

THEORY AND MEASUREMENT OF VISUAL MECHANISMS

VII. THE FLICKER RESPONSE FUNCTION OUTSIDE THE FOVEA

BY W. J. CROZIER AND ERNST WOLF

(From the Biological Laboratories, Harvard University, Cambridge)

(Received for publication, March 19, 1941)

I

Our chief interest in obtaining flicker response contours for excitation of an extrafoveal region has been to modify differentially the parameters of the "rod" and "cone" response curves, and thus to test the general notions already employed for the analytical separation and interpretation of these functions. This involves not merely a test of the respective properties of the two parts of the duplex curve, but also of the interrelations between these components. Such a test can be made in several ways. In one of these, by using an image of the same areal extent (1) centered at the fovea and (2) placed outside it, one necessarily involves changes in the numbers and proportions of cones and rods, as well as changes in the basic excitability *per* (small) unit area and in the area as a whole. The experiment here described was designed to exhibit the resulting differences in the flicker response function, for different wave-length compositions and as a function of the light-time fraction in the flash cycle. These differences are then to be considered in terms of the theory of the nature of the curves. A different manner of carrying out tests of this general import will be considered in a following paper.

To obtain data for the examination of this matter which should be reasonably homogeneous, one observer was used, employing uniocular measurements (W. J. C., left eye) with white, red, and blue lights of the kind already used for the same retinal area (square, *ca.* 6.13° on a side) with foveal fixation, but now fixated with the center of the area 8.37° on the temporal side of the fovea, and $t_L = 0.10$ and 0.90 . In this way it was possible to secure the desired information without too great a time spread. By suitable check measurements it was verified that no appreciable changes in excitability occurred, within the series of tests or in respect to the homologous measurements with foveal fixation already considered.

The technique of the measurements has been described in some detail (Crozier and Wolf, 1940-41 *a, b*), and the description of the instrumentation (Crozier and Holway, 1938-39 *a*) and procedure will not be given again here. We shall

present the data as compactly as possible, without much theoretical comment, before discussing the deductions to be drawn.

TABLE I

Data for flicker response contours with *white*, W. J. C., monocular (left), 6.3° square centered 8.37° on temporal side of fovea, $t_L = 0.10, 0.50, \text{ and } 0.90$; each entry is the mean of 10 observations; I_m and P.E._{-1F} in *millilamberts*. See Fig. 1.

F	$t_L = 0.10$		0.50		0.90	
	log I_m	log P.E. _{-1F}	log I_m	log P.E. _{-1F}	log I_m	log P.E. _{-1F}
<i>per sec.</i>						
2	5.1596	7.5595	5.8616	6.4857	4.4686	6.9235
4	5.3032	7.7701	4.0294	6.5387	4.6726	6.9411
6	5.4763	7.7281	4.1821	6.4865	4.8533	5.3278
8	5.6358	7.9669	4.3150	6.6625	3.0362	5.4631
10	5.7798	6.1906	4.4866	5.0734	3.2030	5.5974
12	5.9848	6.2497	4.6838	5.1519	3.3709	5.6220
14	4.0927	6.5001	4.9302	5.2799	3.5459	5.9528
16	4.3716	6.7843	3.1852	5.6676	3.8090	4.1773
18	4.6821	5.0309	3.4884	5.7830	2.1775	4.3731
19	4.9515	5.2226	3.9179	4.2446	2.5321	4.9132
20	3.6866	4.0672	2.5646	4.8336	1.4118	3.8168
	3.5769	4.0218	2.5895	3.2355	1.3773	3.9123
21			2.7807	3.1543		
22	2.2542	4.5943	2.9294	3.3384	1.7483	2.0447
25	2.3791	4.9142	1.2164	3.7302	1.9556	2.4025
30	2.7372	3.0337	1.5112	3.9822	0.2055	2.6592
35	1.0923	3.4370	1.8644	2.5587	0.5377	2.8508
40	1.5135	3.9188	0.2730	2.8669	0.9807	1.2386
			0.6374	1.6558		
45	0.1501	2.5813	0.8941	1.3195	1.5536	1.7694
48			1.3911	1.8191	2.0962	0.4399
50	1.1062	1.4482	1.7973	0.4452	2.7205	1.0615
	1.0675	1.4890	1.8396	0.3165		
51	1.6218	0.0895	2.4568	0.9644	3.6010	2.0262
	1.7429	0.2821				
52	2.6170	1.0581				
	2.2799	0.8879				

II

Tables I, II, and III contain the data for *white* at $t_L = 0.10, 0.50, \text{ and } 0.90$, and for *blue* and *red* respectively with $t_L = 0.10$ and 0.90 , for the 6.13° square centered 8.37° on the temporal side of the left fovea. A small red dot suitably located and of suitable intensity provided a foveal fixation point. The square image thus located did not overlap the image of the same size when centered at the fovea. In its position for the present observations the field included the

initial flattish part of the curve of "intrinsic retinal excitability" for this observer, as determined by the use of a quite small test area briefly exposed (Crozier and Holway, 1938-39*b*); when *foveally* centered it included the region of markedly least primary excitability. The *red* light was secured by using Wratten Filter No. 70, the *blue* with No. 47, as in the preceding experiments

