THEORY AND MEASUREMENT OF VISUAL MECHANISMS

VIII. THE FORM OF THE FLICKER CONTOUR

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I

The question of the basic analytical form of the flicker recognition curve is of interest in several ways. An acceptable theory of the flicker contour should provide indices of the invariant properties of flicker recognition under different conditions, such as are necessary for the understanding of this kind of visual excitation and for relating its data to other visual measurements. It is also required for the interpretation of the duplex flicker contour as typically found with vertebrates, where two groups of neural effects usually are complexly overlapped in the determination of flicker. The demonstration of the occurrence of the same fundamental form for the flicker curves in each of these two groups independently, in man, is dealt with in the present paper. This substantiates rather directly the procedure already used for the separation of the two groups of effects in duplex flicker contours, and is important for the analysis of their integrative interaction.

An acceptable equation for the flicker contour must first of all describe in a satisfactory quantitative way the interdependence of flash frequency F and flash intensity I critical for the response under a given set of conditions, and with reference to known measures and properties of the variances of the data. A given set of conditions involves effective constancy of wavelength composition of light; the form of the light-dark alternation; the light-time fraction in the flash cycle; the temperature of the organism; and certain other variables, such as the position of the light on the retina, the constancy of the pupil opening, and the degree of homogeneity in the state of the tested individuals during the observations. The acceptable formulation must also, however, and as a necessary condition, exhibit under different circumstances properties of its parameters such as are called for by the notion the equation of the descriptive curve is intended to express. In the present case this involves properties of the variation of the measurements as well. In general, testing the properties of parameters is of course much more significant than the indications from simple criteria of curve-fitting. This is especially so for a multivariate situation, in which the exact relationship between any two significant variables depends upon the magnitudes of a number of others.

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The visual performance contours of most vertebrates characteristically exhibit the well known duplex form of the curves describing dark adaptation; intensity discrimination, flicker recognition, visual acuity, and the like, as functions of intensity and of time. For the analysis of duplex flicker contours it has been found necessary to extrapolate the high intensity segment toward $F = 0$, and to obtain the low intensity contribution by subtraction from the observed course of the data.[1] This procedure depends upon a valid theory of the fundamental nature and form of the flicker contour as it might be observed if there were no overlapping of the two populations of neural effects. It also relies upon the tested interpretation of the resulting properties of the summation (or rather integration) of the two sets of effects in the region where overlapping occurs.

There are two immediate points, namely: (1) the form of the "cone" curve in isolation and (2) the fundamental form of the "rod" curve when not complicated by the overlapping photopic function. The problem is in some respects more interesting when the degree of overlapping of photopic and scotopic effects is typically more complete, as with man,[2] than with certain fishes[3] for which the separation of the two groups of effects is comparatively extreme. The further question as to the mechanism evident in the overlapping of these two groups of effects depends for its resolution upon the satisfactory analysis of these two points. This analysis requires the systematic experimental manipulation of the conditions of visual excitation in such ways as will expose, without overlapping, the forms of the primary "cone" and "rod" curves. The problem of the integration of effects when overlapping does occur is dealt with elsewhere. Throughout we shall for brevity use the labels "rod"- and "cone"-effects respectively for the low intensity and the high intensity segments of the duplex contours. It is not to be presumed that the two segments are taken to describe the intrinsic properties of the retinal rods on the one hand and of retinal cones on the other. We are simply concerned with the fact that two groups of neural effects are involved in the recognition of flicker, and that these two groups have in certain respects demonstrably different properties although integrative relations can occur between them.

II

It has been urged[4, 5] that the basic form of the uncomplicated flicker contour is given by a probability band in which $F \pm \sigma_F$ is a normal probability integral

[1] *J. Gen. Physiol.*, 1936–37, **20**, 411; 1937–38, **21**, 17, 203, 315; 1938–39, **22**, 463; 1939–40, **23**, 229, 667, 677; 1940–41, **24**, 505, 635; 1941–42, **25**, 293.

[2] *J. Gen. Physiol.*, 1937–38, **21**, 203; 1940–41, **24**, 505, 635, etc.

