On comparing monocular and binocular critical points for visual flicker, within the fovea, it was found by Sherrington (1902, 1904, 1906) that for similar phases of interrupted illumination falling synchronously on each retina there was very little reinforcement, so that the binocular fusion frequency was almost the same as when using one eye (or a little higher). The observations were made at a comparatively high flash intensity, and thus at a high flash frequency, save for some incidental tests. No mention was made of differences in critical flash frequency for the right and left eyes of an observer; such differences are always revealed by systematic tests, in our experience, although at the upper end of the $F$-log $I$ contour they may not be easy to detect.

Sherrington's data and the conclusions he drew from them, involving other phase relations in the interruptions of light to the two eyes, are frequently referred to in connection with the general problem of "binocular summation;" doubtless others have noted similar findings; but the basic question seems not to have been carefully re-examined. It has never been made entirely clear just in what respect such observations should be expected to reveal evidence of "summation," and in default of a theory of the flicker response contour naïve expectations might very well be obscure. In now making a re-investigation of the relations between monocular and binocular flicker thresholds a chief point has been to establish under optically simple conditions the relation of the binocular flicker response contour to that obtained for each eye taken separately. This has not heretofore been done. It is necessary also to have quantitative information as to the variability of such measurements. Relatively complete contours must be obtained for each eye taken separately before any real discussion of "binocular summation" can be attempted. It cannot be
predicted that the relations at low flash frequencies, where the frequency of subjective flicker corresponds to the actual flash rate, will necessarily be the same as at high intensities where it does not; nor can the relations between subjective brightness-at-fusion, flash intensity, and critical frequency be adequately studied without knowledge of the whole curve.

We have purposely employed for the present experiments a centrally fixated image large enough to provide an excitable extra-foveal area, thus extending the data to the "rod" segment of the duplex performance curve. The flash cycle used for the main observations gave equally long light and dark intervals. In other experiments, dealt with in communications immediately following, we discuss in detail the effects of altering the retinal position of this image, the rôle of the light-time fraction, and the relations of the several response contours to the wave-length composition of the light.

The interrelation between the influences of these variables is of especial significance for the theory of the flicker effect. For our immediate purpose, however, it is important that the same procedure is shown to be successful in analyzing the response contours obtained in these different experiments; the parameters which this analysis reveals may thus be used with confidence for the general comparison of the flicker excitation functions when one eye, the other, and both, are concerned under the same physical conditions. Two practiced observers were used. Certain reproducible differences exist in the visual performance contours of these two individuals. Many additional data are now available for them, and confirm the finding that the same method of analysis applies when the variable of "individual difference" is concerned. The existence of such quantifiable differences of course shows why it is unwise to "average" data from different subjects; indeed this is really forbidden; only by accident could such averaged data exhibit theoretically significant properties.

The visual discriminometer already described in detail (Crozier and Holway, 1938–1939 a) was employed to form equivalent images in one or the other or both eyes. The right-hand beam in the right-hand arm of the instrument was brought to a focus beyond the mirror $P_1$ (Crozier and Holway, 1938, 1939 a, Fig. 1) in the plane of an accurately cut sector-disc. (This was possible by removal of the brass collar visible in Crozier and Holway, 1938–39 a, Fig. 2.) Beyond the sector-disc the beam was collimated and focused on the slit $S_1$ in the usual way (Crozier and Holway, 1938–39 a, Fig. 1). The disc was driven by a controlled-speed motor and gear system; the revolution frequency was determined from millivoltmeter readings of the potential developed by a sensitive magneto geared to the driving shaft (cf. Crozier and Wolf, 1939–40 d, etc.).
FIG. 1. View of discriminometer with sector wheel in position, driving device, magneto, and lamp ammeter (control desk with millivoltmeter, etc. not shown; observer's cubicle removed); see text.

FIG. 2. Comparison of flicker response thresholds (flash intensity, $I_m$), solid circles; with fusion thresholds, open circles. E. W., left eye, $t_L = 0.50$, white light (the curve drawn is from: Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b).
By using sectors with six or eight openings and a series of interchangeable gears, steady flash frequencies ranging from 2 to about 80 per second could be secured by control of resistances in the motor circuit. The general plan of the apparatus is seen in Fig. 1.

The procedure was to secure observations with the left eye first, then with the right, then with both used simultaneously. The findings were then checked by taking readings with one eye, then with the other, then with both, during single sittings. Each series of measurements was preceded by at least 30 minutes dark adaptation; for work at the lowest (2 to 20) flash frequencies, 45 to 60 minutes. A quite regular procedure of relaxation during the interval of dark adaptation is important in securing regularity of response. Comfort for the observer is insured by the air-conditioned atmosphere of the dark room. A period of several minutes adaptation to each critical fusion intensity level precedes the taking of observations. Each group begins with the lowest flash frequency \( F \) desired in that particular set, and the value of \( F \) is then fixed at successively higher levels by small steps, with appropriate rest periods during the series. Succeeding groups of determinations are so arranged that there is a partial overlapping of the \( F \) ranges; data are taken at eight to ten levels of \( F \) in one sitting per day.

It is important for precise observations, taken in such a way as to make possible the study of the variability of readings, that the observer does not control the apparatus in any way. This permits the observer to enjoy relaxed concentration while reducing the possibility of head and eye movements despite the use of the headrest. It also helps to assure reasonable uniformity in the way in which the end-point is approached. After several preliminary trials at each \( F \) the approximate value of the critical intensity is known to the person operating the instrument. Then, beginning at a flash intensity about 0.20 log unit below this value, the optical wedge (Crozier and Holway, 1938-39 a, Fig. 2) is moved at a nearly constant rate until the observer signals that the intensity for recognition of flicker has been reached. This is repeated until ten readings have been taken. The observer may signal orally, or by means of a foot-switch turning on a small red pilot light.