TABLE II
As in Table I, but for Blue at $t_L = 0.10, 0.90$; See Text, and Fig. 9

<i>F</i>	$t_L = 0.10$		0.90	
	log I_m	log P.E. _{1I}	log I_m	log P.E. _{1I}
<i>per sec.</i>				
2			7.3251	7.1368
4			7.4968	7.7693
6			7.9008	8.3597
8			8.2498	8.7383
10	7.5037	9.9117	8.4504	8.8495
12	7.7343	8.3133	8.8598	7.4266
14	6.1110	8.6641	5.2673	7.6225
16	6.3707	8.6936	5.5998	7.9959
18	6.6867	8.9382	5.8430	6.2127
19	5.3315	8.9047	4.4168	6.7143
20	5.7811	6.1931	4.8688	5.2423
	5.7268	6.1170	4.8374	5.2519
25	4.4925	6.9613	3.4550	5.8431
30	4.7488	6.9968	3.7665	4.1311
35	3.1204	5.6567	2.1808	4.5364
40	3.5448	4.0975	2.6662	3.0945
45	2.1192	4.5759	1.2991	3.8428
48			1.6453	2.0952
50	2.7469	3.2094	1.9514	2.2459
52			0.5305	2.8740
53	1.2842	3.8026		
54			1.3160	1.6953
55	1.8020	2.4312	2.2186	0.4976
58	1.2827	0.2963		
	1.4349	1.6105		

(Crozier and Wolf, 1941-42*a*). The mean intensities given in the tables, and their P.E.₁ values, are in log millilambert units, as obtained from photometric matches with white (below the color level).

The general properties of the F -log I_m contours for the extra-foveal situation are similar to those established under conditions of foveal fixation (Crozier and Wolf, 1940-41*b*, 1941-42*a*). The "cone" F_{max} is lower for the extra-foveal location, the "rod" F_{max} higher. There are a number of quantitative differences in detail. The extent to which these differences can be brought into a

consistent picture of the meaning of the F - $\log I_m$ contour will be considered in the succeeding sections.

Fig. 1 is a plot of the measurements with *white* at the three light-time fractions. It also contains the extrapolations of the "cone" probability integrals, the "rod" difference curves, and certain information about the subjective character of the end-points. Fig. 2 exhibits the "cone" data on a probability grid. The three slopes here (and consequently $\sigma'_{\log I}$) are the same. The

TABLE III
As in Tables I and II, but for Red; See Text, and Fig. 10

F	$t_L = 0.10$		0.90	
	$\log I_m$	$\log P.E._{1I}$	$\log I_m$	$\log P.E._{1I}$
<i>per sec.</i>				
2	5.5203	7.8699	4.6020	5.0275
4	5.7061	6.2467	4.7771	5.2129
6	4.0653	6.5448	3.1661	5.5850
8	4.4467	6.7630	3.5668	5.9410
10	4.7827	5.0589	3.8939	4.3626
12	3.0621	5.4702	2.2316	4.5992
14	3.3065	5.6796	2.4203	4.7719
16	3.5813	5.9914	2.7074	3.0515
18	3.8590	4.2270	2.9648	3.3391
20	2.0886	4.3645	1.2148	3.7706
25	2.4174	4.8357	1.5600	3.8851
30	2.6658	4.9158	1.8154	2.1599
35	1.0142	3.4323	0.1438	2.5210
40	1.3901	3.7272	0.5299	2.8889
45	1.9841	2.4205	1.0956	1.6918
48			1.3704	1.7181
50	0.5677	1.0184	1.7079	1.9552
51			1.9316	0.3439
52	0.9962	1.2723		
53	1.7561	0.0331		

values of the "cone" F_{\max} are again in rectilinear relation to the light-time fraction (Fig. 3), as are also the magnitudes of the abscissa of inflection r' (Fig. 4).

For the same area of test patch the total number of available primary retinal cone units must be presumed less with the extra-foveal location than for the foveally centered location; but without foveal regard the number concerned in recognition of the end-point could well be greater. It has been pointed out (Crozier and Wolf, 1941-42 *a, b*) that there is to be expected, for an increase in the number of these units, a decrease of $\sigma'_{\log I}$ (*cf.* Crozier, 1940, 1941). The values of F_{\max} are a function of the frequencies of effective con-

tributions from these units, as well as of their number. For the foveal and extra-foveal locations we find that the slope in Fig. 2 is actually the greater, and $\sigma'_{\log I}$ consequently smaller, as expected. The "rod" slope (rising; Fig. 5), here presumably representing the participation of a larger population of rods, might be expected to be less, and is actually about identical or insignificantly greater, for the foveal and extra-foveal locations (*cf.* data in: Crozier and Wolf, 1940-41 *b*). (For the "rod" curve the *apparent* F_{\max} is the result of