[3] *J. Gen. Physiol.*, 1937–38, **21**, 17, 313; 1938–39, **22**, 463.

[4] *Proc. Nat. Acad. Sc.*, 1937, **23**, 71, 516; 1938, **24**, 125, 216.

[5] *Proc. Nat. Acad. Sc.*, 1936, **22**, 412; 1938, **24**, 130; *J. Gen. Physiol.*, 1935–36, **19**, 503; 1937–38, **21**, 17; 1939–40, **23**, 101.

in log $(I \pm \sigma_I)$. Ordinarily, F is fixed at various levels and critical intensity I is repeatedly measured; its mean value I_m is computed; F is then exhibited as a probability integral in log I_m. With repeated flashes, $1/t$ (where t is the flash exposure $= 1/F$) is a measure of the capacity to distinguish separateness of flashes. But flicker recognition is also governed by the flash intensity I, and during a finite interval the excitation should be the integral of a frequency distribution of $-I \cdot d (1/I)$, and thus of $d \log I$.[6] This integral is then equatable to $1/t$. The argument for the expected Gaussian form of this integral is the same as with other modes of excitation.[6] Animals possessing but one general kind of retinal receptor cell (cones)—as the turtle *Pseudemys*,[7] the lizard *Phrynosoma*,[8] the zebra finch *Taeniopygia*[9]—give simplex $F - \log I$ contours under various conditions of temperature, light-time fraction, retinal area, and wave-length of light, which are well described by the probability summation. It also applies for an animal possessing only retinal rods,[10] and for invertebrates having uncomplicated simplex performance contours.[11] With arthropods the complication usually due to the gross curvature of the optic surfaces[12] has been satisfactorily accounted for.

The three parameters of the probability summation—F_{max}; abscissa of inflection τ'; standard deviation $\sigma'_{\log I}$ of $dF/d \log I$—while specific for the kind of animal are found to exhibit consistent, non-specific, kinds of relations to temperature, number of retinal units involved, light-time fraction, and wave-length of light. In forms with which adequate cross-breeding experiments can be made these parameters are also found to demonstrate their character as natural invariants.[13]

It will be shown here that when the $F - \log I$ contour (man) is determined entirely within the normal fovea, where by the usual tests cones alone are presumed to occur, it is of simplex form adhering well to the probability summation over the whole testable range. It is also shown that by novel extensions and developments of the procedure for flicker observations the rising, low-intensity, "rod" portion of the typical duplex curve can be observed free from "cone" complication, and that this curve then also follows the probability integral form, as already shown for the "rod" contribution as it has been dissected out by subtraction of the extrapolated "cone" curve.

[6] *Proc. Nat. Acad. Sc.*, 1937, **23**, 71; 1940, **26**, 54, 334, 382.

[7] *J. Gen. Physiol.*, 1938–39, **22**, 311; 1939–40, **23**, 531.

[8] *J. Gen. Physiol.*, 1940–41, **24**, 317.

[9] *J. Gen. Physiol.*, 1940–41, **24**, 625; 1941–42, **25**, 293.

[10] *J. Gen. Physiol.*, 1938–39, **22**, 555.

[11] *J. Gen. Physiol.*, 1938–39, **22**, 451.

[12] *J. Gen. Physiol.*, 1937–38, **21**, 223, 463; 1938–39, **22**, 451, 795; 1939–40, **23**, 1; *Biol. Bull.*, 1939, **77**, 126.

[13] *J. Gen. Physiol.*, 1937–38, **21**, 17; *Proc. Nat. Acad. Sc.*, 1937, **23**, 516; 1938, **24**, 221; *J. Gen. Physiol.*, 1938–39, **22**, 463; *Proc. Nat. Acad. Sc.*, 1939, **25**, 171, 176; *J. Gen. Physiol.*, 1939–40, **23**, 143.

