THEORY AND MEASUREMENT OF VISUAL MECHANISMS

X. MODIFICATIONS OF THE FLICKER RESPONSE CONTOUR, AND THE SIGNIFICANCE OF THE AVIAN PECTEN

BY W. J. CROZIER AND ERNST WOLF

(From the Biological Laboratories, Harvard University, Cambridge)

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The retina of the zebra finch Taeniopygia castanotis (Gould) contains visual cells histologically of one general type only (cones), although some of these are differentiated by oil droplets; some are “double” cones; the retina has a well developed fovea. In keeping with the subsequently observed simplex character of the primary photoreceptor population, the flicker response contour (F vs. log I), with white light and light-time cycle fraction $t_L = 0.50$, was found to be a single symmetrical probability integral (Crozier and Wolf, 1940-41 b). This was confirmed by a number of additional experiments with colored lights (Crozier and Wolf, 1941-42 d). The eye of Taeniopygia contains, however, a fairly large and complex pigmented pecten. The position of this organ (cf. Krause, 1922, Fig. 88) is such that it, or rather the presence of its serrated shadow on the retina, may well be expected to have an effect upon the sensory influence of moving images, as suggested by Menner (1938), although in a recent review of this matter Walls (1942, pp. 367, 520, 648) concludes it to be unlikely that the pecten casts a shadow outside its own base or elsewhere “where it would do any good.” No specific signs of an influence of the pecten could be detected in our measurements with $t_L = 0.50$. The symmetry of the $F - \log I$ contour was not disturbed, and subsequent series of observations at $t_L = 0.10$ with lights from different spectral regions have confirmed this (Crozier and Wolf, 1941-42 d). The very low intensity level at which the $F - \log I$ curve is located, by comparison with that for other vertebrates, is sufficiently accounted for by the bird’s higher temperature (Crozier and Wolf, 1940-41 b), and requires no assumption that the presence of the pecten is responsible.

We were led to believe that study of the modification of the $F - \log I$ curve by systematically changing the light-time cycle fraction ($t_L$), employing the methods already used with various animals (Crozier, Wolf, and Zerrahn-Wolf, 1937–38 d, e; Crozier and Wolf, 1940, 1939–40 b, 1940–41 d), might reveal a distinctly unusual situation. The comparative morphology of the pecten, and the complexity of its shadow on the background of the eye in diverse birds of different habits, strongly suggests (Menner, 1938) that the effect of the pecten might be to increase the sensory action of small moving images. Con-
sequently, the particular effect (if present) should be especially apparent, with
the striped cylinder technic, when using narrower dark stripes and broader light
spaces ($t_L > 0.50$). The proof that this is the case is contained in the present
paper. The systematic changes in the $F - \log I$ contour as a function of $t_L$
are with the zebra finch of a kind not found in other animals lacking a well
developed pecten.

The avian pecten is a membranous organ, highly vascular, rather densely
pigmented, attached to the retinal surface of the eye along the entrance of the
optic nerve. It projects for a considerable distance into the vitreous humor.
Its surface is elaborately plicated. In our birds the ophthalmoscopic appear-
ance of the eye agrees rather well with Wood’s account for members of the
related Fringillidae (Wood, 1917, Plate LIV); the eyeground is bright blue-
green-gray, with bright dots. A great variety of guesses has accumulated
concerning the functional significance of the pecten,—that it is concerned with
the nutrition of the vitreous, or with excretion (cf. Johnson, 1901, 1927);
that it is an erectile organ, and may be involved in the movement of liquid
during lens movements and the accommodation of the eye; that it is a visual
shield, especially for that part of the field in front of and above the bird’s head,
and that it may therefore serve to suppress binocular vision; or that it protects
the retina from too great illumination; or that it is a sense organ. The notion
must be guarded against that the pecten, or any organ, should have a function.
The degree of its development in different birds is apparently coordinated with
the dominance of photopic vision and with the use of monocular rather than
binocular perception. During ophthalmoscopic observation the impression
is very easily gained that the pecten moves about within the vitreous. The
incorrectness of this notion was demonstrated by Beauregard and by Paul
Bert, for pigeon and duck, in 1876. We can confirm their conclusion that the
apparent larger movements of the pecten are actually due to the movements
of the eyeball; the vibratory pulsations of the pecten which can be detected
are mechanically transmitted to the eyeball by the contraction of the muscle
which operates the nictitating membrane. There remain quite minor pulsa-
tions of smaller amplitude which may well be due to fluctuations in the circu-
latory pressure. We find in our quantitative evidence on the reaction to flicker
no indication that the functioning of the pecten as a “light shield” introduces
any modification of the fundamental nature of the flicker response contour.
The effects actually found are of quite another sort.