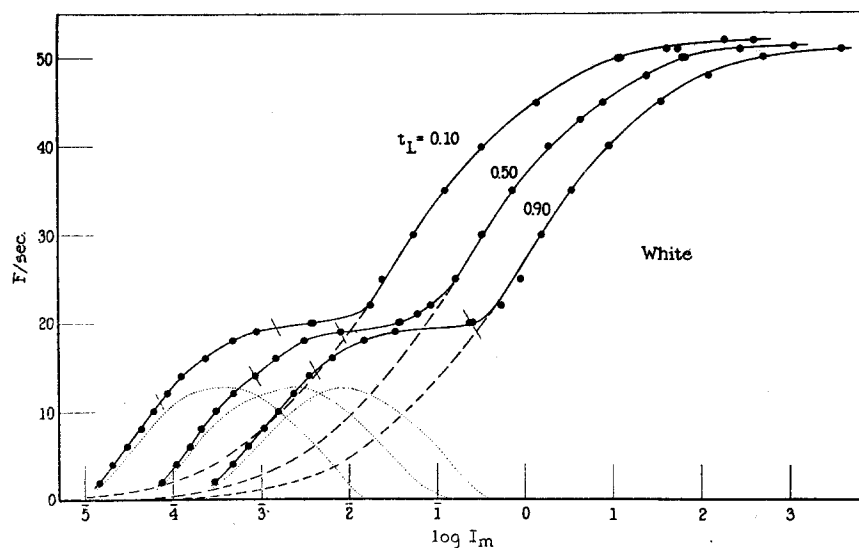


FIG. 1. Data in Table I. Flicker response contours for extra-foveal square, with $t_L = 0.10, 0.50, 0.90$; *white* light; on each curve the lower mark indicates the upper intensity limit of smooth blue-gray fields; the upper mark indicates transition to a smooth field with "foveal" end-point; between these marks the fields are "speckled." For the "cone" portions of the contours the lines are probability integrals as adjusted in Fig. 2; these are extrapolated toward $F = 0$, and the dotted difference-curves ("rod") are also given.

inhibitive "cone" competition; Crozier and Wolf, 1940-41 *a, b*, 1941-42 *a*.) Incidentally, it must be pointed out that in view of the extrapolations (as in Fig. 1, etc.) and difference-taking with curves of different shapes involved in getting at the intrinsic "rod" curves, this kind of quantitative agreement, not expected, is a remarkable fact. It definitely strengthens the view that the procedure used is valid. It may be suggested that, so far as *white* is concerned, the number of effective "rod" units may well be about the same for the two areas studied.

As a test of the general proposition concerning the effect of a change in the number of "cone" units, we note that in the present series F_{\max} is much less

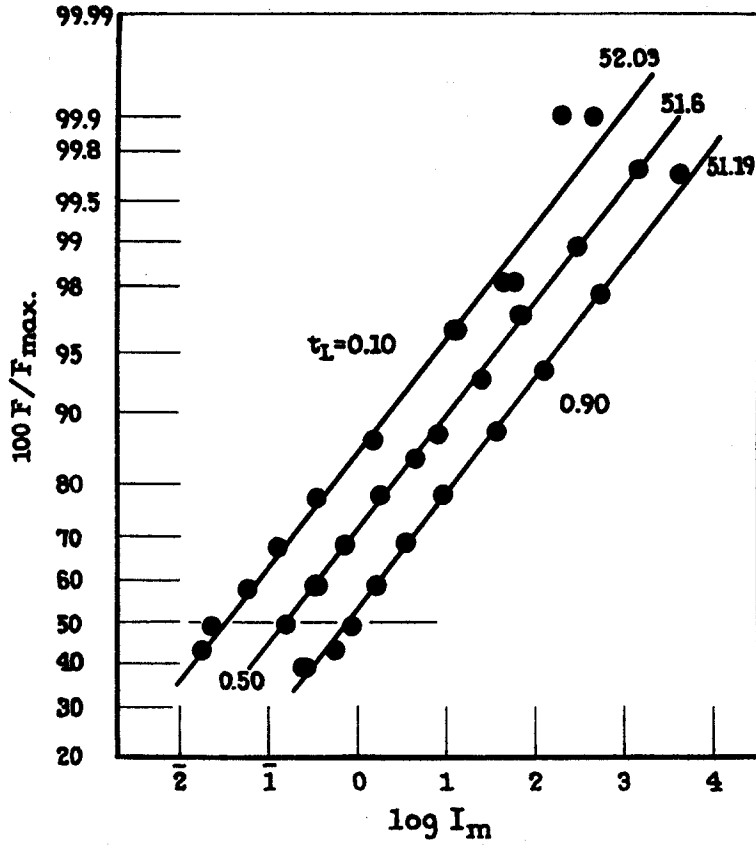


FIG. 2. Measurements in the upper ("cone") parts of the contours in Fig. 1, shown on a probability grid. The number on each graph is the asymptotic value of F_{max} .

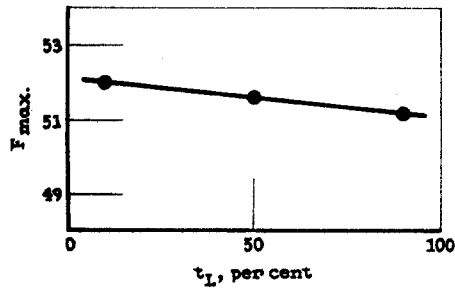


FIG. 3. The rectilinear relation between F_{max} . (Fig. 2) and the light-time fraction t_L .

responsive to change of t_L (Fig. 3; *cf.* Crozier and Wolf, 1940-41 *b*, 1941-42 *a*), although τ' is more responsive.

