33.3	6100.	52.1	45.3
25.7	23.0	21.3	28.2	22.9	22.7	91.2	31.7	28.2	200.	37.3	32.2	676.	41.5	38.0	596.	41.2	37.1	15300.	56.5	44.9
63.1	27.7	25.6	66.1	28.3	26.5	209.	34.8	32.2	479.	41.6	35.7	1320.	45.2	38.8	1460.	45.9	40.7	39400.	59.4	44.7
148.	34.4	31.1	151.	33.7	32.1	479.	39.4	37.2	1175.	47.3	41.0	3090.	48.8	42.0	3670.	51.3	44.0			
331.	37.8	36.4	355.	39.1	35.9	1120.	45.7	42.0	2400.	52.5	43.0	7590.	52.8	44.7	9890.	56.9	45.0			
759.	44.7	40.4	977.	45.0	41.0	3020.	48.8	45.7	5250.	56.2	44.0	19500.	54.6	43.5	27200.	57.5	45.0			
1780.	48.1	44.2	2240.	50.4	44.5	6760.	55.2	48.2	12000.	60.5	43.9	50100.	60.7	44.7	58200.	59.6	44.9			
4370.	54.0	47.1	5130.	56.2	46.2	15100.	54.3	49.2	28200.	63.5	45.0	97700.	61.4	43.7						
8130.		47.3	12000.	57.3	46.6	34700.	57.2	49.8	67600.	64.1										
			27500.	58.5	50.1	79400.	59.3	47.8												
			50100.	61.2	47.5															

of us. The table shows that as the spectrum changes from red to blue, measurements of critical frequency become possible at lower and lower intensities. This is what we had anticipated from the spectral sensibility distribution for the rods and cones.

The information conveyed by the measurements can best be understood from their graphic representation. As Fig. 3 (the data are for S. H.) shows, the data break into two sections. The high intensity portions, which we have identified with cone function, fall together for all the colors. We have graphically superimposed the various cone data on each other, and have compared the results with the superposition achieved on the basis of heterochromic photometry. Only the slightest differences appear between the two methods, the differences being haphazard and well within the errors both of heterochromic matching and of our superposition judgments. The low intensity sections, which we have identified with rod function, are

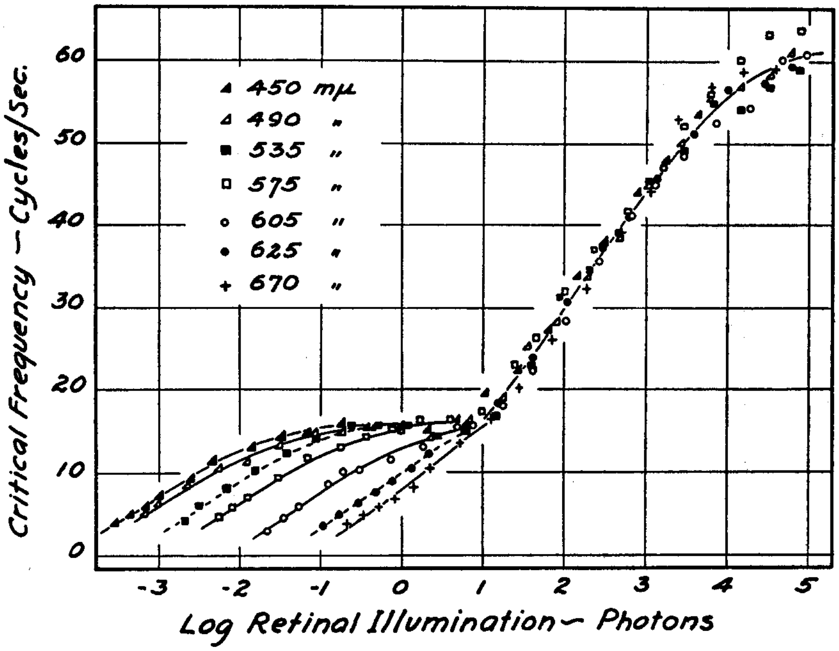

FIG. 3. The data of S. H. showing the relation of critical frequency to log I for the different spectral regions shown.

spread out much as expected, and extend to lower and lower intensities with decreasing wave-length.

