

THEORY AND MEASUREMENT OF VISUAL MECHANISMS

IX. FLICKER RELATIONS WITHIN THE FOVEA

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I

In our examination of some essential propositions of visual theory it has been necessary to determine flicker recognition contours within the human fovea, with reference to light-time fraction (t_L) and wave-length composition as controlled parameters. It is also desirable to consider in this connection the area (and form) of the test patch as well. We give now an analysis of some of the phenomena encountered, although we do not for the present discuss area or form as variables within the fovea. We are to deal subsequently with conclusions arising from the study of reasonably homogeneous data on flicker recognition as a function of flash frequency and flash cycle form, flash intensity, image area and form, retinal location, wavelength composition of the light, and the fraction of the cycle-time occupied by light. It has been demonstrated¹ that the precise relation between flash frequency F and $\log I$ critical for recognition of flicker is defined by a contour of which the properties express the participating influences of quite a number of such variables. The present paper supplies additional data for the theory of flicker recognition in terms of the multivariate nature of visual response.

The character of the rôles of variables such as have been mentioned is, for the human observer, so far as exploration has gone, entirely consistent with the effects obtained on the corresponding contours for forced reactions to perceived moving stripes in a great variety of animals,² and is consequently non-specific. The basic analytical form of the F - $\log I$ contour is the same, a normal probability summation; and so also are the qualitative effects produced on its shape and position, in various animals, by altering the retinal receptive area, the light-time fraction, and the wavelength composition of the light, regardless of the type of eye concerned² ("camera" or "apposition"). The correlated changes in the specific $F - \log I$ contours, and in addition those produced by altering the temperature of the organism³ (which have not yet been tested with man), are directly in keeping with the general theory of the $F -$

¹ 1937-38, *J. Gen. Physiol.*, **21**, 203; 1940-41, **24**, 505, 635; 1941-42, **25**, 89, 293, 369.

² 1936-37, *J. Gen. Physiol.*, **20**, 393, 411; 1937-38, **21**, 17, 223, 318, 463; 1938-39, **22**, 311; 1938-39, **22**, 463, 487, 795; 1939-40, **23**, 143, 531; 1941-42, **25**, 381.

³ 1939-40, *J. Gen. Physiol.*, **23**, 143, 531; 1939, *Proc. Nat. Acad. Sc.*, **25**, 78.

$\log I$ contour which we have advocated.⁴ Quantitatively they support the idea that flicker recognition, as a forced response, is due to the summative action of elements of effect produced in a population of intrinsically fluctuating neural units. The properties of other analytically usable end-points for visual response are consistent with this.⁵ Among these properties not least significant are those of the *variation* of I_c , the flash intensity critical for flicker.¹ They give an objective standard of homogeneity of data⁶ and they also give a means of demonstrating the basically statistical nature of the critical intensity for single discriminatory responses.⁷

In the present observations several wavelength compositions of light have been used with a single small test area in the fovea, and at several light-time fractions. The resulting properties of the $F - \log I$ function are to be compared with those observed for other test areas and different retinal locations, for the same observer, having particular reference to the problem of visual integration. The dynamical nature of visual response cannot be interpreted simply in terms of the shape of the response contours under a fixed set of chosen conditions, because this shape is in general a function of these conditions; it is also a function of the observer and of the eye used; it is not invariant when these conditions are changed. This is likewise true for the relations between the contours for different parts of the spectrum with conditions otherwise the same.⁸ A guiding thought has been to recognize the respective parts taken by (*a*) number of neural units and (*b*) numbers of elements of effect⁹ produced in the determination of the visual effect used as end-point. It is in some important respects possible to improve the analytical conditions by working with simplex (flicker) performance contours, as obtained within the fovea.

II

The observational methods have been described previously, as well as the methods of computation.¹⁰ The same observers (W. J. C. and E. W.) were concerned

⁴ Cf. 1939-40, *J. Gen. Physiol.*, **23**, 531, etc.

⁵ 1940, *Proc. Nat. Acad. Sc.*, **26**, 54; 1939, *Science*, **90**, 405.

⁶ 1937, *Proc. Nat. Acad. Sc.*, **23**, 23; 1938, **24**, 130; 1939-40, *J. Gen. Physiol.*, **23**, 101, etc.

⁷ 1936, *Proc. Nat. Acad. Sc.*, **22**, 412; 1937, **23**, 23.

⁸ 1941-42, *J. Gen. Physiol.*, **25**, 293, 369, 381.

⁹ 1936-37, *J. Gen. Physiol.*, **20**, 393, 411; 1938-39, **22**, 311; 1938-39, **22**, 795; 1939-40, **23**, 531; 1940-41, **24**, 635; 1941-42, **25**, 89, 293, 369, and two following papers.

In a recent book, Bartley gives a figure purporting to show that this rule concerning the effect of the light-time fraction differs from that found by other investigators (Bartley, S. H., 1941, *Vision: A study of its basis*, New York, Van Nostrand Co., p. 122, Fig. 31). In fact, however, Bartley draws graphs on coordinates of F and t_L/t_D , and not of F_{max} and $t_L/(t_L + t_D)$. We gave a fairly detailed account of the necessity for using the latter coordinates, in our first papers on the subject (1937-38, *J. Gen. Physiol.*, **21**, 313, 463).

¹⁰ 1940-41, *J. Gen. Physiol.*, **24**, 505, 635; 1941-42, **25**, 89, 293.

throughout. Monocular data (left eye) are discussed here. For the present experiments a square image measuring at the retina 0.602° on a side was provided by suitable adjustment of the slits in one limb of the visual discriminometer.¹⁰ A very small red dot immediately above this square image was formed by another beam of the instrument illuminating a minute hole in metal foil. By suitable adjustment of the intensity of this image it was seen only as red when within the fovea, and by practice it could be held at the lower margin of this area. This method of fixation is not perfect, but the properties of the data (including the variation of I_c) at the lowermost F range, where alone it was really needed at all, show none of the irregularities to be expected if this procedure had not insured adequate fixation.

When the plots (Figs. 1 and 2) are examined, certain quite minor but systematic departures are observed; thus the value of mean critical intensity I_m for the colored lights at $F = 2$ tend to be a little too high, while those at $F = 5, 8,$ and 10 tend to be slightly too low (by the test of the adjusted probability integral for F vs. $\log I_m$). Minor departures of this kind have been found in other cases,¹¹ and have there been traced to a correlation with properties of particular filters ("neutral") used for the step-wise control of intensity levels. In the present instance they are likely due to the same causes, in part at least. The spectral transmissions by the filters used have been recorded and studied.