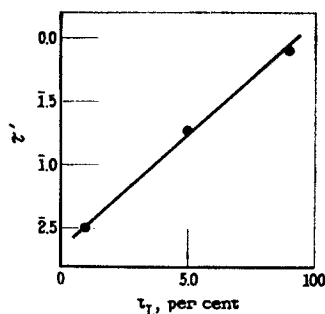


FIG. 4. The rectilinear relationship between the abscissa of inflection τ' of the "cone" probability curve (Fig. 2) and the light-time percentage.

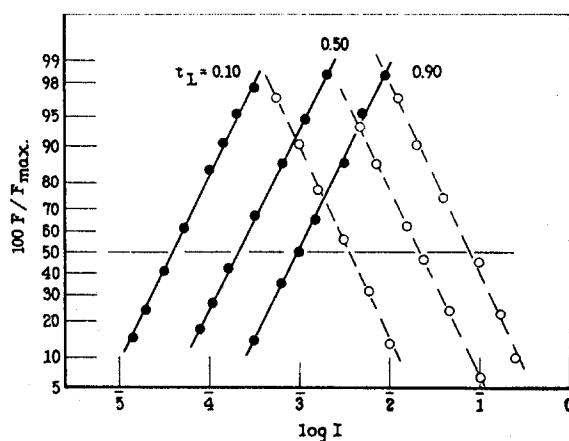


FIG. 5. The rising and descending branches of the difference curves in Fig. 1, shown on a probability grid. Coordinates of points on the dotted curves of Fig. 1 are shown as plotted. The value taken for F_{max} is the same for all three curves, namely $F_{max} = 12.8/sec$.

The variation data (Table I; Fig. 6) exhibit no unusual features (*cf.* Crozier and Wolf, 1940-41 *a, b*). The scatter of $P.E._{17}$ for $t_L = 0.10$ is smaller, relatively, despite the extra-foveal fixation, than might have been expected. The scatter coefficients ($\sigma_{P.E._{17}}$) are low, and their relation to F_{max} does not differ significantly from those expected by extrapolation (Fig. 7) from the relation established for the foveally centered tests. The proportionality constants for

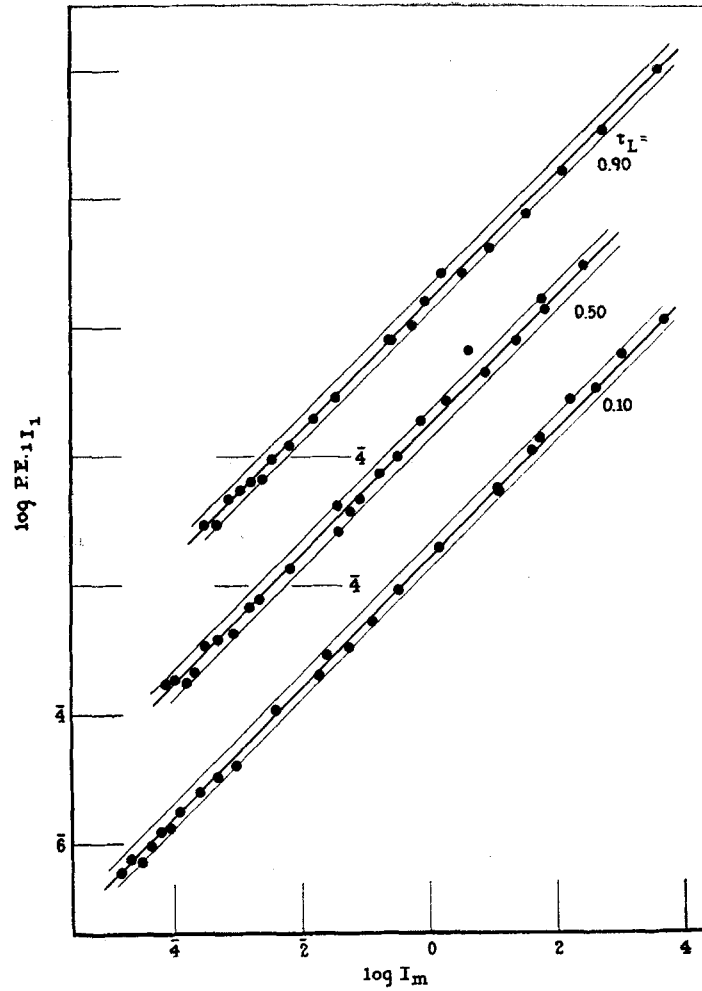


FIG. 6. The relation between $\log I_m$ and $\log P.E.II$ for the *white* data of Table I and Fig. 1. See text.

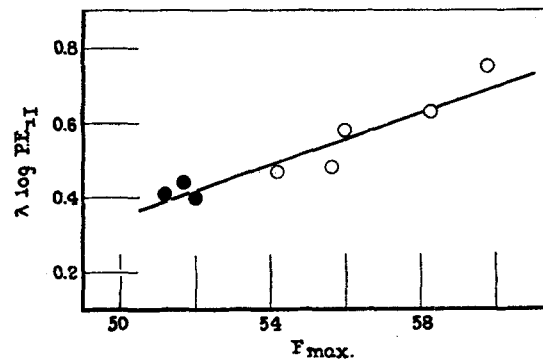


FIG. 7. The relation between the scatter coefficients for $P.E.II$, and F_{max} . The open circles are from previous measurements with the test square foveally centered, the solid dots for the present measurements (Fig. 6) with the extra-foveal square.

$P.E._{17} = k I_m$ are in excellent agreement with those already obtained for the foveally centered patch.