The data given graphically in sections III and IV are drawn from series of measurements concerned with the questions of image area, location, wavelength, light-time fraction, and number of illuminated patches as concerned with flicker. These data will be given in full when discussing these questions systematically in subsequent papers. The apparatus and technique have been described already.[14, 15]

<center>III</center>

Measurements of several types of intensity discrimination have made it clear that with test areas falling entirely within the fovea the performance contours are simplex.[16] These curves are in general accurately described by appropriate forms of the probability summation.[6] The common assumption has been that such contours are simplex because only retinal cones are then involved. The $F - \log I$ contour in the fovea has been determined on several occasions (white light),[16] but somewhat more elaborate tests are required for the purpose here in view.

Fig. 1 contains measurements from series with one practised observer (W. J. C.), for monocular regard (left eye) under the conditions of instrumentation and procedure described in some preceding papers.[14] We have used an area as large as conveniently possible (a square 0.6° on a side), centered at the fovea by means of an appropriately located very small, red, fixation dot of suitable intensity just above the upper side of the square. In general, less scattered determinations are obtained with colored lights, and for these the scatter of σ_I is less[17] although the average value of σ_I/I_m is very nearly invariant, mean σ_m being of the order of 0.4 per cent throughout; each of the plotted points is the mean of ten measurements. The curves drawn are probability integrals (Fig. 2).

When the $F - \log I$ contour is determined at several light-time fractions, with conditions otherwise the same, a better test is obtained than by mere replication. This is because the properties of the parameters can then be examined. On the basis of these properties as seen in the analysis of the integrals adjusted to data of this observer from other and larger image areas giving duplex contours,[2, 18] we expect in Fig. 1 to find $\sigma'_{\log I}$ greater, τ' lower,

[14] *J. Gen. Physiol.*, 1938–39, **22**, 341; 1940–41, **24**, 505, 635.

[15] *J. Gen. Physiol.*, 1937–38, **21**, 203; 1939–40, **23**, 531; 1941–42, **25**, in press.

[16] *Cf.* Hecht, S., and Verrijp, C. D., *J. Gen. Physiol.*, 1933–34, **17**, 251; Hecht, S., and Shlaer, S., *J. Gen. Physiol.*, 1935–36, **19**, 965; Hecht, S., and Smith, E. L., *J. Gen. Physiol.*, 1935–36, **19**, 979; Shlaer, S., *J. Gen. Physiol.*, 1937–38, **21**, 165; Steinhardt, J., *J. Gen. Physiol.*, 1936–37, **20**, 185; and Crozier, W. J., *Proc. Nat. Acad. Sc.*, 1940, **26**, 334, 382.

[17] *J. Gen. Physiol.*, 1941–42, **25**, 89, 293.
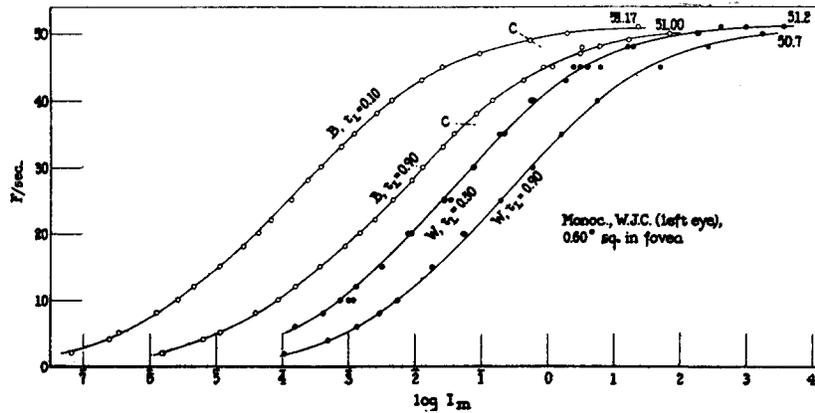
[18] Report in preparation.