There is no discontinuity in the curves describing the data (Fig. 1) even though the fixation point be obliterated at $F = 10$ and above, and there is then no change in the scatter of the individual measurements of critical intensity for flicker (Fig. 3). This is important evidence, because at flash frequencies $F = 2$ to 8 or thereabouts the fovea adapted to the prevailing critical intensity for flicker *fusion* with this area of image can scarcely be said to give rise to the consciousness of light at all, although the incidence of flicker is detected with precision. There is no evidence that, under these conditions, even a very tiny illuminated dot quite nearby should influence the subjective end-point for flicker. This is especially clear since the curves for light-time fractions $t_L = 0.10$ and 0.90 are found to be quite parallel (with each $F_{max.}$ put = 100), as is shown in Fig. 3. It should be pointed out that there is nothing necessarily mysterious about the ability to detect flicker end-points at flash illuminations so low that the fused, non-flickering field is almost or indeed quite below the visual threshold; it is known that judgment of intensive differences can be made with lights not consciously perceived.¹²

III

The observations were planned as part of a larger scheme, now completed, involving the determination of flicker contours with several wavelength zones, with different light-dark proportions, and with a series of image areas on different portions of the retina. The tests are laborious and time-consuming. If the findings are to form a set of intercomparable data, steps must be taken to assure that no serious changes in an observer have occurred during the period concerned. These steps included as an important feature the systematic study of the variability of the observer's performance. The several sets of

¹¹ 1938-39, *J. Gen. Physiol.*, **22**, 311; 1940-41, **24**, 625; 1941-42, **25**, 381.

¹² Cf. Miller, E. G., 1939, *Am. J. Psychol.*, **52**, 562, etc.

measurements obtained were so far as possible designed to give information on the rôle of the variables mentioned with the smallest convenient effort. Thus, only two light-time fractions were used here, since it has been sufficiently well established that for simple test-fields (such as used here) F_{max} and τ' are rectilinear functions of $t_L/(t_L + t_D)$, while $\sigma'_{\log I}$ is invariant,⁹—unless subdivided test images are used with moving stripes¹³ producing flicker; the complications arising in these latter cases we discuss elsewhere.¹⁴ (F_{max} = the upper asymptote of the $F - \log I$ curve; τ' = the abscissa of inflection; $\sigma'_{\log I}$ = the standard deviation of its first derivative, with F_{max} put at 100.)

Visual performance contours for test areas entirely within the fovea are almost without exception simplex; they form single continuous curves, not the duplex functions characteristic of test areas in or including extra-foveal regions. One of several exceptions to this is seen in the relation of (extinction) threshold intensities to image area, within the fovea. (Another exception, which we shall later discuss at length, is found in the dependence of intensity critical for various different end-points upon the exposure-time.) As given, for example, by the data of Graham, Brown, and Mote, and Graham and Bartlett,¹⁵ the simple power function relating ΔI_0 to A changes exponent abruptly (white light, and red) at image areas of *ca.* 6 to 9 minutes diameter. This is paralleled by the behavior of similar data, including those not gotten by the extinction-of-brightness procedure, and for larger areas and in the periphery of the retina (*cf.* Crozier and Holway¹⁵), as is shown in detail in another place (Crozier¹⁵); reasons have been given¹⁵ for not necessarily regarding this change of slope as signifying structural duplexity. Generally, the properties of the simplex foveal contours have been taken to describe the properties of a purely cone receptor population. In comparing the parameters of such foveal flicker contours with those presumably for the cone units of extra-foveal regions, it has been found necessary to assume that the extra-foveal "cone" parameters for flicker are not influenced by concurrent rod excitation, although cone excitation does influence the neural results of rod excitation.¹⁶ In testing this notion, however, data are required for estimating the properties of the flicker contour parameters as a function of at least several variables, since the rôles of area, light-time fraction, and the like are quantitatively altered when the retinal region tested is changed.⁸ Consequently, comparisons of flicker excitability cannot have general theoretical significance if, for example, one has at hand merely curves for F vs. $\log I$ in different retinal locations with the same image area, light/dark ratio, and wavelength composition of light.

A basic clue to the systematic ordering of the properties of flicker contours is found in the consideration that the "elements of neural effect" responsible for the discrimi-

¹³ 1941-42, *J. Gen. Physiol.*, **25**, 369.

¹⁴ 1941-42, *J. Gen. Physiol.*, **25**, 369; and two following papers.

¹⁵ Graham, C. H., Brown, R. H., and Mote, F. A., 1939, *J. Exp. Physiol.*, **24**, 555. Graham, C. H., and Bartlett, N. R., 1939, *J. Exp. Psychol.*, **24**, 574. 1939-40, *J. Gen. Physiol.*, **23**, 101. The kinetics of adaptation, in preparation.

¹⁶ 1941-42, *J. Gen. Physiol.*, **25**, 89, 293, 369; 1941-41, **24**, 505, 635.

nation of flicker are produced by neural units which fluctuate in their capacities to produce neural effects.¹⁷ For a given retinal region $\sigma'_{\log I}$ is a function of the number of units involved, whereas $F_{max.}$, and also τ' at constant temperature, depend on the mean numbers of elements of effect produced by such units.¹⁶ From this standpoint we shall consider the properties of the foveal flicker contours obtained with a white light and with certain color bands filtered from this white. The filters employed have already been used in various tests with a larger image in other retinal regions, and for other organisms.¹⁸

Violet, blue, green, and red lights were produced respectively by filters Corning 511, Wratten 47, 58, and 70. For some tests a special orange-yellow filter was used also. The intensity scale used in Figs. 1 and 2 is one of photometric brightness based on achromatic matches with the standard white; for certain other purposes a relative energy scale is used, based on matching with the standard white by using a vacuum thermopile with galvanometer as a null instrument.¹⁸

Measurements are collected in Tables I-V. Certain subsidiary measurements are referred to subsequently. Each I_m entry is the mean of ten consecutive readings, of which P.E.₁ indicates the dispersion. For each wavelength composition the observations were taken in several overlapping groups. No systematic drifts were detected, and (as shown subsequently) the variability of the critical intensities also retains a consistent character.

IV

Probability integrals adjusted to the data of Tables II-V are shown in Fig. 1. That a simple probability integral describes such foveal data over their whole range has already been shown, with the measurements for *white* and *blue* as examples.¹³ The curves differ slightly in $F_{max.}$ and in $\sigma'_{\log I}$ (cf. Fig. 2), and they also differ in their positions on the $\log I$ axis (τ').

The general rules already noted^{9,18} are again confirmed: $F_{max.}$ declines as t_L is made greater; τ' increases; but $\sigma'_{\log I}$ is specific for each wavelength composition (at fixed image area). The image area is quite small here, and the change of $F_{max.}$ in passing from $t_L = 0.10$ to 0.90 is less than for a larger area (6.13° square).¹⁹ But, as with the much larger square, the rate of change of the white (*W*) $F_{max.}$ as a function of t_L is distinctly greater than for *V, B, G, or R*. For the latter, the change in the *V* $F_{max.}$ is greatest, and the changes in *G* and *R* are least. This order confirms that found with the larger area used.¹⁹ There is one difference, however: with a foveally centered square 6.13° on a side $F_{max.}$ for $t_L = 0.10$ was in the decreasing order *V, G, B, W, R*, whereas here with the square 0.6° on a side the order is *W, B, V, R, G*. The interesting fact that $F_{max.}$ can be higher for a colored light than for the white from which it is filtered is, however, again shown in the present data at $t_L = 0.90$, where the

¹⁷ Cf. footnotes 2, and 12 and 1936, *Proc. Nat. Acad. Sc.*, **22**, 412, 1940, **26**, 54, 334, 382.