We have used systematically the determination of the flash intensity \( I \) critical for recognition of flicker ("Flimmern"), at fixed flash-frequencies \( F \). The curves so produced are of course not quite the same as those for the flicker fusion intensities obtained by lowering \( I \) at fixed \( F \) until fusion is observed; the latter are found to be of the same form but of course tend to be a little below on the intensity scale (Fig. 2); the variability of the critical fusion intensity tends to be a little higher than for the critical flicker intensity.

The discriminometer slit was adjusted to produce on the retina a square image subtending ca. 6.13° on a side. In the present experiments the image was centrally fixated. For work at the lowest intensities, a minute red dot produced by a beam in the left-hand arm of the discriminometer (cf. Fig. 1; and Crozier and Holway, 1938-39 a, Figs. 1 and 2) served as a fixation point in the center of the square. Its intensity could be so adjusted as to make it visible only when focused in the fovea (relaxed accommodation). The cross-section of the beam at the eye-ring is such that its area is less than that of the fully contracted pupil (cf. Crozier and Holway, 1938-39 a). The square image extending \( 3° + \) vertically and horizontally from the fovea includes that part of the retina known for the particular observers to be of highest intrinsic threshold. Some data for W. J. C. are in Crozier and Holway (1938-39 b, 1939-40); the exact form of the curve for threshold intensity as a function of distance from the fovea, of course, depends on the size of the test-patch and on the exposure time, as we know from other work with
these observers; and the excitability of a given retinal area as a whole behaves as a unit in which the observed excitability is determined by the concurrent excitation of spatially contiguous regions (cf. Crozier and Holway, 1939-40).

III

Data obtained by the procedure outlined in section II, for E. W. and W. J. C. as observers, are listed in Table I. In considering the properties of such data we have first to deal with the question of intrinsic reliability. This has two separable aspects. These are (1) the reproducibility of the mean values of the critical flicker intensities, and (2) the quantitative properties of the variation among the individual readings. The possible rôle of a particular apparatus and manipulative procedure can be checked, in evaluating the matter of reproducibility, by studying the form of the $F$-log $I$ contour as already obtained for the same observers by a quite different technic (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b).

We are fortunate in having sets of data on two trained observers of dissimilar ages, obtained with two different pieces of apparatus. We also have indices of the observed dispersions in the homogeneous sets of measurements of which the averages are utilized for the analysis. It should scarcely need emphasis, but apparently still does, that in the absence of measures of scatter there is really no objective criterion of curve-fitting to test a descriptive hypothesis. It is a characteristic of much of the literature of visual theory that this basically significant information is practically never provided. Lacking it, any statement that the curve derived from a specified theory of the underlying mechanism "describes" the observations is, strictly speaking, without meaning unless the parameters of the proposed description can be demonstrated by independent tests to possess the properties the hypothesis implies.

There are two organically different sources of variation in measurements of the kind which concern us here. These are (1) the differences between individuals, and (2) the fluctuating performance of an individual. We are excluding for the moment those variations and differences due to instrumental or manipulative causes; these appear partially in (2), but can influence (1) also, since different individuals may of course react diversely to manipulative differences. It has been a very general practice to seek to increase the significance of measurements of visual excitability by using a large number of observers (again, usually without dispersion indices). Since the several parameters of an excitability function can and do vary quite independently, the quantitative significance of these mean data is in doubt even if the same individuals are employed the same number of
### TABLE I

Mean critical flash intensities $I_c$ (millilamberts) for response to visual flicker at different flash frequencies $F$ per sec. Each log $I_c$ is the logarithm for the average of 10 (ml) readings of $I_c$; the logarithm of the dispersion of these 10 is given as log P.E.:F. For each of the two observers data are given as derived from the use of the left eye, of the right eye, and of both eyes under conditions of binocular fusion, in independent series of measurements.

<table>
<thead>
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<th>$F$</th>
<th>Obs.: W. J. C.</th>
<th>Obs.: E. W.</th>
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</thead>
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<td></td>
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<td>Right eye</td>
</tr>
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</table>
times, with the same procedure, at each of the points on the excitability contour. All that can then be said, really, is that such data partially express the experimenter's conception of the "normal state." However great the value of this might conceivably be, it is after all not the primary concern in researches supposedly designed to elucidate the nature of visual excitability. Cases do arise in which a group of individual organisms can be shown by analysis to be effectively a homogeneous group as regards excitability (cf. Crozier, 1935; Crozier, Wolf, and Zerrahn-Wolf, 1936–37 a, b, 1937–38 a, 1938–39 a, etc.). This cannot in general be done for groups of human observers. The only basis for sense in this matter is the use of adequately numerous data on single observers, with the indices of variation permitting use of objective criteria as to whether a sufficient degree of homogeneity in the measurements does exist.

Just how serious differences can be between observers surely "normal" is sufficiently exemplified in Fig. 3. "Averages" from such curves would be meaningless. The contrasts apparent in Fig. 3 are of an order quite different from the fluctuations of successive determinations with one observer. The properties of these fluctuations are quantitatively definable in a simple way, and have a usable significance.