The demonstration that the highly exceptional properties of the zebra-finch
$F - \log I$ curve to be described in relation to $t_L$ are really due to the presence
of the pecten shadow cannot be made by removing the pecten. Nor can a
veritable pecten be put into the eyes of other forms. But the same effect can
be produced by projecting an appropriate shadow on the human retina. It is
shown that in this way the specifically peculiar properties of the bird’s flicker
response contours can be essentially reproduced. The experiment provides a proof of the visual significance of the avian pecten. It also opens the way to the experimental analysis of the problem of visual integration through the use of subdivided patterns, of which we shall have something to say in later papers.

The consequences of breaking up a visual area (in man) into several parts can give a proof of the separability of the two general factors we have conceived to be operating in the production of a given level of visual excitation, namely (1) the number of neural units concerned and (2) the mean number of elements of sensory effect produced in each unit. Some practical consequences will be briefly referred to. Since the pecten effect is one apparently directly involving only the “cone” response contour, it becomes possible to separate experimentally the human “cone” and “rod” contributions, with a result confirming in important respects the conclusion from previous analytical interpretations.

II

With an insect (Anax, nymph), sunfish (Enneacanthus), turtle (Pseudemys), and man, reduction of the light-time fraction in a flash cycle of given form increases $F_{\text{max}}$ of the $F - \log I$ curve and decreases the abscissa of inflection, each in rectilinear proportion to $t_L$. The third parameter, $a' \log t$, the S.D. of $dF/d \log I$ with $F_{\text{max}}$, put $= 100$, is not modified at all. The statistical basis for the generality of this rule has been indicated in earlier discussions. The S.D. parameter is demonstrably (in man) a function of the number of available neural units, while $F_{\text{max}}$ measures the total number of elements of sensory effect producible under the conditions. Reduction of the $t_L$ fraction means that, in virtue of the correlated increase of the percentage dark-time, each flash has a greater chance of finding less refractory units to work upon; hence a given level of effect ($\alpha F$) is achieved with a lower flash intensity, although the total number of available and participating units is not changed.

The observations with the zebra finch were made in the way described in our account (Crozier and Wolf, 1960–41 b) of the flicker response contour with white light at $t_L = 0.50$, by the use of the initiation of head nystagmus as an end-point. Series of striped cylinders providing $t_L = 0.10, 0.25, 0.50, 0.75$, and 0.90 were used in the present tests. The method and general procedure are discussed in the paper by Crozier and Wolf, 1939–40 b. Four selected individual male birds were used throughout. No consistent differences were noticed in the excitabilities of these four. (Two females were also used at $t_L = 0.50$ and 0.90; cf. Table II.) At each flash frequency $F$, three observations were made of the critical flash intensity $I$ with each bird, averaged, and the means and P.E.'s of these averages appear in Table I.

The relations of $\log I_m$ to flash frequency $F$ are shown in Fig. 1. The set of curves does not have the character found for Anax, sunfish, turtle, and man. From $t_L = 0.10$ to 0.50, $F_{\text{max}}$ declines and $\tau'$ increases pretty much in the regu-
lar way; but with \( t_L = 0.75 \), and more extremely with 0.90, the asymptotic maximum is increased, \( r' \) is less, and the slope is markedly greater, so that the two latter curves cut across the other three.

Despite the changing shape of the \( F - \log I \) contour with alteration of \( t_L \), the curves are still well described by a normal probability integral (Figs. 1 and

### TABLE I

Critical intensities (white), as \( \log I_m(l.m.) \), for response to flicker by the zebra finch (Taenio-

pygio castelnoci), with different proportions of light-time (\( t_L \)) to cycle time (1/\( F \)), as a function of flash frequency \( F \). Each entry is the mean of twelve measurements, three on each of four male birds. Under \( t_L = 0.50 \) entries are also given in Fig. 1 from a previous experiment (Crozier and Wolf, 1940-41b) with other individuals. Each entry is accompanied by its log P.E.