Fig. 3 resolves the mystery of Ives' old findings (Ives, 1912) that the low intensity portions of critical frequency data for different parts of the spectrum may be represented by straight lines which differ in slope, the red being steepest and the violet being practically horizontal.

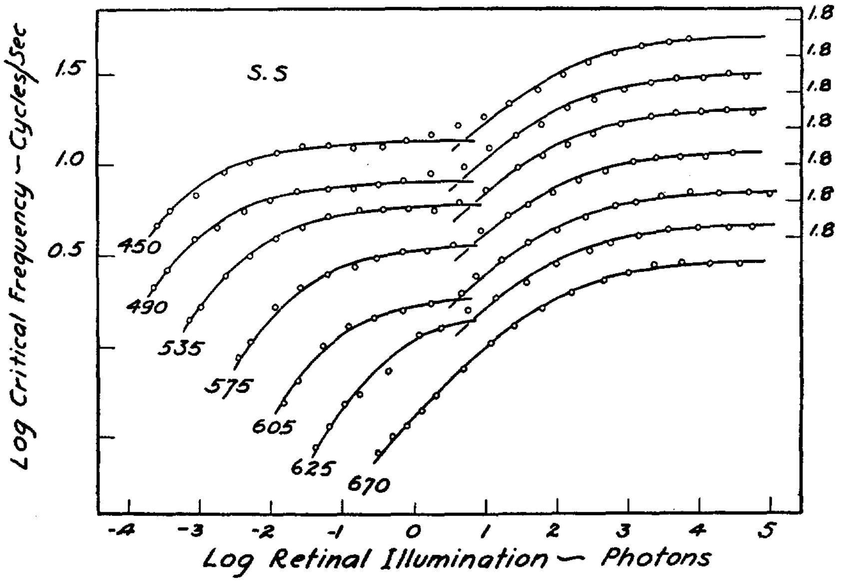

FIG. 4. The data of S.S. plotted as log frequency against log I for the different spectral regions. The numbers on the ordinates to the left apply to the topmost data alone; for convenience the other data have been moved down in steps of 0.2 log unit, and their exact positions are indicated to the right. The curves are from equation (1) for the high intensity cone portions, and from equation (2) for the low intensity rod portions.

It is apparent in Fig. 3 that for short stretches near the rod-cone transition, straight lines can be drawn through the rod data, showing different slopes for the different wave-lengths.

The real phenomenon, however, is something quite different. It is that the separation of rod and cone sections as a whole increases as the wave-length decreases. This is shown strikingly by Fig. 4 in which the data of S. S. are plotted as the logarithm of the critical frequency against the logarithm of the intensity. The data for 670 mμ fall on a single, continuous curve, whereas the data for all other parts of the spectrum are best described by two separate curves. The high intensity curve is in the same position for all colors, and the only effect of changing the spectral composition of the light is to shift the position of the low intensity, rod curve along the intensity axis, without in the least changing its form. From our first measurements (Hecht and Shlaer, 1935) we were inclined to believe that the rod curve shifts along the vertical axis as well. However, the average data of S. H. show no vertical shift at all, while those of S. S. show a slight displacement which is sufficiently haphazard and small to be neglected as within the range of variation.

The transition between rod and cone portions is quite sharp for all but the blue and violet data. On either side of the transition, the identification of rod function and cone function is borne out by subjective observation. The test field, being 19° in diameter, contains the whole macula as well as periphery. At low intensities and below the critical fusion frequency the flicker is distinctly located in the peripheral portion of this field, so that the field resembles a flickering doughnut. As the critical frequency is approached, the last appearance of flicker is always in the periphery. With increasing intensity, the first sign of approaching cone function is the appearance of color in the field, which becomes identifiable with certainty about 0.5 log unit below the actual inflection point of the measurements. At the intensities around the transition and near the critical frequency, two separate centers of flicker are very often apparent, one in the periphery and the other in the center, and it is difficult to predict which will disappear later and thus determine the critical fusion frequency. As a result, this is a region of difficult measurement, and of daily variation. At intensities higher than the transition intensity but near it, flicker usually persists longest in the center, but beyond these intensities the last trace of flicker may be in any part of the field. Obviously the rods determine the low intensity section, and the cones the high intensity section, but the specific cones which set the critical frequency are not necessarily the same throughout the high intensity section.