FIG. 1. Flicker response contours for square image 0.60° on a side, within the fovea. To the left, curves for blue (Wratten Filter No. 47), $t_L = 0.10$ and $t_L = 0.90$. To the right, curves for white light with $t_L = 0.50$ and $t_L = 0.90$. The points marked C on the B curves are the flash intensity levels at which color is just perceptible along the fusion contour. The curves drawn are probability integrals (see Fig. 2), computed to the maximum indicated at the tops of the curves. Each point is the mean of ten determinations. Flash intensities are in millilamberts, blue being matched with white below the color threshold.
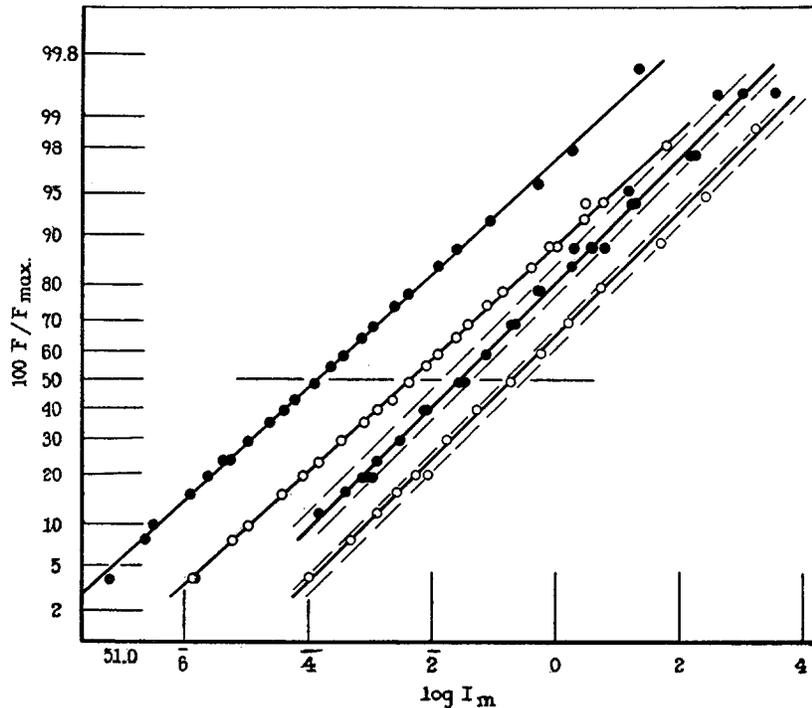

FIG. 2. The data of Fig. 1 displayed on a probability grid.

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and $F_{max.}$ lower than with larger areas, both for the white (W) and for the blue (B); $\sigma'_{\log I}$ should be greater and τ' should be less for B than for W, $F_{max.}$ greater for B than for W; and for each light-time (t_L) fraction used $\sigma'_{\log I}$ should be the same, for W and for B. These relations are found. In addition, if the properties of the "cone" segment of duplex contours are of the same kind as those of the exclusively foveal simplex contours, the appearance of color at the fusion point should be, for example, at a rather high flash-intensity separated by log 9 units on the $t_L = 0.10$ and 0.90 graphs. This is seen in Fig. 1. There are other facts connected with the subjective experiences along these flicker contours, and likewise with the scatter of $\sigma_{1\,I}$, which are consistent with the essential likeness of the properties of these simplex contours and those of the "cone" branches in the duplex cases. We may conclude that the simplex "cone" curve is adequately described over its whole extent by the probability integral.

<div style="text-align:center">IV</div>

Two methods have been used to obtain directly the practically pure rising "rod" portion of the duplex flicker contour. In one, colored light is used to form a flickered image of suitable area at some distance from the fovea. In the other a flickered field containing several illuminated patches is employed. Qualitatively, the results are of the same kind. The theoretical consequences of the experiments with the second procedure are of considerable interest, but will not be enlarged upon here. One point should, however, be mentioned: under the conditions used it can be shown that the flicker contours due to the non-homogeneous but simultaneous excitation of suitably separated retinal areas are also simple probability integrals, both for the "rod" and for the "cone" segment, and that the rules already found[2] for their integrative overlapping continue to apply. This is manifestly consistent with a central nervous control of the flicker end-point, and clearly with the theory of its statistical determination, rather than with the idea of its government by retinal photochemistry—since the several areas, taken singly, provide quite different contours.