¹⁸ Cf. 1941-42, *J. Gen. Physiol.*, **25**, 89, 293, 381.

¹⁹ 1941-42, *J. Gen. Physiol.*, **25**, 89, 293.

TABLE I

Data for flicker contours with "white" light, W. J. C., monocular (left eye), square image $0.602^\circ \times 0.602^\circ$, in the fovea; $t_L/(t_L + t_D) = 0.50$ and 0.90 . Each I_m is the mean of ten values, I_1 ; P.E.₁ is the dispersion of these ten; I_m = mean flash intensity, in millilamberts.

<i>F</i> per sec.	<i>White</i>	
	$t_L = 0.50$ $\log I_m$ $\log P.E._1$	$t_L = 0.90$ $\log I_m$ $\log P.E._1$
2		$\bar{4}.0233$ $\bar{6}.3971$
4		$\bar{4}.6901$ $\bar{5}.2030$
6	$\bar{4}.1870$ $\bar{6}.6839$	$\bar{3}.1208$ $\bar{5}.5228$
8	$\bar{4}.6125$ $\bar{6}.9542$	$\bar{3}.4646$ $\bar{5}.9376$
10	$\bar{4}.8739$ $\bar{5}.4003$	$\bar{3}.9681$ $\bar{4}.2958$
	$\bar{3}.0820$ $\bar{5}.3892$	$\bar{3}.7322$ $\bar{4}.4296$
	$\bar{3}.0730$ $\bar{5}.5443$	
12	$\bar{3}.1169$ $\bar{5}.5552$	
15	$\bar{3}.6047$ $\bar{5}.8568$	$\bar{2}.2526$ $\bar{4}.9085$
20	$\bar{3}.8919$ $\bar{4}.1956$	$\bar{2}.7221$ $\bar{3}.1713$
	$\bar{3}.9434$ $\bar{4}.4365$	$\bar{2}.7292$ $\bar{3}.1380$
25	$\bar{2}.6392$ $\bar{4}.8819$	$\bar{1}.2869$ $\bar{3}.8409$
	$\bar{2}.4390$ $\bar{4}.8530$	
30	$\bar{2}.8781$ $\bar{3}.3892$	$\bar{1}.7728$ $\bar{2}.2509$
	$\bar{2}.8871$ $\bar{4}.2774$	
35	$\bar{1}.2953$ $\bar{3}.7950$	0.2097 $\bar{2}.6973$
	$\bar{1}.3722$ $\bar{3}.7568$	
40	$\bar{1}.7455$ $\bar{2}.0639$	0.7526 $\bar{1}.1602$
	$\bar{1}.7547$ $\bar{2}.2431$	
	$\bar{1}.7705$ $\bar{2}.2655$	
43	0.2819 $\bar{2}.7266$	
45	0.6182 $\bar{2}.9669$	1.7122 0.2311
	0.6075 $\bar{1}.0783$	
	0.2960 $\bar{2}.8244$	
	0.8016 $\bar{1}.3600$	
48	1.2169 $\bar{1}.9516$	2.4344 0.9652
	1.2991 $\bar{1}.7701$	
50	2.2835 0.8726	3.2477 1.7208
	2.2667 0.9207	
	2.2831 0.9022	
51	3.0046 1.4475	
	2.6233 1.3101	
	3.5670 1.9652	

order is $B > V > R > W > G$; the differences are of course small, but it is clear that (as we have already emphasized¹⁹) comparisons cannot be made unambiguously unless contours are obtained over a range of values of each of the significant variables. For instance, the relative magnitudes of F_{max} for the particular colored lights at a given t_L are really dependent on the different specific changes of F_{max} as a function of t_L , image area, and retinal location.

The fact that, in Fig. 1, the several values of $F_{max.}$ are really so very similar makes it possible to study the change of τ' as a function of t_L almost independently of the influence on $F_{max.}$ When the temperature of an animal can be altered (which does not change $F_{max.}$) it was found⁸ that τ' is an interpretable function of the temperature, and the corresponding function for mean intensity flux can be at least qualitatively indicated for the present data. It is true that the procedure for work with lower animals, where the relations of the $F - \log I$ contour have been studied, involved illumination of the whole eye. It would be interesting to know if the apparent temperature characteristic for the position of the human $F - \log I$ curve depends on the size of the test-patch,

TABLE II

Conditions as in Table I, but violet light and $t_L/(t_L + t_D) = 0.10$ and 0.90 .

Violet

F per sec.	$t_L = 0.10$		$t_L = 0.90$	
	$\log I_m$	$\log P.E._1$	$\log I_m$	$\log P.E._1$
2	$\bar{6}.0040$	$\bar{8}.3071$	$\bar{5}.5643$	$\bar{7}.9818$
5	$\bar{6}.6905$	$\bar{7}.2610$	$\bar{4}.2239$	$\bar{6}.7316$
10	$\bar{5}.5649$	$\bar{6}.0103$	$\bar{3}.0940$	$\bar{5}.3953$
15	$\bar{4}.2316$	$\bar{6}.7745$	$\bar{3}.7964$	$\bar{4}.3296$
20	$\bar{4}.7701$	$\bar{5}.1152$	$\bar{2}.3396$	$\bar{4}.7900$
25	$\bar{3}.2336$	$\bar{5}.6454$	$\bar{2}.8378$	$\bar{3}.2892$
30	$\bar{3}.7612$	$\bar{4}.4302$	$\bar{1}.2893$	$\bar{3}.9005$
35	$\bar{2}.2424$	$\bar{4}.6415$	$\bar{1}.8151$	$\bar{2}.2842$
40	$\bar{2}.7967$	$\bar{3}.2260$	0.3534	$\bar{2}.8196$
45	$\bar{1}.5578$	$\bar{2}.0748$	1.1182	$\bar{1}.6836$
48	0.1485	$\bar{2}.6221$	1.9260	0.2192
50	1.5091	$\bar{1}.9363$	3.0869	1.7002
51	2.6949	$\bar{1}.6287$		

and on the retinal location. It might not be difficult to supply reasons leading to the expectation that this could be the case for ranges of area in which A and $F_{max.}$ are not in simple proportion and in which $\sigma'_{\log I}$ is a function of A , indicating inhomogeneity. But, disregarding this possible complication, we have pointed out that the temperature characteristic for the percentage light-time required to produce a constant value of τ' , with the same flash-intensity at different temperatures, must be the same as that for $1/I$ at any fixed F and fixed t_L fraction. Put in another way,²⁰ "for a given change $\Delta\tau'$ the necessary change in the dark-time percentage is a declining rectilinear function of the change in $1/T^\circ$ required to produce the same change in τ' when $F_{max.}$ is constant." The particular point which can then be examined in the present data is the relation of τ' to t_L in the case of light from different regions of the spectrum. The argument in view is more reasonable when $F_{max.}$ does not change greatly

²⁰ 1939-40, *J. Gen. Physiol.*, **23**, 531 (p. 548).

with t_L , as in the present data; because then one is not concerned with the secondary correlations possible between $F_{max.}$ and τ' . But a still different complication remains, namely that the test must ideally be restricted to cases in which the number of units concerned is the same, as would be indicated by the constant value of $\sigma'_{\log I}$.