IV

Theory

The curve which in Fig. 4 is drawn through the data for 670 mμ represents the equation

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

in which I is the intensity and f the critical fusion frequency. K is a constant, which in a log I-log f plot determines the position of the curve on the intensity axis, just as f_{max} determines its position on the vertical frequency axis, neither K nor f_{max} having any influence on the shape of the curve from the equation. It is apparent that the equation describes the entire 670 mμ data with precision. The same curve has been drawn through the cone portions of all the other parts of the spectrum, even though it slights the transition points for the blue and violet. The rod portion of all the measurements has the curve drawn through it from equation

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

in which the symbols have the same meaning as before.

Although equations (1) and (2) may be considered as purely empirical expressions to describe the data, they nevertheless can be derived from the familiar reversible photochemical system which has been useful in describing many aspects of vision and the photosensory process (Hecht, 1934). Generalizing the derivation previously made (Hecht and Wolf, 1932; Hecht and Verrijp, 1933 *c*), the steady state, when the light and dark periods of the intermittent illumination are of equal duration, may be written as

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

where m and n are the reaction orders of the photochemical and dark reactions respectively.

If we make the critical frequency f proportional to the concentration x of photoproducts at the steady state, then equation (3) becomes the flicker equation (1) for the cones, provided $m = n = 2$,.as shown by the data of intensity discrimination (Hecht, 1935). Similarly, when $m = 2$ and $n = 1$, equation (3) becomes the same as (2) used for describing the rod data.

The assumption (Hecht and Verrijp, 1933 *c*) that f is proportional to x^2 has to be discarded because it requires the intensity factor to enter the equations as I^2, and Arnold and Winsor (1934) have definitely shown that I must enter as the first power if Talbot's law is to hold. This change introduces nothing new for the rods since the rod dark reaction at the steady state is also proportional to x ($n = 1$) and the resulting equation (2) is almost identical with the old one (Hecht and Verrijp, 1933 *c*). For the cones, however, the data persist in showing two contradictory things. According to theory, the critical frequency should be proportional to the velocity of the dark reaction. The data clearly show (see particularly the following paper) that for the dark reaction $n = 2$, so that f should be proportional to x^2. Yet the data follow equation (1) only when f is made proportional to x.

One way of resolving this contradiction is to suppose that the proportionality of f to x indicates the dependence of the critical frequency for the cones not on the dark reaction which re-forms the sensitive material, but on the secondary dark reaction which follows the photochemical one in time and which uses the photoproducts to form impulses that leave the cell. There is no reason to suppose that the velocity of this reaction is anything but directly proportional to the concentration of photoproducts rather than to their square.

SUMMARY

1. An optical system is described which furnishes large flickering fields whose brightness, even when reduced with monochromatic filters, is capable of covering the complete range of the relation between critical frequency and intensity.

2. For a centrally located test field of 19° diameter, with light from different parts of the spectrum, the data divide into a low intensity section identified with rod function, and a high intensity section identified with cone function. The transition between the two sections is marked by an inflection point which is sharp, except for 450 and 490 mμ where, though clearly present, it is somewhat rounded.

3. The intensity range covered by the flicker function is smallest in the red, and increases steadily as the wave-length decreases. The increase is due entirely to the extent of the low intensity, rod section which is smallest (non-existent for S. S.) in the red and largest in the

violet. The high intensity cone portion for all colors is in the same position on the intensity axis, and the only effect of decreasing wavelength is to shift the rod section to lower intensities without changing its shape.

4. The measurements are faithfully described by two similar equations, one for the rods and one for the cones, both equations being derived from the general stationary state equation already used for various visual functions.

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