For each of the observers in the present experiment we already have available (Crozier, Wolf, and Zerrahn-Wolf, 1937–38 b) flicker response contours with the left eye, using a quite different apparatus. The centrally fixated image was square, and larger (14.3° on a side) than in the present case. The "rod" component of the duplex curve is therefore more prominent. For the older observer (W. J. C.) there is in the "cone" branch of the curve (Fig. 4) no real difference between the new data (Table I) and those already published. For E. W., younger and more likely to be at an age for more rapid visual change, a real although slight difference is evident. For the rod (i.e., extra-foveal) part of the response contour we have a rather striking difference between E. W. and W. J. C.; for the latter the rod segment runs to lower intensities. Qualitatively, this difference is likewise seen in the older data, where the larger test-area is responsible for a larger rod segment with each observer. The important point is that the cone data are shown to be essentially reproducible, quantitatively (with due respect to the age factor), and likewise the qualitative character of the relative rod contribution, independently of the apparatus used and over a period of several years.

Referring once more to Fig. 3, a further comment must be made concerning homogeneity, averaging, and the estimation of comparative excitabilities. It is obvious that when the homologous performance contours for
Fig. 3. Comparison of (binocular) flicker response contours for two observers, under the same conditions of observation (Table I).

Fig. 4. Comparisons of $F$-$\log I_m$ contours obtained with two different pieces of apparatus, at an interval of 2.5 years, for two observers. Open circlcts, data from Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b; solid dots, data of the present paper (Table I). The older data with a 14.3° square field, the newer field 6.13° on a side; $t_c = 0.50$, white light. See text.
two individuals cross one another—a situation not at all unusual—the only possibly valid method of comparing their performance capacities involves and depends upon the theory of the contour as a whole (cf. Crozier and Pincus, 1929-30; Crozier and Wolf, 1938-39, 1939-40 a; etc.). It is also clear that no simple transformation of the curves, such for example as equating the maximal or the median excitabilities, will bring the two curves into even approximate uniformity. In a similar way the comparison of excitabilities using the right and left eyes of one individual is also faced with the necessity of using complete performance contours.

IV

The data of the flicker response threshold for the comparison of results using one eye, the other, and both, with white light (Table I), are plotted in Figs. 5 and 6. For each of the observers it happens that in ordinary use the left is definitely the dominant eye. Yet, as we know from much other data (especially for W. J. C.), “absolute” visual thresholds under given conditions are lower for the right eye. They also tend to be lower for E. W. than for W. J. C., although at given levels of $I_1$ the values of $\Delta I$ are lower for W. J. C. As already shown in Fig. 3, the $F$-$\log I$ contours for the two observers cross. For each of them the log $I_m$ values are persistently lower for the right eye than for the left, while at the fusion frequency and intensity the field presented to the right eye ($R$) is subjectively brighter than that seen by the left ($L$), although the intensity is lower. These effects are in general accentuated when colored lights are used. They cannot be accounted for by imperfections of the binocular head of the discriminometer or its matched oculars. This is easily checked by repeating the tests with one eye through the ordinarily opposite limb of the head.

The difference between $R$ and $L$ is systematic and statistically significant, but it is not constant. It is a matter of the form of the entire $F$-$\log I_m$ curve, just as in the comparison illustrated in Fig. 3. For E. W., the $R$ and $L$ curves actually cross near the upper end. We shall consider the form of the $R$ and $L$ curves in some detail before taking up the binocular ($B$) curves, since the intercomparisons depend upon the use of assignable values of the parameters. The analysis of the variation data is then separately considered, in section VI, since it has an important bearing, of a kind apparently not hitherto suspected, upon the decisions which can be made concerning binocular summation.

It has been shown for an adequate variety of organisms that when there is evidenced the visual activity of a simplex performance system the
Fig. 5. $F$-log $I_m$ contours, white light, $t_L = 0.50$, for W. J. C. (Table I); left eye, right eye, and with binocular fusion. (At $F = 30$ and 38 extra determinations not entered in Table I have been plotted.)

Fig. 6. As in Fig. 5, but for observer E. W.
relation between $F$ and log $I$ is accurately described over its whole extent by a normal probability integral (Crozier, Wolf and Zerrahn-Wolf, 1938-39 a, b, c; Crozier and Wolf, 1940-41 a, b). The external form of the optic surface in the typical arthropod eye distorts this curve, in a predictable way (Crozier, Wolf, and Zerrahn-Wolf, 1936-37 b, 1937-38 c; Crozier and Wolf, 1939, 1939-40 a). The use of this particular descriptive function rests only in part upon its obvious success in adhering to the data; a more decisive justification is found in the nonspecific rules for the modification of its parameters when the temperature of the organism, the light-time fraction in the flash cycle, and certain other variables, are systematically altered (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 d, 1938-39 a; Crozier and Wolf, 1939-40 d, etc.).

By the use of this function a separation has been made of the two groups of neural effects apparent in the duplex performance curve typically obtained with vertebrates (e.g., Crozier and Wolf, 1938-39, 1939-40 b). This procedure has also been applied to flicker response data for man (Crozier, 1937; Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b). In the case of various fishes studied, the analysis provides descriptions of groups of neural effects so widely separated on the log $I$ axis that no interference is detectable between the rising curves of the two populations (Crozier and Wolf, 1938-39, etc.). This is proved by the fact that the shape of the curve gives the same form constant when the curve as a whole has been shifted by altering the temperature or the light-time fraction in the flash cycle, even when the two portions of the duplex contour are not affected to the same extent. The important point in this connection has to do with the invariance of the shape constant for the low intensity segment of the curve. The behavior of this constant in cross-breeding experiments with fishes is—like that of the shape constant for the upper segment—entirely consistent with the idea that for these cases the shape constant in question is an organic invariant (cf. Crozier and Wolf, 1938-39, 1939-40 b).