TABLE III

Conditions as in Table I, but blue light and $t_L/(t_L + t_D) = 0.10$ and 0.90 .

Blue

F per sec.	$t_L = 0.10$		$t_L = 0.90$	
	$\log I_m$	$\log P.E._1$	$\log I_m$	$\log P.E._1$
2	8.8261	9.2943	6.1911	8.7038
			6.2111	8.7243
4	7.3796	9.9040	6.8084	7.3294
5	7.5229	9.8340	5.0734	7.6386
8	6.1086	8.7360	5.5914	6.1383
10	6.4168	8.9361	5.9418	6.3762
12	6.7653	7.3316	4.2213	6.3394
15	5.0433	7.4782	4.5878	5.0066
18	5.4028	7.9671	4.9447	5.5579
20	5.6465	6.1416	3.1674	5.7170
22	5.8260	6.3006	3.3996	4.0671
25	4.1329	6.5779	3.6609	4.0649
28	4.3788	6.9027	3.9461	4.3361
30	4.5747	5.0881	2.1061	4.5873
33	4.8925	5.5004	2.4199	4.9361
35	3.0786	5.3460	2.6005	4.9413
38	3.4191	5.8582	2.9256	3.1361
40	3.6883	4.2569	1.1790	3.5737
43	2.1072	4.5549	1.6434	2.0733
45	2.4260	4.8995	0.0665	2.4652
			1.9334	2.3325
47	2.9631	3.5711	0.4917	2.9403
48			0.5279	1.0808
			0.7922	1.2781
49	1.7331	2.2983	1.2264	1.6974
50	0.3139	2.7549	1.8513	0.3232
51	1.3813	1.8253		

The argument is, briefly, that if the change $\Delta\tau'$ for a given change Δt_L is the same for different spectral regions, then temperature characteristics for the flicker contours obtained for these lights of differing wavelength composition should be the same, as already indicated—provided $\sigma'_{\log I}$ were the same for the different spectral regions. If the rate of change of τ' for change of t_L should be the same for V , B , G , R , and W , one could then conclude that the chemical mechanism governing the production of flicker recognition elements

is controlled in the same manner. In the data of the present experiment it is clear that the calculated $\Delta\tau'$ between $t_L = 0.10$ and 0.90 is largest for W , smallest for R , and very nearly the same for V and B . The values are:

$(W - \Delta\tau' = 1.72)$	
V	1.49
B	1.51
G	1.56
R	1.45

There is thus a close parallelism between $\Delta\tau'$ for the several spectral regions and white and the respective values of $\sigma'_{\log I}$ (Fig. 2). From the inverse order

TABLE IV

Conditions as in Table I, but green light and $t_L/(t_L + t_D) = 0.10$ and 0.90 .

Green

<i>F</i> per sec.	$t_L = 0.10$		$t_L = 0.90$	
	$\log I_m$	$\log P.E._1$	$\log I_m$	$\log P.E._1$
2	$\bar{7}.6293$	$\bar{8}.0600$	$\bar{5}.1730$	$\bar{7}.5697$
5	$\bar{6}.3404$	$\bar{8}.6912$	$\bar{5}.8771$	$\bar{6}.3849$
10	$\bar{5}.1988$	$\bar{7}.6877$	$\bar{4}.7282$	$\bar{5}.2678$
15	$\bar{5}.8286$	$\bar{6}.3444$	$\bar{3}.3977$	$\bar{5}.9163$
20	$\bar{4}.4143$	$\bar{6}.8957$	$\bar{3}.9312$	$\bar{4}.4444$
25	$\bar{4}.9302$	$\bar{5}.2787$	$\bar{2}.4464$	$\bar{3}.1081$
30	$\bar{3}.3676$	$\bar{5}.8836$	$\bar{2}.9102$	$\bar{3}.2590$
35	$\bar{3}.8839$	$\bar{4}.4824$	$\bar{1}.4204$	$\bar{3}.9409$
40	$\bar{2}.4376$	$\bar{3}.0052$	$\bar{1}.9762$	$\bar{2}.4541$
45	$\bar{1}.2095$	$\bar{3}.8190$	0.7499	$\bar{1}.2878$
48	0.1557	$\bar{2}.4833$	1.5185	$\bar{1}.7951$
50	1.1384	$\bar{1}.3652$	2.7144	1.3601
51	2.2895	0.6951		

of the latter quantities it is deduced that the relative numbers of neural units concerned are

$$W > G > V, B > R$$

This is consistent with the effect of simply enlarging the area of the test-patch, as then $\sigma'_{\log I}$ and $\Delta\tau'$ are again inversely related.²¹

The behavior of $F_{max.}$ indicates no real correspondence with that of either $\Delta\tau'$ or $\sigma'_{\log I}$, the order being $W > B > V, R > G$. $F_{max.}$ is a measure of the total number of elements of effect obtainable and this quantity is determined by two independently varying things: the number of units concerned, and the mean frequency of elements of effect contributed by each. It is already known that $F_{max.}$ and $\sigma'_{\log I}$ can be caused to vary independently.⁹

²¹ Cf. paper on area vs. $\Delta\tau'$ and $\sigma'_{\log I}$ in preparation.

The inference is thus permitted that if the numbers of *units* could be made the same, the values of $\Delta\tau'$ for $t_L = 0.10, 0.90$ at different wavelengths would not differ significantly. (Note that $\sigma'_{\log r}$ for B and V do not really differ and that $\Delta\tau'$ is essentially the same for each.) The observed values of $\Delta\tau'$ do not depart significantly from rectilinear proportion to $1/\sigma'_{\log r}$. Thus there is no reason in these data to question the proposition that the chemical mech-

TABLE V
Conditions as in Table I, but red light and $t_L/(t_L + t_D) = 0.10$ and 0.90 .