As illustrating the complex character of the relationships appearing in a multivariate system of this sort, it is useful to compare the $F - \log I_m$ curves with the same test area in the two locations used. The essential points appear for any level of t_L ; we take for illustration (Fig. 8) $t_L = 0.10$. It is obvious

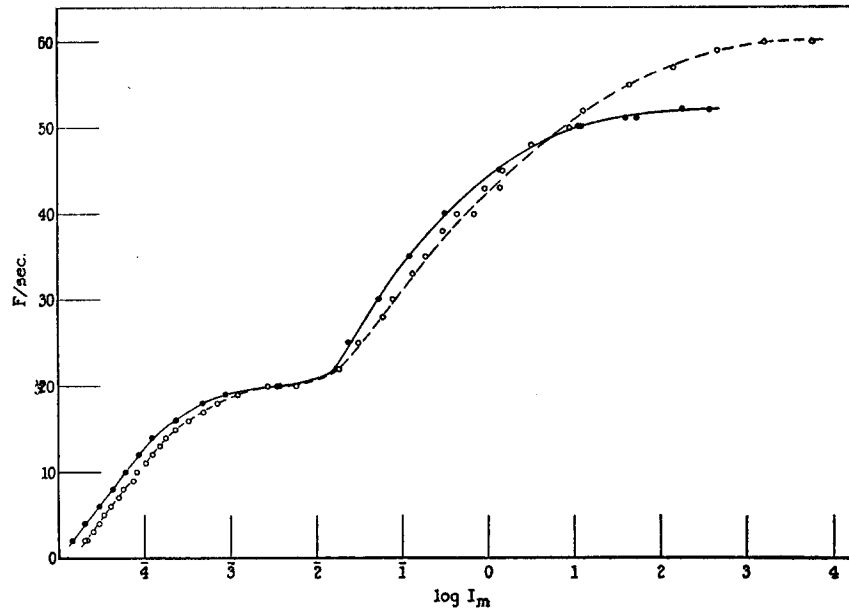


FIG. 8. Comparison of flicker response contours, $t_L = 0.10$, for the same square test area centered at the fovea and on the temporal side of the fovea; *white* light, W. J. C., monocular (left eye); open circlets, test square centered at the fovea, solid dots, centered 8.37° on temporal side of the fovea.

that any real comparisons must depend upon the properties of the function as a whole.

III

The curves for blue and red corresponding to Fig. 1 for white are given in Figs. 9 and 10 (Tables II and III). As with the *white*, the F_{\max} for both *blue* and *red* is less with the foveally centered square; in each case the value of F_{\max} is *greater* than for *white*. The values of τ' , for each t_L , are well below those for the *white*. The variation indices follow the rules already discussed, and the mean ratio $k = P.E._1/I_m$ has the same value (Fig. 11).

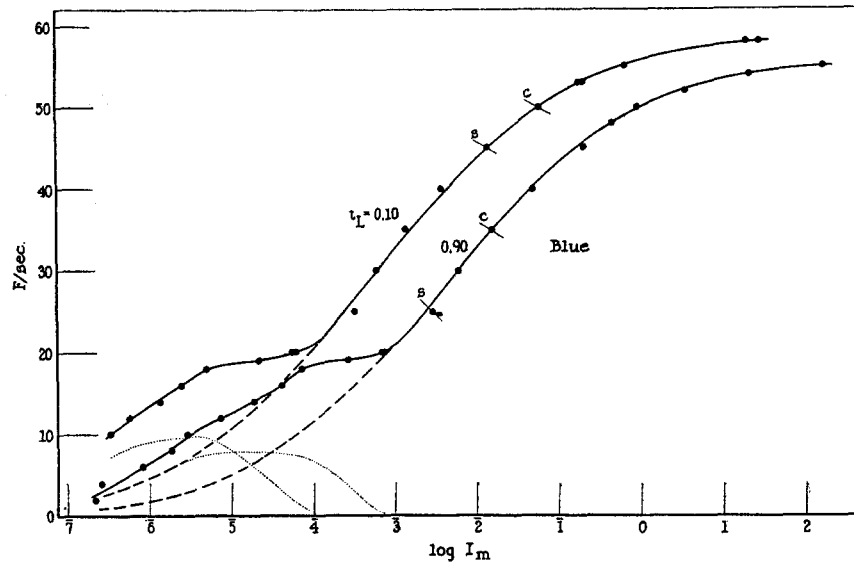


FIG. 9. Flicker response contours for *blue*, extra-foveal test square, with $t_L = 0.10$ and 0.90 . Data in Table II. Above the marks *c*, the end-point fields are colored; above *s*, "smooth."