The situation is significantly different for some vertebrates in which the overlapping of the low and high intensity populations of effects is more complete (as seen with man, frog, Triturus, Fundulus: Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b; Crozier and Wolf, 1939-40 c, e, f). In these latter cases there is reason to believe (cf. particularly the following paper: Crozier and Wolf, 1940-41 c) that the actual form of the rising low intensity segment of the $F$-log $I$ curve is the outcome of neural integrations resulting in the partial suppression of effects in the low intensity group. The evidence for this is chiefly derived from experiments in which both wave-length of light and the light-time fraction are varied, and in different
retinal positions. The general properties detected in these experiments are kept in mind in the subsequent analysis.

In these discussions we have been well aware of the traditional assumption that the low intensity segment of such duplex curves of vertebrate visual performance is due to the activation of retinal rods, the high intensity segment to the activation of retinal cones. This assumption has tended to take the form (cf. Hecht, 1937) that the quantitative properties of the two segments directly represent and measure respective quantitative properties of the rods and cones as excitable units. For this proposition, in this ex-
treme form, no real basis whatever can be found. As a matter of convenience in reference, however, we have used the designations "rod" and "cone" for the two sections of the duplex contour; the quotation marks signify that we do not take the form of the curves to represent in any direct way the characteristics of the retinal sensory cells.

![Graph 9](image1)

**Fig. 9.** The extrapolation of the curves in Fig. 7 and the difference curves obtained by subtraction from the data of Fig. 5.

![Graph 10](image2)

**Fig. 10.** The lower segment of the data for E. W. (Fig. 6) analyzed as in Fig. 9, on the basis of Fig. 8.

The cone portions of the data of Figs. 5 and 6 are shown on a normal probability grid in Figs. 7 and 8. Confining attention for the moment to the R and L measurements, it is seen that in each case the value of $F_{\text{max}}$ required for an adequate fit is definitely higher for $L$. With W. J. C. the slope constant ($\alpha'_{\log I}$) is a little higher and the abscissa of inflection $\tau'$ a little lower (0.15 log unit) for $R$. With E. W. the situation is essentially the same. The criteria for an adequate fit are rectilinearity on the probability grid and the parallel margins of scatter of the points. The basis for the use of the latter criterion is indicated in section VI.

Following the process already used in the study of many other cases already referred to, the probability integrals of Figs. 7 and 8 have been
extrapolated toward $F = 0$ (Figs. 9 and 10); by ordinate differences the rod contributions shown as dotted lines are then obtained. The rising...
declining curves do not differ much in $\sigma'_{\log I}$ or in $\tau'$; the evidence for considering the form of these declining curves as resulting from inhibition of rod effects by cone effects is considered elsewhere (Crozier and Wolf, 1938–39; 1940–41 c, d).

Figs. 5 to 12 inclusive also contain the measurements for the mean binocular (B) flicker thresholds. We shall consider the B parameters in relation to those for R and L before dealing with the variation data (section VI). Both are necessary for the theoretical analysis, and they supplement one another in perhaps unexpected ways. It is necessary also to record some subjective effects concerning brightness.

As shown in Figs. 5 and 6, the mean B thresholds for E. W. adhere rather closely to, or are a little below, those obtained for the eye (R) with lower threshold, over most of the F range; at the two ends of the range, however, they agree rather well with those for the other eye (L). For W. J. C. the B data fall in between the R and L measurements except at the very top; it cannot be said that they are the arithmetic mean or the geometric mean of the R and L figures, however; as with E. W., the form of the B curve is not the same as that for either eye used alone. Obviously, no statement comparing simply the effects of monocular with binocular flicker excitation can be unambiguous in the absence of detailed information over the entire explorable range. While it is true that conditions can be found (as near the crossing point of the R and L curves for E. W., Fig. 6) such that a very small difference exists between B and R, L, this is not the characteristic state of affairs. Although it is true, as Sherrington (1904) described, that $B$ vs. $R$, $L$ difference is slight, it is nevertheless real and systematic.

The B contours are analyzed into their constituent branches in Figs. 8 to 12. The probability integral formulation is just as efficient as for the monocular data. It emerges that with W. J. C. the B cone value of $F_{\max}$ is definitely higher than for R or L, the slope constant $\sigma'_{\log I}$ is intermediate, and the abscissa of inflection $\tau'$ is exactly intermediate. With E. W. on the other hand, the B $F_{\max}$ is not certainly different from that for L, $\sigma'_{\log I}$ is less than for either R or L, but $\tau'$ is again intermediate. It is to be added that when the light-time fraction is systematically modified, and for a given wave-length composition, in a given retinal region, the value of the $\sigma'_{\log I}$ for the rod (rising) curve as analyzed out is found to be invariant despite the unequal shifts of the rod and cone contributions; the significance of this for the statistical basis of the observed functions is
mentioned elsewhere (Crozier and Wolf, 1940-41 c, d, e). Thus the statement which can be made for these two observers is that log \( I_m \) for the inflection of the binocular cone \( F \)-log \( I \) contour is rather precisely intermediate between that for the right and the left eye monocular observations. It is exhibited in these results that there is no necessary correlation between the changes in the three parameters of the probability summation,—as is also clearly demonstrated by the various experiments in which the curve is modified experimentally (cf. Crozier and Wolf, 1940-41, c, d, e).

The "B" rod curves obtained in Figs. 9 and 10 are analyzed in Figs. 11 and 12. For the W. J. C. curve the \( B F_{\text{max}} \) is about that for \( L \), but the rising curve does not differ otherwise from that with \( R \). The E. W. rising \( B \) curve is also quite like the \( R \). (The general nature of the declining branches has been referred to already.) It is to be mentioned that in our earlier experiment, with a larger test area centrally fixated, the rod curve is one with a higher \( F_{\text{max}} \), a lower \( \gamma' \), and a much greater \( \theta' \log \Gamma \) (cf. Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b).