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<th>( F ) per sec.</th>
<th>( t_L = 0.10 )</th>
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2). The slight departures are nevertheless systematic. Near the inflection point the departures tend to be in excess, and half way above it in defect. This is clearer below \( t_L = 0.75 \). Although any one of these departures is only barely significant statistically, their reality is attested by their further occurrence in our data with colored lights (Crozier and Wolf, 1941-42 d). Several factors are possibly concerned in producing them. For the control of light intensity in the apparatus it was necessary to use filters; these are very nearly
Fig. 1. Flicker response contours for the zebra finch (Taeniopygia castanotis [Gould]) with different light-time fractions in the flash cycle, 0.10 to 0.90. White light. Data in Table I. The curves drawn are probability integrals (Fig. 2).

Fig. 2. The data of Fig. 1 on a probability grid. At the left the different curves are separated arbitrarily for clearness. On the right the lines drawn are shown in their natural relative positions.
Fig. 3. The proportionality between $I_m$ and $P.E.1$ in the data of Table I is direct (that is, on the double log grid the points form a band of unit slope). The proportionality constant does not significantly depend on $t_L$.

Fig. 4. The abscissa of inflection ($r'$) of the curves in Fig. 1 is directly proportional to the percentage light-time from $t_L = 0.10$ to 0.50; for higher values of $t_L$ it becomes smaller.

"neutral" for the normal human eye, as shown by spectrophotometric measurements, but are not necessarily so for the bird. Again, in covering the range of
flash frequencies use is made of rotated cylinders with 5, 10, 20, or 40 stripes, in different parts of the range. There is no absolute correlation of the slight systematic departures with either of these influences, but it is possible that in view of the action of the pecten they may play a part. There seems no basis for suspecting that the iris is involved in the departures, although they seem lessened at \( t_L = 0.90 \).

The variation of \( I_L \) as a function of \( I_m \) shows no real correlation with \( t_L \) (Fig. 3).

The change of \( \delta' \) with \( t_L \) is shown in Fig. 4, and of \( F_{\text{max}} \), in Fig. 5. The changes are rectilinear in \( t_L \) up to 0.50, then alter direction abruptly. This is correlated with the constancy of \( \delta'_{\text{log}} \) for \( t_L = 0.10, 0.25, \) and 0.50, and its abrupt decrease beyond that point (Fig. 2).

The interpretation given for the \( t_L \) data in cases thus far known was applied to situations in which the retina is comparatively free from fixed shadows. The eyes of the gecko and of \( \textit{Phrynosoma} \) have minute simple pectens, it is true; but that of the zebra finch is very much more elaborately developed. In each of the instances mentioned the simplex flicker response contour is quite symmetrical (Crozier, Wolf, and Zerrahn-Wolf, 1938–39 a; Crozier and Wolf, 1938–39 b, 1939–40 b). This is consistent with the present findings, and has an important bearing on the interpretation of visual data in general (cf.}
section V). But in the presence of a fairly elaborate pecten shadow it is clear
that the parameters of the flicker response function (moving stripe method)
suffer a kind of dependence on $t_L$ which is not otherwise found. The experimental proof that the pecten shadow does involve this sort of effect is given in
section IV.