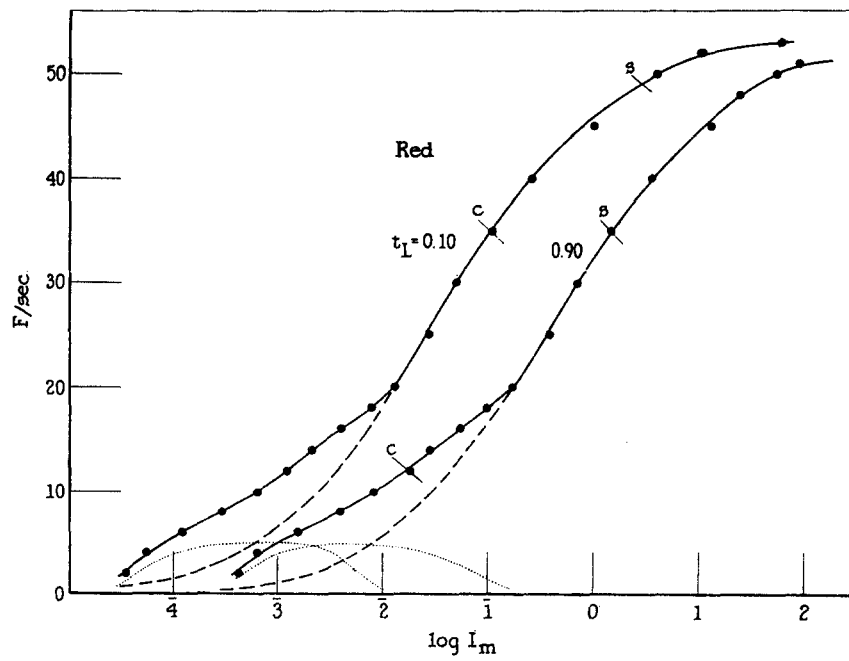


FIG. 10. As in Fig. 9, but for *red*. Data in Table III.

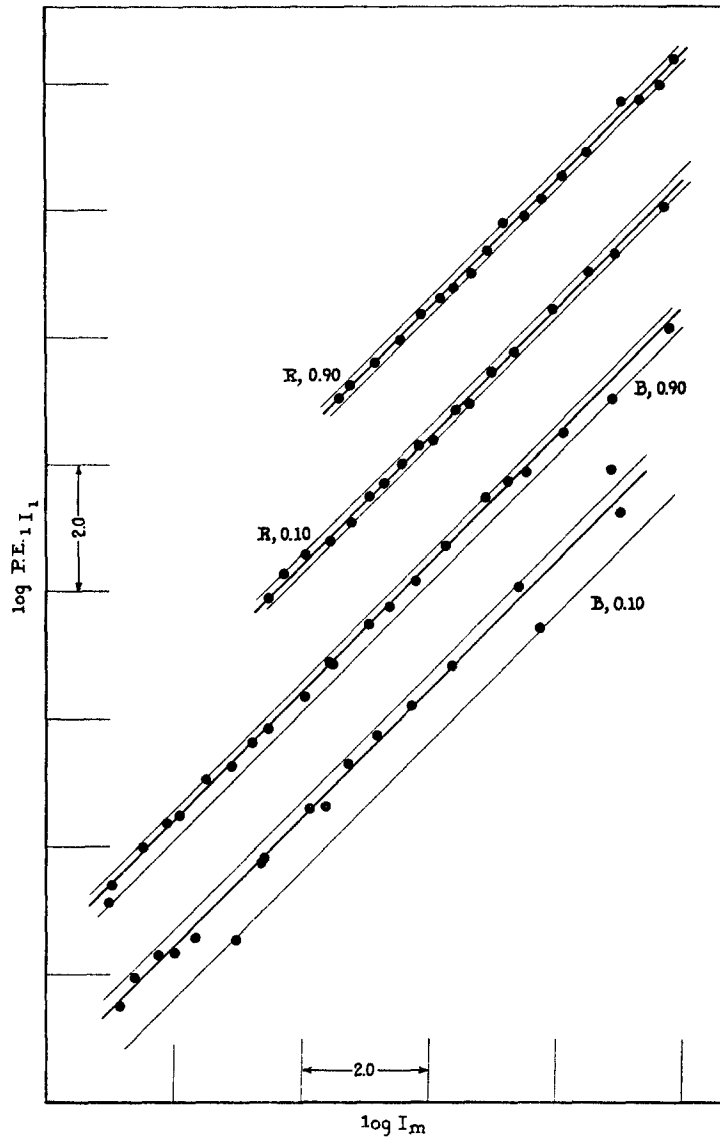


FIG. 11. Variation data for red and blue, Tables II and III. See text.

The probability integrals adjusted to the red and blue data ("cones") show that (Fig. 12), as for the foveally centered case, $\sigma'_{\log I}$ for the blue is greater than for the red. The red $\sigma'_{\log I}$ is, like that for white, less than for the square foveally centered; the blue $\sigma'_{\log I}$, however, is a very little higher in the present

series,—although the difference is not very significant. Some further information is given by the fact that while in the foveally centered series the *blue* and *red* F_{\max} are about equally affected (the *blue* a little more) by change of t_L