The general conclusion to which Sherrington (1904) came from his experiments with symmetrical binocular flicker and brightness was that the binocular perception results from the combination of fully "elaborated unioocular sensations," and is the product of "already elaborated sensations contemporaneously proceeding." With this we agree. In Sherrington's observations he found reason to doubt whether the well known slight excess of binocular brightness over that of the unioocular components was really to be explained as due to summation of the intensities of effects at the corresponding points of the two retinas, and that, most often, the binocular brightness was not perceptibly different from that of either of its co-equal unioocular components. Under the conditions of the present observations there is no possible complication due to the consensual pupillary reflex, or to changes of accommodation, and care was always taken to continue comparisons until no differential effect of adaptation could play a part. Yet we find that the \( L \) and \( R \) subjective brightnesses just at fusion are not equal, that for \( R \) being the greater in these tests, and that the \( B \) subjective brightness at critical fusion is always above that for either eye taken alone—yet the \( R \) critical intensity is characteristically lower than the \( L \) while the \( B \) critical intensity over most of the range either agrees with that for \( R \) or lies between the \( R \) and \( L \).

Obviously, the relation between \( F \) and \( \text{log } I_m \) is not determined by the subjective brightness alone. This conclusion is well reinforced by the consideration of data in which wave-length of light and light-time fraction in the flash cycle are involved as variables (Crozier and Wolf, 1940-41 c, d).
With the apparatus we have used it is also possible to show that not even binocular fusion of uniocular images is required for the effects discussed. By separation of the ocular barrels of the discriminometer head (Fig. 1; and cf. Crozier and Holway, 1938–39 a) a little beyond the distance for binocular fusion the observer sees two illuminated squares, each centrally fixated. The differential $R$, $L$, brightness is then obvious, but both fields are seen to flicker simultaneously at the critical flash intensity characteristic of the binocularly fused image (for the same $F$), whether this be below or between the $R$ and $L$ values. Central integration of effects simultaneously arising from the two eyes must consequently be taken as proved, and as independent of subjective fusion of the images.

The possibility existed that $R$, $L$ differences might perhaps bemagnified
under certain conditions. Since the whole $F$-log $I$ contour is enlarged and shifted toward lower flash intensities when the light-time fraction is reduced (Crozier and Wolf, 1940-41 c, d), and also by using blue light, an experiment was done with blue light (Wratten Filter No. 47) and a flash cycle with 0.10 light-time. The absolute scatter of the determinations of critical flash intensity is also lower under these conditions. The data are given in Table II and in Fig. 13. W. J. C. was used since in the data with white light (Fig. 5) his $B$ figures were more nearly intermediate between the $R$ and $L$. It is shown in Fig. 13 that the separation of $R$ and $L$

### TABLE II

Size and location of retinal image as in Table I—6.13° square, centrally fixated; blue light (Wratten Filter No. 40); light-time = 0.10 of the cycle time. Left eye ($L$), right eye ($R$), and binocular ($B$) determinations ($n = 10$) of mean critical flash intensity for flicker and of P.E.I; observer, W. J. C. The intensities (mL) are in terms of a photometric match against white light (below the color threshold). See text and Fig. 13.

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<thead>
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<th>$B$</th>
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<tr>
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</table>

is of exactly the same general sort as with white light (Fig. 5), and that $B$ is again intermediate. It is important that under the conditions of this particular test the blue color threshold is not reached until just below $F = 50$ on the curve, and the typical "foveal" appearance of the flicker recognition point not until ca. $F = 43$ along the curve. A fuller analysis of these indications is attempted in following papers, but their significance for the classical use of ordinary criteria for rod and cone function is highly interesting. For present purposes the measurements show that the relationships between $L$, $R$, and $B$ measurements already discussed for white light and $t_x = t_y$ are in fact independent of wave-length composition of light and of the light-time fraction, and of the brightness level.

Analysis of the variation of $I_c$, the critical flash intensity, and of the scatter of the indices of this variation, supplies further important criteria which the theory of neural integration for binocular flicker must satisfy.
The recognition of flicker is a form of intensive discrimination; the fact that at high flash frequencies the critical flash frequency does not correspond, subjectively, to the physically impressed frequency is no bar to this interpretation. One of the aspects of the homology of the flash intensity with $\Delta I_0$ and $\Delta I$ as ordinarily determined is the parallel way in which $I$, like $\Delta I_0$ or $\Delta I$, is directly proportional to its own index of variation ($\sigma_I$ or $P.E.I$), as shown for many series of measurements (Crozier, 1935–36; Crozier and Holway, 1937, 1938, 1939–40; Crozier, Wolf, and Zerrahn-Wolf, 1937–38 a). There are two aspects of the interdependence of $I$, and $P.E.I$, namely the mean magnitude of the proportionality constant and the manner of distribution of the values found in the band of slope = 1 relating $\log P.E.I$ to $\log I$. For sufficiently homogeneous data the distribution is such that the line giving the mean value of the proportionality constant divides the $\log P.E.I$ width of the band arithmetically in half. For non-homogeneous data with a single observer, such as result from the massing of observations taken over a period of some days, this line simply divides the $\log P.E.I$ span equally. The position of the median line and the positions of its margins can be objectively determined by projecting the positions of the points along a $45^\circ$ slope to a common ordinate and determining the mean and the S.D. for the frequency distribution of the intercepts (cf. Crozier and Holway, 1937, 1938). For the two observers the mean $P.E.I/\sigma_I$, here obtained is (W. J. C.) a little lower and (E. W.) a little higher than in the older series with other apparatus (Crozier, Wolf, and Zerrahn-Wolf, 1937–38 b). (The absence of a "break" in the present variation plot is correlated with the small rod group.)