Fig. 3 gives an illustration of results with the first method, using blue light. By comparison with the contours obtained for images closer to the fovea, the form in Fig. 3 is at first sight peculiar. With smaller test areas in the retinal periphery the shape of the contour becomes still more distorted. In the absence of tests with intermediate areas and other retinal locations the extrapolation of the "cone" curves would scarcely be attempted here, but we do have these data. The parameters of the empirically fitted "cone" integrals have the expected interrelations. Their extensions approach $F = 0$ at just about the intensity where the "rod" curve reaches its maximum (Fig. 3). It is shown that the "rod" data, without subtractive correction for "cone" effects

in this case, are here directly described by the probability integral (Fig. 3). The "rod" $\sigma'_{\log I}$ is the same for $t_L = 0.10$ and 0.75; $F_{max.}$ does not perceptibly change, but even for the "cone" branch this change is quite small with colored lights; the shift in τ' is slightly greater than for the "cone" curves. As for the various cases[2] in which the "cone" curve more or less underlies the whole of the "rod" part, the declining "rod" curve is also given by a probability integral.
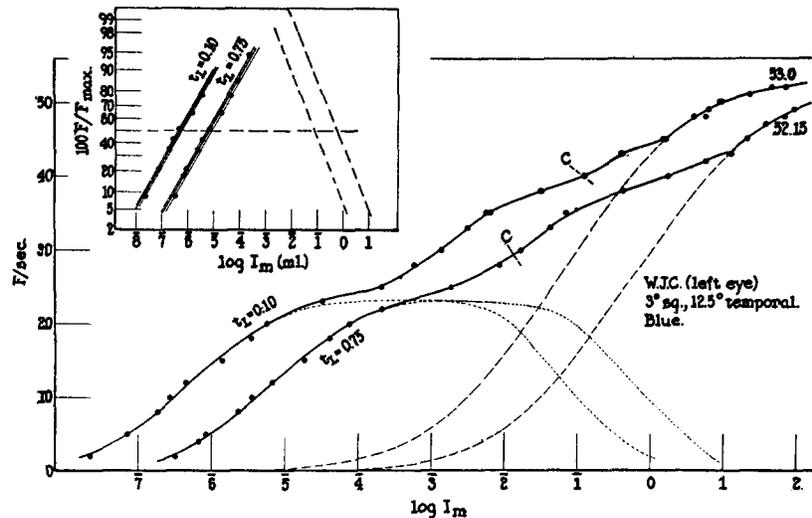

Fig. 3. Flicker response contours for a 3° square centered 12.5° on the temporal side of the fovea, with $t_L = 0.10$ and $t_L = 0.75$. Probability integrals are adjusted to the uppermost short segments, and the "rod" contributions are determined by difference. The inset figure shows that the rising "rod" branches, computed to $F_{max.} = 23.3$, and the declining contributions obtained by ordinate differences, are well described by the probability integral. Flicker contours with structures intermediate between those of Fig. 1 and these of Fig. 3, as well as more extreme instances, are provided by the use of other test areas and retinal locations.

The second procedure used to free the basic "rod" curve from "cone" involvements uses the striped cylinder technique[15] and a subdivided test-field such as is shown in Fig. 4. With high values of t_L the contours obtained are of the general form seen in Fig. 4. Despite the subdivision of the field the "cone" and "rod" segments are smooth, simple functions which shift systematically when t_L is changed. The significance of these facts for the theory of visual integration is developed elsewhere. For the present purpose it is sufficient to show that by this procedure the "cone" curve may be made so steep that the rising "rod" branch is almost completely exposed (cf. Fig. 4). The extrapola-

tion of the "cone" integrals (Figs. 4 and 5) requires almost no subtraction from the rising "rod" curves, for which the data adhere to the probability summation as shown in Fig. 6.