By testing separately and in combination the influence of image area, location, exposure time, temperature, light-time fraction, and wave-length composition it has been shown that three independently modifiable parameters are required for the description of the visual excitability function (cf. Crozier, Wolf, and Zerrahn-Wolf, 1937-38 a; Crozier, 1939; 1940 a, b; etc.). For the “cone” curves it is found that increasing the number of cone units available for excitation causes a decrease in $\sigma_0 \log I$ (cf. Crozier, 1940 a; Crozier and Wolf, 1941-42 b). This is the effect found with the zebra finch at $t_L = 0.75$ and 0.90. On the other hand, $F_{\text{max}}$, is also increased by augmenting the mean contribution from each unit, but without change in $\sigma_0 \log I$. It may thus tentatively be deduced that with narrow dark bands and wider light bands, as in our tests with longer light-time intervals, the production of the end-point effect for the bird is due to the activation of a larger number of neural units, regardless of whether the excitation of these units is then more effective in the sense that larger numbers of elements of effect are obtained from them. This means that $F_{\text{max}}$, must tend to pass through a minimum as $t_L$ is increased (Fig. 5). The pecten shadow produces a serrated light-dark line along which contrast is enhanced. The interruption of light by superimposed dark-light transitions moving across this pecten shadow must be expected to produce an enhancement of the sensory effect if the dark intervals are brief by comparison with the alternating light intervals. Consequently the end-point effects must for short dark-times be expected to increase, especially along the illuminated edge of the pecten shadow. This corresponds exactly to the subjective effect when the human observer is provided with a “pecten shadow” on the retina (see section IV). It is thus easily explained why the unusual effect seen in Fig. 1 occurs only with short dark-times, and is greater with $t_L = 0.90$ than with 0.75. When such comparatively small dark-times are used the retinal effective area is enlarged, an increased contribution to the end-point effect then arising along the margin of the pecten shadow because the units there located are involved in a contrast situation which enhances their neural efficiency.

The phrasing of this interpretation implies that the neural effect determining the end-point response is taken to be located central to the retina. In this connection we have to note that for all the light-time fractions used the curve is smoothly symmetrical. It is pointed out subsequently (sections IV and V) that the same thing is found when a number of flickered patches on the human retina are separated by darkness. The synthesis implied cannot very well be understood unless a central nervous locus be accepted for it.
The changing form of the $F - \log I$ curve as a function of $t_L$ cannot be attributed to a rôle of the bird's iris. Several kinds of evidence support this assertion. With no pupil correction possible or required, the corresponding data with *Anax*, *Enneacanthus*, and *Pseudemys* show the constancy of $\sigma'_{\log I}$ when $t_L$ is altered, just as with man when an effective artificial pupil is used. With elimination of the pupil variable and the introduction of a "pecten shadow," the human curves (section IV) show as a set the properties of those seen in Fig. 1. It is also consistent with this that, in the case of the zebra finch, $\sigma'_{\log I}$ with $t_L$ constant is not noticeably a function of spectral region (Crozier and Wolf, 1941-42 d).

In passing it may be remarked that if one were to attempt the interpretation of the form of the flicker response curve from the standpoint of the theory of the retinal photostationary state (Hecht, 1937), and if one had in hand only one of the curves of Fig. 1, the system of reaction-orders one would assume would necessarily be quite different say for $t_L = 0.10$ and 0.90,—neglecting the fact that the equations do not really describe the full range of the data in any case (cf. Crozier, Wolf, and Zerrahn-Wolf, 1938-39 a, b; Crozier and Wolf, 1939-40 a). This is equally true for the curves in the corresponding experiment with man (section IV). The direction of the shift of the curve with increase of $t_L$, of course, negatives the whole conception in any case (Crozier, Wolf and Zerrahn-Wolf, 1937-38 d, e, etc.).

From these findings it is apparent that a definite functional significance can be assigned for the pecten: it increases the sensory action of small moving shadows. This is entirely in agreement with deductions made on the basis of the nature of the pecten shadow in birds of different visual habits, and from some not altogether conclusive experiments with man (Menner, 1938). In sections IV and V it will be shown that no direct effect of a "pecten shadow" can be demonstrated for the "rod" $F - \log I$ curve in man. This might be correlated with the small size of the pecten in nocturnal birds (cf. Wood, 1917; Franz, 1934; Menner, 1938). It can be tested in a more significant way by examining the responses of a bird exhibiting visual duplexity, as we do in the following paper. Another kind of test is also possible, because if the theory is sound the "pecten" effect should be reduced by using a flash cycle of different wave form in which the light-dark transitions are less abrupt.