The study of the properties of the variation of $\Delta I$ and of $\Delta I_0$ (Crozier and Holway, 1938; 1939–40) has shown that this variation, under uniform conditions of test, has properties which must be regarded as an organic product of the performing system under test. These considerations reappear in the data of the present experiments. From measurements of $\Delta I$ at different levels of $I$, it was shown (Crozier and Holway, 1939–40) that with monocular measurements, at different areal exposures and for different wave-lengths, $\sigma_I \Delta I$ and $\Delta I$ were in the same statistically constant proportion and slightly lower than for corresponding measurements made binocularly. For the binocular determinations, however, $\Delta I$ measurements at a given level of $I$ are lower than the mean of the values for the two eyes individually (Crozier and Holway, 1939–40), in a mean ratio a little less than the 1.41 obtained for "absolute" thresholds with the same apparatus and general procedure (Crozier and Holway, 1938–39 b).
The variation data in Table I are plotted in Figs. 14 and 15. It is shown, in the first place, that the proportionality constants for monocular P.E. vs. \( I_m \) are not the same for the two eyes, being a little lower for R; the breadth of the scatter band is a little greater, however, for R. In each case the mean ratio for the binocular measurements \( B \) is definitely lower than that for either R or L taken alone.

The mean values of \( \frac{P.E.}{I_m} \) are for W. J. C.: R, 3.62; L, 4.67; of \( \sigma_1 \) of the sets, R, 1.45, L, 1.41; the \( B \) mean ratio is 2.99, its \( \sigma_1 = 1.34 \). The average of the ratios for R and L = 4.15, which is 1.39 times the value for \( B \). (These values are all lower than found for determinations of \( \Delta I \) and \( \Delta I_0 \) under the same conditions with this observer.)

With E. W. the corresponding values for the means are, for \( \frac{P.E.}{I_m} \): R, 9.31, L, 10.06, B, 6.68; the average for R and L is 1.45 times greater than the value for \( B \), as compared with 1.39 for W. J. C. For R and L, \( \sigma_1 \) is 1.466 and 1.471, for \( B \), 1.34.

The values of \( \sigma_{log P.E.} \) for W. J. C. and E. W., which are the proper basis of comparison of the monocular and binocular dispersions since the data are non-homogeneous to the extent that they comprise compound fluctuations, are in the \( \frac{(L + R)}{2} B \) ratio of 1.25 and 1.37.

Thus both the mean value of the precision and of the scatter of the determination of \( I_m \), with the intensity level automatically corrected out, is definitely less for the binocular measurements than for either of the contributory uniocular processes taken singly. The value for the \( B \) data is found to stand in the ratio of 1.39 (W. J. C.) and 1.45 (E. W.) to that for the average values for the respective right and left eyes. It is very doubtful if either of these values departs significantly from their mean, 1.42. The variation data in Table II, for W. J. C. with blue light and \( t_o = 0.10 \), tell essentially the same story, although they are not sufficiently numerous for analysis. This is the kind of result clearly to be predicted on the basis that discriminatory precision is a consequence of the number of elementary units involved in a statistical discrimination (Crozier, 1936), and if in the binocular measurements the numerical potency of these discriminatory elements is doubled, the precision is accordingly increased in the ratio \( \sqrt{2} \) to 1.

We have to note that only when the procedural errors are held reasonably constant, and when the correlation between \( I_m \) and \( \sigma_{1t} \) can be used to exhibit their relationship independent of intensity, can this type of demonstration really be made. It is important to remark, however, in view of the fact that different operators were in control of the instrument for the E. W. and W. J. C. series, that the quantitative relationship between
Fig. 14. The dispersion indices for the values of $I_1$ averaged to give $I_m$ are rectilinearly related to $I_m$; log P.E.1 $I_1$ vs. log $I_m$ gives a band of statistically constant height and slope = 1. Data for W. J. C. (Table I); the bands are separated vertically for clearness. The proportionality constant is less for B (in the ratio 1.39 to 1), and the relative scatter of P.E.1 $I_1$ is less. See text.
Fig. 15. Variation data for E. W. (Table I); as in Fig. 14; see text.
P.E.-112 and $I_m$ is not (within reasonable limits, at any rate) a function of the manipulator. Nor, as we know from adequate tests, is it modified essentially by changes in the procedure used in approaching the end-point. A chief possible source of such modification lies in the level of adaptation adopted as the standard from which to approach the end-point, and in the rate of this approach. For W. J. C. the standard method was to increase the flash intensity from ca. 0.18 log unit below the critical region. The mean value of $I_m$ can be made 0.10 log unit lower by beginning from a lower level of adaptation, at 0.90 log unit below the critical region. This is, of course, to be expected, but the important fact is that P.E.-112 then still has the same relationship to $I_m$. With E. W. each measurement was begun from a level of intensity proportionately lower than with W. J. C.; but this cannot explain the differences found in their variability functions.

### VII

The evidence described may now be considered in reference to the theory of binocular summation in symmetrical flicker. The data show that there are systematic differences between the binocular flicker recognition contours and the contributory uniocular contours determined separately. The differences cannot be adequately described simply by saying that the B data are intermediate between those for R and L; the shapes of the contours differ. For the cone segments the parameter $r'$, the log $I_m$ abscissa of inflection of the curve, is rather precisely intermediate between those for R and L. The analyzed properties of the rod segments show their forms to result from complex interaction between cone and rod elements of effect, in the sense that progressive increase of cone effects inhibits the action of rod effects. The rising branch of the pure rod contribution to the duplex curve, obtained by deducting the cone effect in the region of their overlapping, is found to show the B curve following pretty closely that for the eye (R) with lower $I_o$. That a real neural integration is involved in the production of these findings is shown by the synchronous behavior of the endpoint for non-binocularly fused images in the two eyes.