Red

<i>F</i> per sec.	$t_L = 0.10$ log I_m log P.E. ₁		$t_L = 0.90$ log I_m log P.E. ₁	
	2	7.9890	8.4614	5.5054
4	6.6105	7.1335	4.1344	6.5511
5	6.8601	7.2780	4.3971	6.8684
8	5.4310	6.0119	4.9300	5.4489
10	5.7366	6.2613	3.2509	5.7145
12	5.9965	6.4227		
15	4.3930	6.8373	3.9168	4.4054
18	4.8054	5.3459		
20	3.0346	5.5870	2.5231	3.0742
22	3.2277	5.6903		
25	3.7245	4.1840	1.0373	3.3739
	3.5765	4.1324		
28	3.8896	4.5258		
30	2.1016	4.6297	1.5680	2.1563
	2.0906	4.4727		
33	2.3476	4.7675		
35	2.4999	3.1089	0.0407	2.6219
38	2.8581	3.3258		
40	1.0852	3.4245	0.6419	1.1103
43	1.5434	2.0155	1.0934	1.6001
45	0.0078	2.5243	1.5511	1.9914
47	0.4869	1.0395		
48	0.7803	1.0778		
49	1.2210	1.6881		

anism of excitation is the same for different spectral regions, although the shape of the flicker contour is definitely not the same for different retinal regions, sizes of image, or spectral compositions.

It has been attempted to deduce the kinetics of primary photic excitation from the *shape* of the performance contour, as in the case of flicker,²² part of the argument resting on the asserted invariance of the shape of this curve in terms of a 2-parameter function. It is now pointed out that (as in other cases²³) 3

²² Cf. Hecht, S., 1937, *Physiol. Rev.*, **17**, 239.

²³ 1940, *Proc. Nat. Acad. Sc.*, **26**, 54, 334, 382.

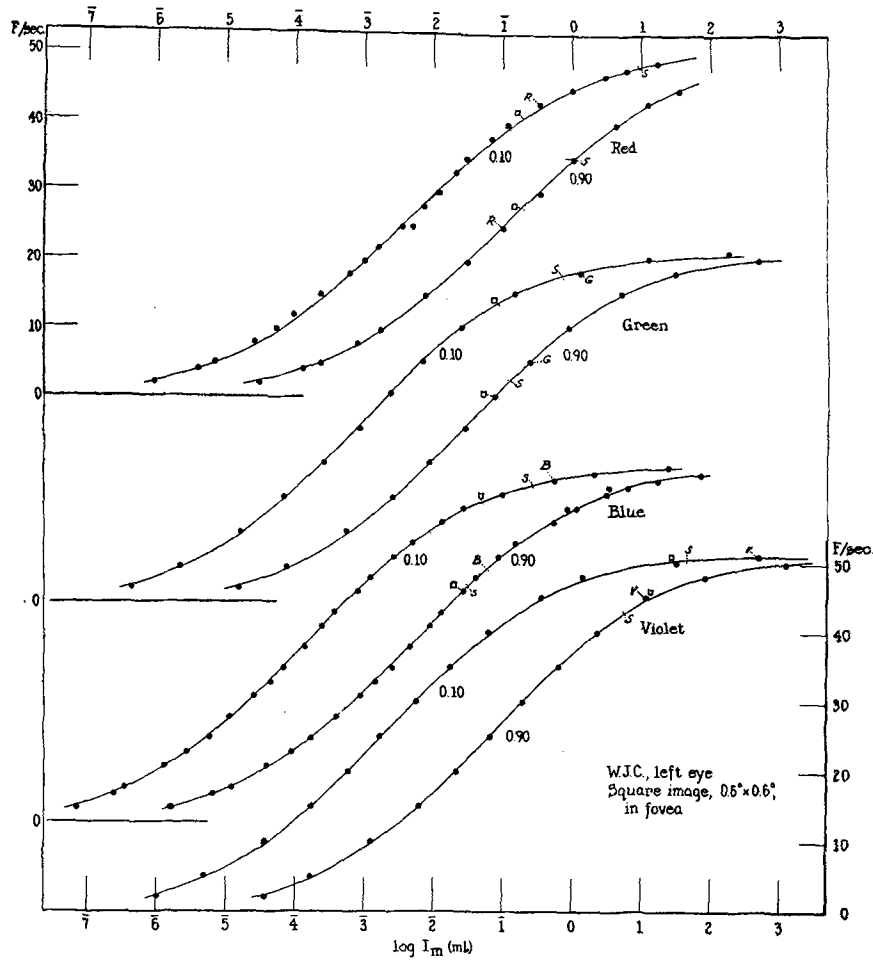


FIG. 1. Flicker response contours within the fovea; square image subtending 0.602° on a side, left eye, W. J. C.; for violet, blue, green, red; with light-time cycle fractions $t_L = 0.10$ and 0.90 . Data in Tables II, III, IV, and V. At the points on the curves marked by the specific symbol (V, B, G, R) the proper color is apparent. At the points marked S the critically fused field is smooth. At the points marked by a square, the outline of the test patch is clearly visible at critical fusion. The curves drawn are normal probability integrals (compare Fig. 2).

parameters are required, as with the probability formulation, but that this in fact does not lead to a conclusion that the simple basic physicochemical control of the production of elements of sensory effect is a complex function of area, retinal region, observer, eye, or wavelength. So far as concerns the deduction of the physicochemical primary properties of excitability, it is required to first dissect out those observable features of the measurements of responses mediated

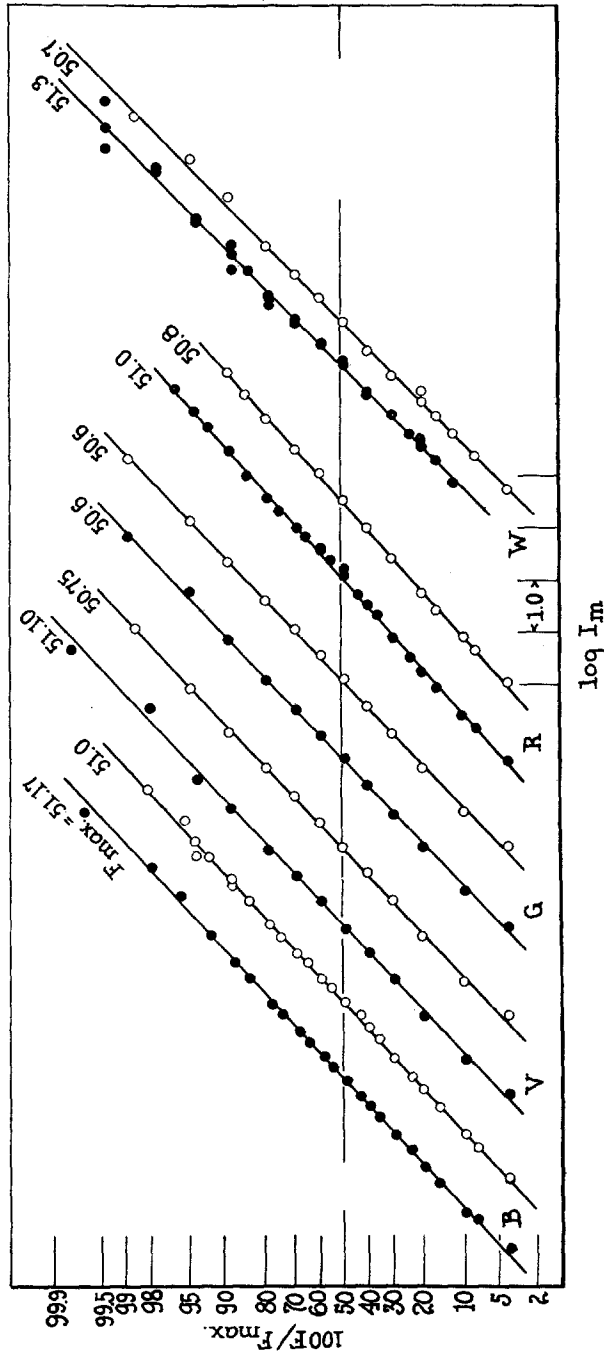


FIG. 2. The data of Fig. 1, and in addition data on white (W) for Table I, put on a probability grid. The respective values of the asymptotic upper maximum F are indicated. The pairs of curves are displaced laterally for convenience; the $\log I$ separation in each pair of curves is correct. In each pair the data for $t_L = 0.10$ (or for W , $t_L = 0.50$) are shown as solid dots, the data for $t_L = 0.90$ as open circlets. The parameters of these functions are discussed in the text.