The probability summation equation applies non-specifically to the relation between F and log I for a great variety of animal types, and for a number of systematically varied conditions. Its three parameters have been experimentally caused to change in such ways as to show that these three independent
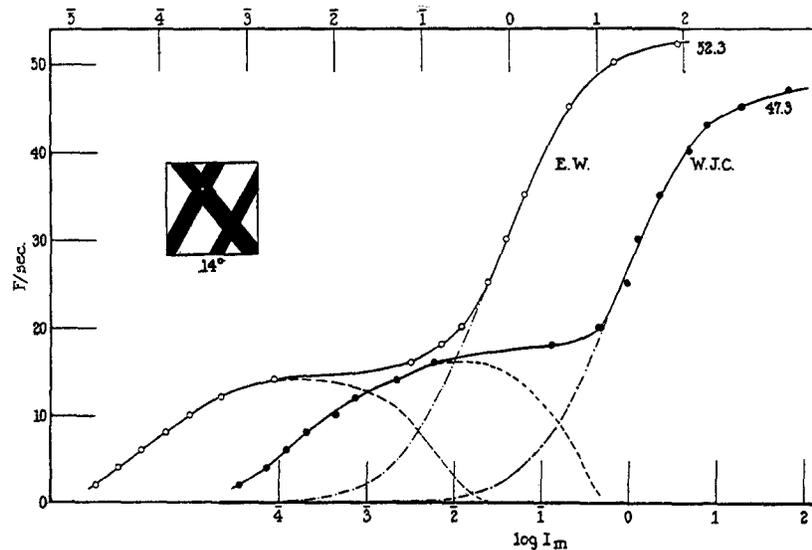

Fig. 4. Monocular flicker contours (left eye, white light) for two observers, employing the method of moving stripes, $t_L = 0.90$, and a divided field 14° square with the pattern shown in the inset. The "cone" probability integrals with the indicated maxima are shown in Fig. 5.

parameters are necessary and sufficient. Its derivation is based upon the conception that a large number of neural units are concerned in the flicker response, and that these units fluctuate both in momentary excitability ($1/I$ for response) and in their capacities to produce elements of neural effect for the determination of the result used as index of response. The analysis of dark adaptation[19] and of intensity discrimination shows that at each instant during the course of progressive changes of excitability a population of neural effects forms a unitary statistical assemblage. This is basically confirmed by the properties of the variation of the critical intensity.[19, 20]   It is also strikingly

[19] *Proc. Nat. Acad. Sc.*, 1940, **26**, 334, 382.

[20] *J. Gen. Physiol.*, 1937–38, **21**, 17; 1939–40, **23**, 101; 1940–41, **24**, 505, 635; 1941–42, **25**, 89, 293.

confirmed by the integrated action apparent in our experiments with sub-divided fields (Fig. 5, etc.). The statistical basis for the integration of "rod" and "cone" effects along the flicker contour is likewise consistent with this view. As already indicated, the inhibition of some "rod" effects in the zone of overlapping on the duplex curves[21] also follows the simple probability law in all cases examined.
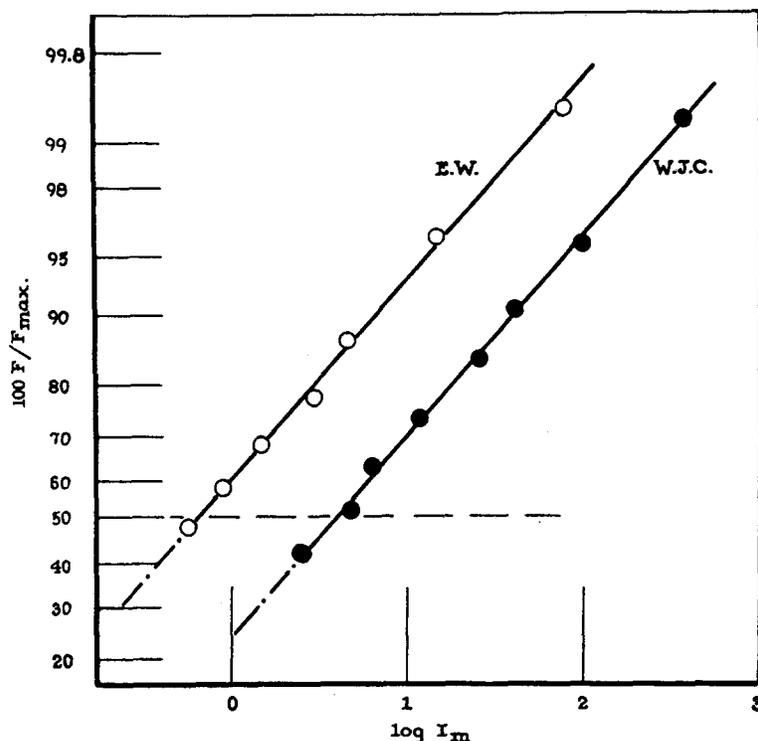

Fig. 5. The upper segments of the curves in Fig. 4 shown on a probability grid.