We have also the fact that the binocular brightness is certainly greater at all critical fusion levels than that for either eye alone. The R images at fusion were subjectively brighter than the L and $I_o$ was lower. The relations between the R, L, and B critical intensities are the same when the determinations are made with blue light in a flash cycle with 10 per cent light-time. Under these conditions the level of brightness for the $F$-log $I_m$ curve as a whole is very low, the fusion color threshold being at ca. $F = 50$, but $I_o$ is far below that for the white light cases already con-
sidered. Consequently, the critical flash intensity cannot be considered to be determined by the general or relative brightness.

The further and quite significant general fact provided by the measurements is revealed in the relationships of the mean values of $I_s$ to their indices of precision, or, more exactly, the rectilinear relations of $P.E._{11}$ to $I_m$. For $B$, the relative scatter of $I_1$ is less than that for $R$ or $L$, in the general ratio of 1:1.43. Moreover, the scatter of the values of $P.E._{1}$ is less. Now we know (Crozier and Wolf, 1940–41d) that when the light-time ratio is varied the scatter of $P.E._{1}$ as a function of $I_m$ is less the larger the light-time fraction; the relationship is rectilinear. In this case the $P.E._{11}$ span is directly proportional to the value of $F_{max}$, a fact confirmed by tests in different parts of the retina as well (Crozier and Wolf, 1940–41d). This sort of thing cannot be entirely a matter of statistical dependence or accident, since in general theory $\sigma$ and $\sigma_n$ must be in simple proportion. When $\sigma_n$, corrected for $I$, is found to be directly proportional to $F_{max}$, as in the experiments involving retinal position and the light-time fraction, with area of image constant, the notion arises that the breadth of the variation band is decreased with increase of the brightness level and with decrease of the total population of elements ($d F/d \log I$) involved. There is some support for this in corresponding data with colored lights, which we describe in a subsequent paper. But it is clear that the factor of subjective brightness level and the factor of "size of population" do not necessarily work concurrently. This is abundantly shown by the colored light data. For the $B, R, L$ cases the $B$ fusion brightness is greater, but $F_{max}$ is only slightly or not at all increased; in conformity to the increase of brightness, $\sigma_{I_n}$ decreases, and $\sigma_n/I_m$ is reduced as $1/\sqrt{2}$—although when monocular brightness is increased by increasing $I$, it does not change. At the same time, the $B$ subjective fusion brightness is certainly not doubled, and we suspect that its ratio to the mean of $R$ and $L$ fusion brightnesses is a function of the intensity level.

To rationalize these somewhat confusing relationships it is necessary to suppose that brightness is one kind of sensory effect, while $F_{max}$ measures another. The relations between them are complex. The values of $P.E._{1}$ and the scatter of $P.E._{1}$ are not determined by the brightness level for the function as a whole, and are not determined by $F_{max}$, although in different circumstances they may appear to be correlated. The fact that the two statistical indices are independent of $I_m$ along any one contour can be best understood on the basis that in the determination of the critical intensity, at any level of $I$, the whole population of elements potentially available under the conditions is actually at work. This is the essence of the con-
ception of statistical fluctuation used in the derivation of the expectation that the form of the contour will be given by a probability summation (cf. Crozier 1937; 1940 a, b). For binocular flicker the number of these elements is doubled in some fashion, as the variation indices prove, and the fusion brightness is somewhat increased (correlated with a decrease in the scatter of P.E.), but this does not materially increase $F_{\text{max}}$. In other words, the potential effectiveness of each element is doubled, but the total number is pretty much the same. This is not dependent on subjective fusion of the images from the two eyes.

The fact that the probability summation effectively describes the flicker data and their modifications under different conditions of retinal area, location, wave-length of light, light-time fraction, and temperature, in a wide diversity of animals, and for monocular and binocular presentation, is of course a potent argument for the propriety of using it. In the various experiments made with arthropods, lower vertebrates, and birds, surrounded by a rotated cylinder with vertical stripes, binocular stimulation is necessarily used. (This of course does not mean binocular fusion of the field of regard.) Certain particular problems arising in this connection, by reason of the fact that the animal is free to move about within the cylinder, have been discussed on the basis of experiments with the crayfish *Cambarus* (cf. Wolf, 1940; Wolf and Crozier, 1940-41). If the essential dynamical properties of such data are determined centrally, and they must be so regarded in the binocular instance, then two possibilities exist: either the properties of the uniocular data are also determined centrally, or else the nature of the measurements has a similar character whether determined centrally or peripherally. The demonstration of a statistical basis for the nature of the data is of course by itself consistent with either possibility. The composition of two probability distributions gives another probability distribution; the Gaussian function is apparently the only one having this property (Cramér, 1937). Unquestionably this is the source of its general capacity to account for the data in these complex situations.

There arises naturally at this point the question as to the manner in which the central nervous composition of two independently produced uniocular effects could be expected to show itself. In the interpretation of complex visual effects considerable general use has been made of the terms “inhibition” and “summation.” It is preferable to speak rather of *integration*, since this may be done without theoretical prejudice. This conception avoids the troubles arising in the situation depicted in Figs. 4 and 5; inhibition with respect to one eye is often summation with respect to the other; the intermediate value of the $B$ cone $r'$ (and the $B^*\log i$) certainly
denotes integration rather than anything else. Difficulties are also avoided when dealing with the rod-cone overlap: if our analysis of the situation is sound, inhibition of some rod effects is simultaneously accompanied by summation of cone effects with the remainder.