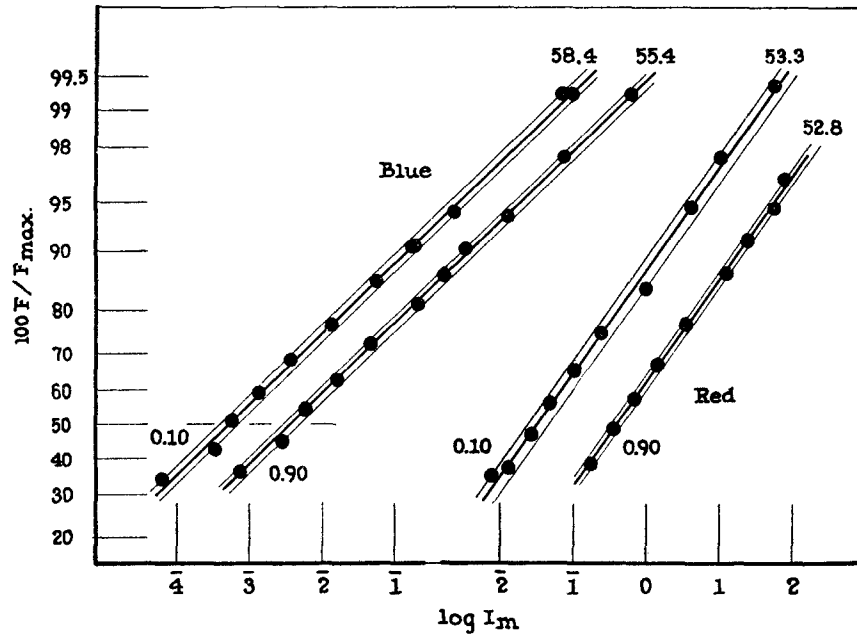


FIG. 12. The upper ("cone") branches of the data in Figs. 9 and 10 put on a probability grid. The associated values of F_{\max} are indicated.

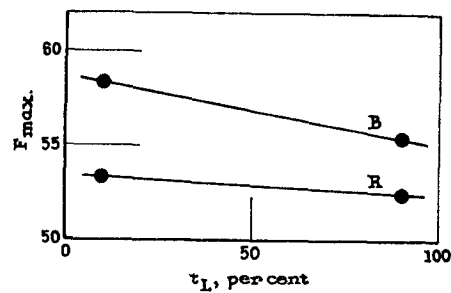


FIG. 13. The relation between F_{\max} and the light-time fraction, for the *red* and the *blue*.

(Crozier and Wolf, 1941-42*a*), in the present case the effect on the *red* values is proportionately much less (Fig. 13) and less than for the foveally centered test patch, whereas with the *blue* it is slightly more. This is correlated with the fact that the displacement of the test patch to the temporal side of the fovea

reduces the *red* F_{max} , more than it does the *blue*, and with the further fact that the effect of change in t_L upon τ' (Fig. 14) is no greater for the *red* and is less for the *blue* than in the centered field.

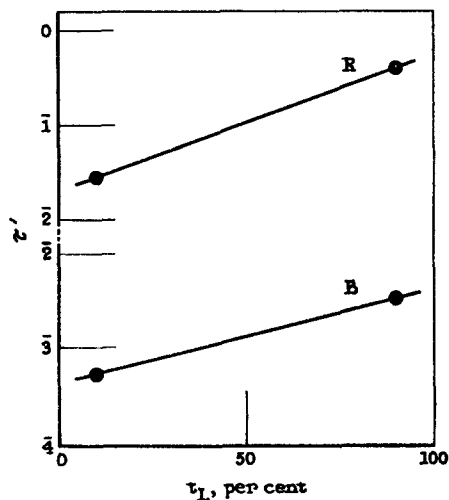


FIG. 14. The relation of "cone" τ' to the light-time percentage, for the *red* and the *blue*.

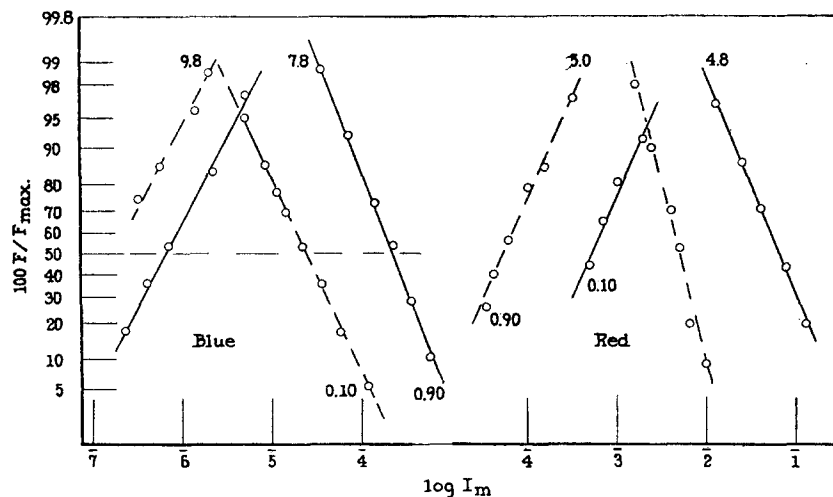


FIG. 15. The "rod" difference-curves of Figs. 9 and 10, for *blue* and *red* respectively, shown on a probability grid.

The dissected-out "rod" curves (Figs. 9 and 10) have been transferred to a probability grid in Fig. 15. The separation of the "rod" and "cone" populations of effects is here great enough so that in each case the apparent "rod"

F_{\max} declines as t_L is made greater (*cf.* discussion in: Crozier and Wolf, 1940–41 *b*). The rising “rod” $\sigma'_{\log I}$ (independent of t_L) is *greater* for the *red*, and *less* for the *blue*, than in the foveally centered series. In terms of the view that one expression of the neural integration of “rod” effects is the increasing value of σ' as the number of units involved is made greater, whereas for the “cone” units the reverse is observed (Crozier, 1940; 1941), this could be taken to mean that in moving out from the fovea we have a larger number of red-excitabile “rod” units and a smaller number of blue-excitabile “rod” units.