by this excitability which arise from the fact that the retinal mosaic and the visual system as a whole are a complex of cellular units.

As a consequence of this situation it is clearly necessary, for a determination of a valid spectral "visibility curve" for the flicker sensory effect as a function of wavelength, to obtain measurements of effect as a function of t_L and of stimulated area under conditions such that the values of $\sigma'_{\log I}$ and of F_{max} can be found the same for different wavelengths. Entirely analogous conditions hold for the use of neural end-points other than recognition of flicker. This is sufficiently indicated by the data on visual intensity thresholds as a function of λ when A and exposure time are varied.²⁴ It has been clear from the flicker data already described that with A constant and F_{max} made the same by suitably changing t_L , the correlated dependence of τ' for different spectral zones is not the same for different retinal regions. This could perhaps be explained on the basis of differential pigmentation (*e.g.*, the presence of macular pigment), and in our data on a bird certain differences as compared with man have been successfully accounted for on this basis.⁸ These comparisons have been by way of the properties of τ' as a function of λ with F_{max} constant or nearly so. They thus involve the brightness or the mean energy required to activate one-half the potentially excitable flicker elements of fixed number and ignore the differences of $\sigma'_{\log I}$ for different λ -zones. As already pointed out here, this does not enable us to get very far in disentangling the questions concerned with the effects of λ on (*a*) numbers of units and (*b*) numbers or frequencies of elements of effect from each unit.

Using a foveally centered 6.13° square (observer, apparatus, and filters being the same as for the present paper) we found⁸ that $\sigma'_{\log I}$ ("cones") for white was intermediate, the numbers of cone units for the several kinds of light as deduced from the (inverse) order of $\sigma'_{\log I}$ being: $R > W > B, G > V$; for the present series the corresponding seriation is: $W > G > V > B > R$ (0.603° square). Thus, as regards *numbers of units* affected for a given potential magnitude of sensory effect in relation to discrimination of flicker, W was intermediate with the larger square but is clearly greater for the very small square. We can also compare with these seriations the less complete results independently obtained in another, extrafoveal, region of the retina,⁸ $B > W > R$ (6.13° square).

Only if the effectiveness of the *white* is regarded as some kind of synthesis of competing effects of spectral regions can such differences be understood.⁸ It cannot be decided without further investigation to what extent other visual data must also be regarded from this standpoint, but it is certainly legitimate to consider that the phenomena of flicker recognition give a proper basis for preliminary considerations. In terms of the numbers of neural units excited, and their retinal locations, white light may be more effective than R or B , or it may be intermediate between them. In terms of the total sensory effect ob-

²⁴ Results to be presented elsewhere.

tained it may be intermediate, or greater than R or B , and the relative efficiencies of R and B can be quite reversed. It is obvious that in comparing the several retinal parts here concerned the mere presence of the yellow macular pigment cannot wholly account for the results. It is true that certain parallelisms can be indicated in terms of visual thresholds. Thus at the fovea ΔI_0 , the dark adapted threshold intensity, is in energy terms least for lights from the G region of the spectrum and increases for B and R in that order, corresponding to the respective numbers of foveal neural units here deduced from the flicker data,²⁵ and the curves of ΔI_0 as a function of distance from the fovea do show crossings corresponding to the reversals of R and B in flicker.²⁵ These properties of ΔI_0 are also functions of A and exposure time, however, and no real analysis can be made until these functions have been explored.²⁴

In terms of the intensities required to activate half the potentially excitable elements of ("cone") flicker effect, with $F_{max.}$ made the same by altering t_L , it was found⁸ that W was intermediate in the case of the foveally centered 6.13° square, just as was the slope constant $\sigma'_{1 \log I}$. In the present data with the 0.603° square, τ' for W is higher than for any of the colored lights, in keeping with its smaller value of $\sigma'_{1 \log I}$ and consequently larger number of excited units. The values of τ' (photometric) at $t_L = 0.90$, for example, where the values of $F_{max.}$ are all very nearly the same, are

W , τ'	$\bar{1}.320$ (ml.)
V	$\bar{2}.820$
B	$\bar{3}.683$
G	$\bar{2}.462$
R	$\bar{1}.040$

The corresponding values simply for $t_L = 0.10$ with the larger foveally centered (6.13°) square, no adjustment being made for $F_{max.}$, are in the order $B < V < G < R < W$, exactly as in the present data, while⁸ for the same square centered 6.4° on the temporal side of the fovea the values of τ' were also in the order $B < R < W$, just as for the present series.

Series of measurements with another observer (E. W.) show that, for the same small image area, left fovea, the "yellow spot effect" is much more marked. At $t_L = 0.50$ the curves are all steeper than for W. J. C., $F_{max.}$ is higher, and the values of τ' are higher. The interpretation of the rôle of this effect in flicker is complex, but what we have chiefly in mind here is displayed in the relative positions of the B and R curves. For the data on W. J. C. the τ' separation of B and R is $1.38 \log I$ units, the B curve τ' being smaller. For E. W. the R curve is 1.19 units below the B . Tests were also made with a special yellow-orange filter. In each case the Y and W curves are close together. For E. W. the Y curve is situated at the lowest intensities, for W. J. C.

²⁵ Cf. Wentworth, H. W., *Psychol. Monogr.*, **40**, 1930; and footnote 21.

the B . Yet for retinal regions 6° to 10° off the fovea, or for images 3° square at the fovea, the order of effectiveness with each observer is just that already mentioned for W. J. C., τ' being in the sequence $B < Y < R$ and agreeing closely in the absolute values for the two.

When the values of ("cone") τ' are considered on the basis of relative energy, by way of the thermopile measurements, W with the 6° square was found intermediate when t_L was adjusted to make $F_{max.}$ the same, but at $t_L = 0.90$ it is higher than for any of the spectral zones tested; this is also true of the present measurements with the 0.6° square, just as for the zebra finch.⁸ By this test R and W are *relatively* more effective for flicker, within the fovea alone as compared with the larger field, than are G , B , and V , in that order.