Since three parameters are required for description of the flicker contour, and since the shape constant $(\sigma'_{\log I})$ can be changed by simply going to another part of the retina or by subdividing the image field, it cannot be held[16] that the photochemical theory of visual data accounts for the form of the curve even under fixed conditions of temperature, light-time fraction, retinal location, and the like. When simplex performance contours are naturally available[7, 9, 11] or are experimentally uncovered, as in the present instances, their forms do not agree with the requirements of photochemical theory any more than do the

[21] *J. Gen. Physiol.*, 1940-41, **24**, 635; 1941-42, **25**, 89, 293, in press.

properties of their parameters;[1, 2] when duplex flicker contours must be dealt with, the transitions from "rod" to "cone" branches are not analyzed at all by the photochemical hypothesis.

In many situations, perhaps in most, which have to be considered by quantitative biological theory it is obvious that many cellular and other structural units are acting at the same time.   It has long been recognized that these units
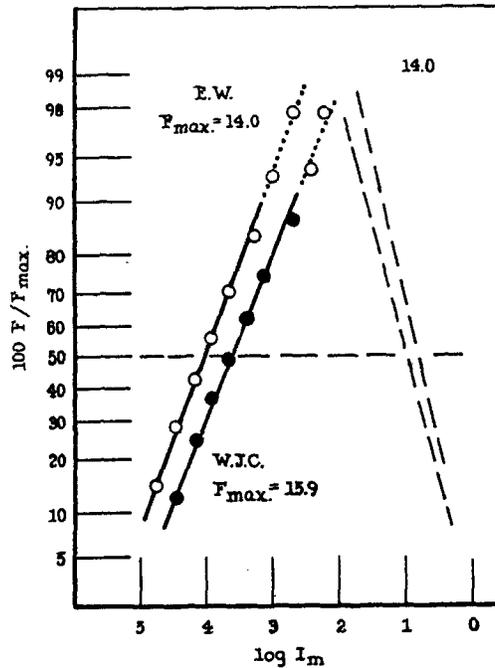

FIG. 6. The "rod" segments of the contours in Fig. 4, on a probability grid. The values of $F_{max.}$ are indicated.

are probably never quite identical, and that they spontaneously fluctuate in threshold excitability as well as in performing capacity.   There is good reason to believe that the analysis of visual data can illustrate the operation of these factors, under especially favorable circumstances.   A primary objective must be the separation of non-specific statistical properties of assemblages of units from those properties which can be used to further the interpretation of intrinsic cellular events, such as those involved for example, in sensory excitation.[22] This procedure will often be confronted by complex interactions and compoundings of the activities of different groups of acting units.   Instances, like those

[22] J. Gen. Physiol., 1939–40, **23**, 143; Proc. Nat. Acad. Sc., 1937, **23**, 71; 1939, **25**, 171, 176; 1940, **26**, 334.

discussed in this paper, in which the nature of such integrations can be exposed have therefore a particular interest for the theory of quantitative biology.

<div align="center">VI</div>

<div align="center">SUMMARY</div>

Flicker response curves (man) obtained with images formed entirely within the fovea are like those secured with lower animals having only one general class of retinal receptors. They are normal probability integrals (F $vs.$ $\log I_m$), and the properties of their parameters agree with those for visually simplex animals and for the "cone" portions of contours exhibiting visual duplexity.

By several different procedures, involving experimental modifications of the "cone" curve, the "rod" part of the typical human duplex curve can be obtained free from overlapping by the extrapolated "cone" curve. It then has the probability integral form which the lower segment does not directly exhibit when combined with "cone" effects.

These results are discussed with reference to the statistical nature of the fundamental form of the flicker contour and to the interpretation of duplex curves produced by the neural integration of two independently modifiable groups of sensory effects.