We refrain from discussing the question of rod wave-length excitation in detail, because it is obvious that one would require determinations with a series of wave-length compositions and a range of test areas in several different locations. Nevertheless it must be pointed out that the rapidity of the drop of the (small test area) “absolute” threshold for blue, in moving out from the fovea, is considerable,—whereas that for red drops very much more slowly (or, under certain conditions, rises—*cf.* Crozier, Holway and Wolf, 1941–42). This can be made consistent with the indications herein obtained from the properties of the dissected-out “rod” curves, if we remember that the apparent “rod” curve in flicker recognition is the result of a competition with “cone” effects; the proof of this can be obtained by the study of divided fields (Crozier and Wolf, 1941–42 *b*). We note that, in contrast to the situation with the foveally centered patch (Crozier and Wolf, 1941–42 *a*) the $\log I$ separation of the “rod” and “cone” branches is more extensive for the *red* and rather less for the *blue*.

IV

Certain questions raised in our preceding account of the $F - \log I_m$ contours with the foveally centered test area must be briefly considered in the light of the present measurements, although they cannot as yet be adequately resolved. It was pointed out (Crozier and Wolf, 1941–42 *a*) that a comparison can be made of the energies required to activate one-half the potentially excitable elements ($dF/d \log I$). This was made by estimating the values of t_L which for various colors and white would bring the (“cone”) curves to the same F_{\max} , and also the corresponding values of τ' . In this respect the mean energy flux for the *white* lay between that for the *red* and the *blue*. In terms of the properties of $\sigma'_{\log I}$, also, *white* was intermediate between *blue* and *red*, and thus might be taken to involve numbers of units in the order $B > W > R$. The same is true in the present series, the *blue* $\sigma'_{\log I}$ having increased (a little) in the extra-foveal series and the *red* $\sigma'_{\log I}$ having decreased.

While it is certainly too early to discuss the possible bearing of these considerations upon the nature of “white,” for example, it can be pointed out that if white is taken to be a competitive synthesis of blue, red, *etc.*, then the kind of result here obtained can be rationalized: the intermediate value of the white

$\sigma'_{\log I}$, the smaller value of its F_{\max} . under given conditions, and the intermediate value of the mean energy flux for half-activation of the elements of effect potentially excitable. This conception can be more profitably exploited in other connections. Before it can be done efficiently it is desirable to show that the methods used for the analysis of the excitation contours are such as possess generality. There are two distinct aspects to such a demonstration. The nature of the micro-heterogeneous neural mechanism involved in the visual excitation-response phenomena requires that the methods for its analysis have to be non-specific; that is, they must be quantitatively applicable to different kinds of animals. This first requirement is obviously met, with reference to the types of contours obtained for a quite varied assemblage of animals and with reference to the dependence of these contours upon such variables as area excited, temperature, and light-time fraction; we can add to this the essential conformity in the effects of wave-length composition of light (unpublished).

It is equally necessary to show that there prevails the same kind of inner consistency of the analysis when, as can be done with man, different regions of the retina, with known different intrinsic properties, are examined in a single individual. A sign of this consistency is found in the rational relations of the parameters of the complex contour to variables such as those used in the present test. The system of relationships of which this test gives a glimpse is the significant thing, rather than the particular relations between any two variables under conditions otherwise fixed. It has been emphasized that a basic feature of the analysis demands the separation of the properties determined by the *number* of units of a given class potentially excitable, from those properties due to the *frequencies* with which these units contribute to the total effect measured. A procedure for illustrating this separation, and its experimentally measured consequences, is considered in some detail in a following paper (Crozier and Wolf, 1941-42*b*). The meaning of its results can then be utilized for further studies of excitation as a function of wave-length.

V

SUMMARY

The several parameters of the flicker response contour ($F - \log I$) are considered as a function of wave-length composition (white, blue, and red) and light-time fraction, for an extra-foveal region (monocular, temporal retina). These data are compared with those secured for the same image area centrally fixated at the fovea. The systematic changes in the parameters are shown to be in rational relation to other relevant excitability data. Since for two retinal regions the primary contours are quite different, the systematic nature of the behavior of the parameters in the two cases is a real test of the power of the analysis proposed. Theoretical interpretation is required to

deal with the properties of sets of performance contours under systematically varied conditions, and cannot rely simply on the comparison of (for example) two contours under the same arbitrary conditions at two retinal locations. In particular it is emphasized that a qualitative separation must be made of the two factors of (*a*) number of units and (*b*) the frequencies of their actions, before the wave-length problem can be dealt with effectively.

CITATIONS

- Crozier, W. J., 1940*a*, *Proc. Nat. Acad. Sc.*, **26**, 54; 1940*b*, **26**, 334; 1941, in preparation.
Crozier, W. J., and Wolf, E., 1940–41*a, b*, *J. Gen. Physiol.*, **24**, 505, 635; 1941–42*a*,
J. Gen. Physiol., **25**, 89; 1941–42*b*, **25**, in press.
Crozier, W. J., and Holway, A. H., 1938–39*a*, *J. Gen. Physiol.*, **22**, 341; 1938–39*b*,
22, 351.
Crozier, W. J., Holway, A. H., and Wolf, E., 1940–41, in preparation.