In making this comparison, as for others, it has to be kept in mind just what it is that one is testing. The frequencies of neural effects contributed by each unit at the point of flicker recognition can vary independently of the number of units excited, as is shown by the rôles of t_L , A , λ , and retinal position. Presumably the recognition of flicker is immediately due to the total number of the acting effects; but the circumstances of stimulation determine the number of units producing these effects and the intensity required to activate them. This may be seen in the comparison of the data for the 0.6° and the 6° squares foveally centered. By the $\sigma'_{10g I}$ test, the larger square involves a larger number of "cone" units, and as indicated by $F_{max.}$ a larger total number of elements of effect. This is true for all the wavelength compositions, although the changes in $\sigma'_{10g I}$ are greater in the sequence $R > G > V > B > W$; yet the change in t_L required to give the same change in $F_{max.}$, for example, is obviously much greater for the smaller area.

V

The variation of I_1 is of the same general order as that previously found for the same observer in similar experiments.¹ For a 6.13° square, foveally centered, with white light, $P.E._1/I_m$ was 0.0340 ± 0.005 , independent of intensity, and λ , and t_L . In the present data it is 0.0317; this corresponds to a mean precision of *ca.* 1 per cent in I_m . There is evidence that the difference between the two series, although small, may be significant, and is correlated with the lower levels of $F_{max.}$, and of the numbers of units, in the present series; it probably cannot be exclusively a function of $F_{max.}$, as the data on colored lights have already shown.¹

When dealing with samples of uncorrelated data from the same unrestricted universe, elementary statistical theory indicates that the scatter of σ_1 (or of σ_m for equivalent random repeated samples of the same size n) is given by $\sigma_\sigma = k\bar{\sigma}/\sqrt{2}$, where $\bar{\sigma}$ is the average of the standard deviations of the samples. But if by reason of internal correlations among the data, due for example to the lawful intrinsic fluctuation of the mechanism responsible for the data, and

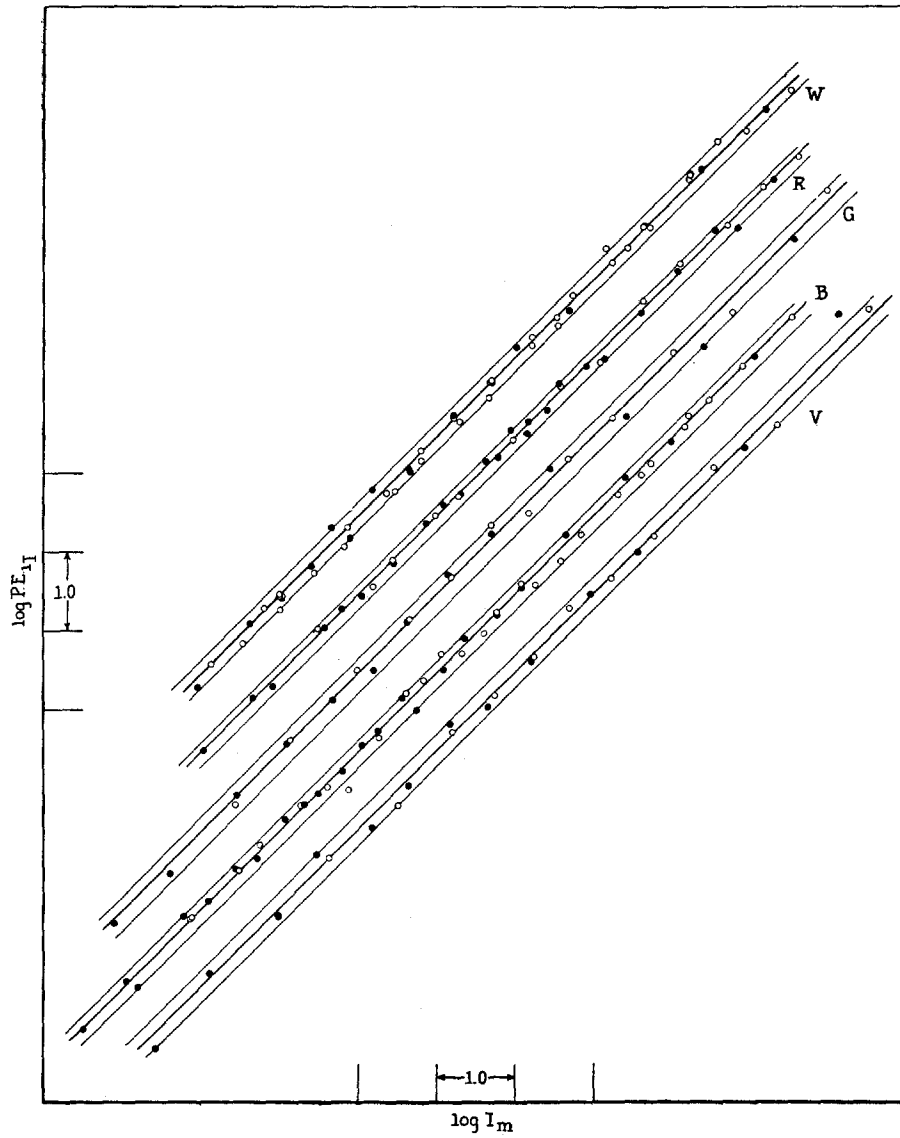


FIG. 3. On a double log grid the relationship between $P.E.I_V$ and I_m is shown for the data of Tables I to V. The plots are displaced vertically for convenience. The intercept of the central lines which bisect each series of points is not the same. The mean value of σ_m is 1.46 per cent of I_m , and not > 2.6 per cent anywhere. The scatter of the points about the central lines is discussed in the text.

when this same mechanism is repeatedly tested, then it is also known that we must correct for this by including a measure of the intrinsic control of scatter. This correction takes the form

$$\sigma_{\sigma} = \bar{\sigma} \sqrt{1 - r} / \sqrt{2}.$$

In sufficiently homogeneous data, on flicker for example, it has been shown empirically that the *scatter* of the variation indices (σ , or P.E.) in plots such as those in Fig. 3, is not invariant. Thus, it is a function of F_{max} . when t_L is varied.¹ It is reduced, together with σ_1 , by binocular stimulation.¹ It is also a function of λ when t_L is constant,¹ although σ_1 is not. As the total size of the potentially excitable group of ("cone") units is increased, the precision with which σ_1 is exhibited is definitely diminished.¹ In the present case, we can roughly test this visually by comparing the breadth of the scatter bands in Fig. 3, which indicate the relative magnitudes of σ_{σ} independently of the intensity level. The mean values of P.E.₁/ I_m , and the scatter of this ratio, can of course be calculated directly.⁷ For the four color bands, where F_{max} is very nearly the same and changes so little with t_L , we find that these breadths are in the order $G > V > B > R$, which is precisely the order already deduced for the numbers of neural units excited. When, however, the number of units ($\sigma'_{log I}$) remains the same but the mean frequencies with which they contribute are caused to change, we also find that the breadth of the scatter band increases as F_{max} increases.¹

It is clear that this can be developed as an independent test of the degree of internal correlation in the data. An important instance has to do with the measure of neural integration ("interaction") as affected by changes of retinal excited area, location, and form, which will be considered subsequently. Since enlargement of image area increases the ("cone") value of $1/\sigma'_{log I}$, and the relation between A and F_{max} is not simple, experimental conditions must again be found for the analytical separation of these two factors. But this appears to be possible, and can obviously lead to an unequivocal objective index of visual integration. The properties of the variation of I_1 plainly show that the total number of units and of elements potentially excitable are concerned in the discrimination of flicker at all levels of F for any one contour. This is clearly consistent with the central nervous control of the recognition point, rather than with its determination by a progressively larger number of excited retinal units as F is increased. The index of integration supplied by the behavior of σ_{σ} is thus independent of the intensity level, and of the level of light adaptation to which the observer is adjusted along the flicker contour.