The determination of visual threshold intensities shows that for the "absolute" threshold the effect of doubling area in one retina is qualitatively like that produced by viewing the same area simultaneously with both eyes under conditions of binocular fusion (Crozier and Holway, 1938–39 b). For understandable reasons, in part (i.e., fixation), the binocular mean variation is increased, but the ratio of mean \((\Delta I)_B\) to the mean for \(L\) and \(R\) is not certainly different from 1.41. There is reason to believe that this ratio may be a function of the exposure time; when \(\Delta I\) is obtained for finite levels of \(I\), it is influenced only slightly by the intensity level; the effect on \(\Delta I\) of enlarging the retinal area illuminated is quantitatively the same for binocular and uniocular presentation (Crozier and Holway, 1939–40: Crozier, 1940 a). It is greater than the ratio obtained for symmetrical doubling of area on one retina. The examination of the exposure time function shows, on the other hand, that within the fovea enlargement of area of test-patch beyond a certain limit brings about an increase of variability in the population of cone effects (Crozier, 1940 a). The same result appears in \(F\)-log \(I\) contours when retinal location or test-patch area are changed to include different sized populations of cone effects (Crozier and Wolf, 1940–41 d): \(\sigma'_\log I\) for the cone curve is increased when the cone population is reduced. For the rod populations the opposite result is obtained: enlargement of the rod population of units brings with it an increase in \(\sigma'_\log I\) for the rod curves (Crozier, 1940 c), as already shown for dark adaptation (Crozier, 1940 b) under different conditions modifying the size of the dark-adapting population of elements. The homologous result in the two sets of flicker experiments with different areas that we have earlier discussed (section IV) is confirmatory. Both the enlargement and the reduction of \(\sigma'_\log I\) as a result of increasing the number of the respective retinal units, by different methods of modification of the conditions of test, signify interaction and integration of neural effects at some level, but cannot reasonably be discussed in terms of inhibition and summation. The closest analogy for the basic binocular effect in flicker is found in the data on binocular vs. monocular \(\Delta I_B\) and \(\Delta I\). The ratio is about 1.41, but the quantitative result of enlarging retinal area illuminated is the same in both cases (Crozier and Holway, 1938–39 b, 1939–40). This proves that in the discrimination of \(I_B\) from \(I\), the binocular effect is doubled, although for a given \(\Delta I\) the size of \(\sigma_{1\alpha I}\) is not much affected, if at all. It has
been possible to show (Crozier, 1940b) that \( \Delta I \) is really determined by the size of the population of effects available for further excitation, under the conditions given, so that \( 1/\Delta I \), the measure of excitability at any level of \( I_1 \), is a declining probability integral in terms of \( \log I_1 \). In the flicker case the magnitude of the level of "sensory effect" must be taken as directly proportional to \( F \); but this measures the discrimination of the effect of flash intensity from the effect of flash after image (cf. Crozier, Wolf, and Zerrahn-Wolf, 1936-37b). If as a consequence of binocular regard the flash effect is increased, so also is its after influence. Consequently one must expect, it seems, on this basis, that the log critical flash intensity \( (r') \) for activation of one-half the total number of elements should appear as the mean of those for the two uniocular components,—and, in the case of the raw rod curves, the \( B \) curve for the observed result should be the average of the two composite rod effects, which is seen. On the other hand, the precision with which the light-dark discrimination is statistically made should be, for a given value of \( I_1 \), increased by the factor \( \sqrt{2} \) if the potency of each element concerned in making it is doubled. This the data show to be the fact.

VIII

SUMMARY

Comparison of monocular and binocular critical flash intensities for recognition of flicker, using a centrally fixated square image subtending ca. 6.13° on a side (white light), shows that for the cone segment of the response contour the inflection point of the probability integral correlating flash frequency \( F \) (for symmetrical flicker) and log mean critical flash intensity \( I_m \) is with the binocular measurements exactly intermediate between those for each eye separately. This does not mean that in general the data are intermediate; they are not; the binocular asymptotic \( F_{max} \), agrees with or lies above the greater one of the two uniocular curves. The entire contour must be considered for valid intercomparisons, as is also true if homologous curves for different observers are to be compared. For the measurements in the predominantly rod region the binocular data are more or less intermediate. The rod curves result, however, from the integrative interplay of rod and cone effects for which the intrinsic curves overlap. The resultant rod curve as measured is determined by the partial inhibition of rod effects by cone effects, and by the summation of the remaining rod contributions with those labelled cone in origin. It is pointed out that in this respect, as in others, it is desirable to consider the rôles of retinal area,
and location, from the standpoint of integration of neural effects. These phenomena are essentially independent of the light-time fraction and of the spectral (λ) quality of the light used.

For binocular, as for uniocular excitation, the normal probability summation provides an efficient general description, under diverse conditions of size and location of retinal image, wave-length composition of light, light-time cycle-fraction, and kind of animal. It is pointed out that this is the only function abstractly likely to exhibit this kind of efficiency.

That a summation of veritable effects independently generated by simultaneous, symmetrical uniocular excitation does occur in the recognition of flicker is specifically demonstrated by the fact that for a given mean critical flash intensity the associated variation is lower for binocular than for either or the average of the single-eyed presentations,—and in the ratio not statistically different from 1:1.41; the relative scatter of the binocular indices of dispersion is also reduced below the uniocular. Since the mean variation of the critical intensity is statistically in a constant ratio to \( I_m \), in appropriately homogeneous series, independent for example of the brightness level and of the light-time fraction, this signifies an essential doubling of the effectiveness (potential) of each of the elements concerned in the discrimination of flicker when binocular excitation is concerned, although the total number of these elements is only slightly or not at all affected. The potential in question is not exclusively correlated with subjective brightness-at-fusion, which is, however, increased with binocular regard.

CITATIONS


1906, The integrative action of the nervous system, New Haven, Yale University Press.