The pecten is probably not stationary; its slight movements in addition to those of the head as a whole, and of the eyes, may well play a part in causing small images to sweep across the retina. The same general enhancement of acuity for smaller images should be produced by movement of the pecten shadow even if the image and the eye as a whole are stationary. This we have tested for the human eye, with interesting indications already at hand. It is not impossible that the lobulated iris of some forms (e.g., camel, goat) may function in a similar way. One thinks also of the experience of those who have
had to do with long-haired dogs; there is a general impression that the hair in
front of the eyes is actually a visual aid. The present interpretation of the
visual role of the pecten shows that this is not implausible. (A suggestion of a
different sort has been made by Swindle (1917) for the function of the "eye
appendage" hairs of the cat and other animals, namely that they aid ocular
fixation.) The matter can be tested with dogs. Finally, the thought occurs
that the barred or patched patterns of the males of certain types (as the zebra
finch) exhibiting pronounced sex dimorphism could conceivably be connected
with a sex differential development of the pecten or of its effect. We mention
this because the data of Table I were obtained exclusively with male Taeniopygia
(some 17 individuals). However, careful tests with two females at $t_L = 0.50$
and 0.90 (Table II) show no trace of significant divergence from the measure-
ments with males (Crozier and Wolf, 1940–41 b, and Table I of the present
paper).

| TABLE II |
| Critical flash intensities (white) for $t_L = 0.50$ and 0.90, with 2 female zebra finch; each $I_m$ is the average of six measurements. Cf. Table I, and text. |
| $P$ per sec. | $t_L = 0.50$ | $t_L = 0.90$ |
| log $I_m$ | log $I_m$ | log $I_m$ |
| 10 | 4.12 | 4.18 |
| 20 | 3.12 | 3.68 |
| 30 | 2.86 | 3.08 |
| 40 | 2.65 | 3.42 |
| 50 | 1.96 | 3.94 |

With a test area of sufficient size, the human $F - \log I$ contour exhibits the
fundamentally duplex character of the typical vertebrate visual mechanism.
The curve is a complex of two partially overlapping $S$-shaped components
(cf. Hecht and Verrijp, 1933; Hecht, Shlaer, and Smith, 1935; Crozier, Wolf,
and Zerrahn-Wolf, 1937–38 b; Crozier and Wolf, 1941–42 b). The essential
properties, and the quantitative form, of the "cone" segment of the duplex
curve are the same with different methods of producing flicker (Crozier and
Wolf, 1940–41 c; Crozier, Wolf, and Zerrahn-Wolf, 1937–38 b). The low
intensity segment of the duplex curve is ordinarily the additive resultant of
"rod" and "cone" contributions. By means of observations in two different
regions of the retina, involving the use of $t_L$ and of wave-length composition
as variables (Crozier and Wolf, 1940–41 d, 1941–42 a, b), it has been demon-
strated that the separation of the essential "rod" contribution to the $F - \log I$ contour can be successfully effected analytically by the procedure already
used for various other vertebrates (Crozier, Wolf, and Zerrahn-Wolf, 1937–38 a, e, 1939–40 c; Crozier and Wolf, 1938–39 a, 1939–40 a), including forms
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in which the overlapping of "rod" and "cone" effects is not so complete. The $F - \log I$ curve is the same, and its changes with $t_L$ are the same, when flicker is produced (1) by sectoring a light beam at a focus (Crozier and Wolf, 1940-41 c) and (2) by the use of the striped cylinder technic; in the latter case the eye of the observer is optically placed within the striped cylinder by the use of telescope and prisms (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b).

A distinction must be carefully made, however, between certain other properties of the two stimulus situations just mentioned. Thus when flicker with a subdivided field is produced by method (1), the change of $r'$ as a function of $t_L$ is of the type about to be described and already seen in the tests with Taenopygia; but $a'_{\log I}$ does not then change at all (Crozier and Wolf, 1943-44 b), in sharp contrast to the case with procedure (2) when a "pecten shadow" is present. It scarcely requires emphasis that tests of this kind demonstrate qualitatively the existence of essentially three independently modifiable parameters in the equation of the flicker contour. (It will be of considerable interest to learn whether in these two cases there appear differences in the behavior of the contours with respect to the influence of temperature, for example, or oxygen pressure.) In any case, we have evidence supporting the conception of the importance of "sliding contact" between moving images and the margins of the pecten shadow.