VI

The various properties of the $F - \log I$ contour are independent of subjective color. There are no discontinuities of the curve nor any changes in the varia-

tion of I_1 which could be correlated with perception of color. When a flickered square test-patch 6.13° on a side was used with various spectral bands a distinct "rod" component was present in the duplex contour. Color appeared at a rather high flash frequency and consequently at a high flash intensity along the fusion contour. It might conceivably have been argued that concurrent rod excitation could in some fashion be responsible for the high color threshold, although the effects of varying the light-time fraction¹⁹ would make this peculiarly difficult to understand. The $\log I$ separation of the approximate color thresholds on the different t_L curves for each color was such as to show that the color threshold along the contour for critical fusion is for each color governed by the mean intensity flux.

With simplex, foveal flicker contours the case may be considered without reference to possible "rod" complications. The observations show that even though only the foveal area is involved the color thresholds at flicker fusion are located at comparatively high flash frequencies (and flash intensities). One problem arising here is of course related to the often debated matter of the "photochromatic" or "achromatic" interval. It has been held for the foveal center that in the extreme red this interval between achromatic and chromatic thresholds is so small that it does not occur (as is true with some observers, but emphatically not for others). It is a simple matter, however, to show that even at the fovea this interval is a function of image area and of exposure time.²⁴ As ordinarily tested for, the foveal achromatic interval with our red is very small (0.01 log unit) for E. W., much larger for W. J. C., over exposure times for *single* flashes ranging from 0.0003 second to 0.5 second. Even with E. W., however, it is not until a comparatively high flash intensity is reached ($\log I$ (*ml.*) = 2.53 for $t_L = 0.50$) that the red color is detected, corresponding to an achromatic interval of *ca.* 1.5 log I units along the flicker contour (for W. J. C., 1.20 is color threshold for this red, an achromatic interval of *ca.* 4 log units).

At the fovea the general order of (energy) intensities for the threshold of color is $R > V > B > G$ (dark adapted), or $R > V > G > B$ (light adapted). For our color bands the color thresholds appear along the flicker contours (W. J. C., $t_L = 0.90$) in the order of intensities (photometric)

$$\begin{array}{ll} R > G > V > B & \text{for the } 6.13^\circ \text{ square, and} \\ V > G > R > B > Y & \text{for the } 0.602^\circ \text{ square.} \end{array}$$

For the data on E. W. the order (0.6° square) is: $V > G > B > Y > R$; here the R color threshold is lower than for W. J. C., the G , B , and Y higher, V about the same. It is to be remembered that a factor in the incidence of the color threshold may well be the fusion of a direct color impression due to flashes of light with the after-image color impressions produced in the dark intervals; as we have earlier noted, these complementary color impressions can be obtained just below the proper color threshold at fusion.¹⁸

The sequence of subjective effects obtained as one goes up the $F - \log I$ fusion contour has been described for larger test-fields.¹ It is of some importance that on the present simplex contours precisely the same general sequence is obtained as F is increased: (1) the critically fused field is gray-blue; (2) it is granular or speckled; (3) it is "frosted"; (4) the outline of the square is clearly seen, and the field is smooth; (5) color is apparent. The order of this sequence, some features of which have been indicated in the graphs of Fig. 1, is not fixed; with R , for example, (5) occurs at lower fusion intensities than (4). The general point is to be made that this succession of phenomena cannot possibly be employed as diagnostic for the entrance of cone function in duplex contours.⁹ Nor can it be alleged that the well known scotopic bluish gray effect is due exclusively to excitation of rods.

The critically fused intensity level at which the *outline* of the square test-image is just perceptible may be taken as an index of visual acuity. It was recorded previously¹⁸ that while the color points on the $F - \log I_m$ curves at different values of t_L fall pretty closely at the same average intensity flux, for each color, the points at which the fused field becomes smooth and uniform tend on the whole to fall at about the same *flash* intensity. This is more definite when the criterion of clear vision of the margins of the foveal square is used. In a general way it is known that visual acuity (steady light) is said to decrease in the order $W < G < R < B < V$. The brightness of flashes producing discrimination of the square boundary, on the flicker fusion contour, ranged in the present experiments from $\log I_m = 2.65$ (W) to 1.00 (V) in the sequence of effectiveness $(1/I_m) = W > B > G > R > V$. In view of the quite different criteria of acuity implied, no complete parallelisms could be expected; this will be more fully examined in a following paper.

VII

SUMMARY

Flicker response contours (F vs. $\log I_m$) for a square image subtending 0.602° on a side, located in the fovea, are simplex probability integrals for a "white" and for four (five) spectral regions filtered from this white, and with different light-time fractions in the flash cycle. The subjective phenomena (the appearance of the field, the intensity threshold for color, and others) at the fusion points along these contours parallel in a variety of ways those obtained on duplex flicker contours resulting from the use of larger or eccentrically placed flickered images. These phenomena therefore cannot be held to indicate involvements of "rod" excitation.

The scatter of the index of variation of I_1 is such as to demonstrate the full participation of all the potentially excitable neural units at all levels of flash frequency, for each kind of light. The magnitude of this scatter, a measure of neural integration in visual performance, is a function of the *number* of these

units (with F_{max} nearly constant); the two quantities vary together when wavelength composition of light is altered.

The properties of the contours for a white light and for the spectral regions filtered from it show that, for the image within the fovea, different numbers of units are excitable in flicker recognition according to the wavelength band used, and different mean frequencies of elements of effect under fixed conditions. The changes in the mean intensity for activation of these units as a function of the light-time fraction in the flash cycle are correlated with the numbers of these units; when this is corrected for, it is pointed out that despite the differences in shape of F vs. $\log I$ it cannot be concluded that the mechanism of excitation differs for different wave-lengths. It is indicated that "white" must be regarded as a synthesis, not a mere summation, of effects due to different spectral regions. Certain differences are pointed to as between foveal and more peripheral regions tested, and as between observers differing in the degree of the "yellow spot effect," with regard to the relative effects of wavelength and of image area. A general consequence is the outlining of conditions required for the precise comparison of excitabilities as a function of wavelength in the multivariate visual system.