We desired to create a condition for the human observer which would mimic in certain essentials the normal state of the eye in a bird with well developed pecten shadow. To do this we provided in the field of view of our "periscopic" telescope (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b, Fig. 1) a cross-barred diaphragm of copper foil. Its appearance is given by the scaled drawing in Fig. 6. The slanting angle of the bars was arranged to give inclined edges across which the vertical images of the revolving cylinder stripes would pass. At the point indicated in Fig. 6 a minute hole provided a fixation point. Thus the image field fell chiefly on the temporal side of the fovea and below the horizontal meridian.

The square field as a whole subtended an angle of 14.3° at the retina. The illuminated parts of the field aggregated ca. 140.2 square degrees, or 59.8 per cent of the total square field. It is of interest that, as shown subsequently, $a'_{\log I}$ is a little greater than for the full 14.3° field centrally fixated, in correla-
tion with its smaller size; this cannot be fully interpreted, however, until more is known of the process whereby the synthesis of critical effects from distinct, simultaneously flickered patches is effected.

Data were obtained with two observers, monocularly (left eye). As in previous measurements with this particular apparatus, no pupil correction is required; the reason for this (although not stated in our earlier paper, as it should have been; Crozier and Wolf, Zerrahn-Wolf, 1937–38 b) is that the diameter of the light beam at the eyepoint is about 1.8 mm. The measurements are given in Tables III and IV, as log \( I_m \) and log \( P.E.1 \) (millilamberts). The flicker response contours are plotted in Figs. 7 and 8.

It is apparent that the presence of the “pecten” grid produces a set of human \( F - \log I \) contours with \( t_L \) as variant which in a qualitative sense imitates the peculiarities of the set obtained with zebra finch (Fig. 1). In the usual situation, with no “pecten shadow,” the curves obtained for the several values of

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**Table III**

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<th>( F ) per sec.</th>
<th>( t_L = 0.10 )</th>
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form a group in which the "cone" segments have the same shape constant $a'_{\log I}$ (Crozier and Wolf, 1940–41 d). This is obviously not the case in Figs. 7 and 8. Quantitatively, the distortion is not the same for the two observers. For W.J.C., with larger $a'_{\log I}$ and lower values of $F_{\text{max}}$, although lower values of $C$, and consequently a proportionately smaller number of elements of neural action produced, the pecten effect is relatively less pronounced. This might

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well be taken as a difference entirely in keeping with the analysis proposed in section III. It will be pointed out in the detailed consideration of the data of Figs. 7 and 8 that there is no reason to suspect a specific influence of the "pecten" shadow on the curves of "rod" performance, which perhaps accords with the general conception of the association of the development of the avian pecten with the accentuation of cone efficiency. The slight changes in the "rod" curves can be shown (section V) to be due secondarly to the interaction of "rod" and "cone" effects. The same is true in our data on the sparrow (Crozier and Wolf, 1943–44 b). On the basis of the differences between Figs. 7 and 8 there would seem to be no doubt that in other individuals more or less
FIG. 7. The measurements of Table III (W. J. C., left eye) giving flicker recognition contours (moving stripe method) with different light-time fractions (tL) using the divided field diagrammed in Fig. 6.

FIG. 8. The measurements of Table III (E. W., left eye) giving flicker recognition contours (moving stripe method) with different light-time fractions (tL) using the divided field diagrammed in Fig. 6.
Fig. 9. Log $I_n$ and log $P.E._1$ are rectilinearly related with a slope of 1, in the data of Fig. 7.
extreme manifestations of the "pecten effect" could be found. There would also seem every reason to believe that with other kinds of "pecten" shadow more pronounced distortions could be produced. Still it is of interest that,
as with the bird, the curves for $t_L$ 0.10, 0.25, and 0.50 have the same slope constants and that their $F_{\text{max}}$ and $\tau'$ change with $t_L$ in the normal way; only with $t_L$ extended to 0.75 and 0.90 is the distortion obvious. In all these respects the human "cone" curves, when the "pecten" shadow is present, behave like those found with the zebra finch. The general parallelisms with the bird measurements strengthen the basis for speaking of the response contours obtained with lower animals as flicker contours.

In one other respect, also, the data have similar properties. In Figs. 9 and 10 the variation of flash intensity critical for flicker is considered as a function of the mean critical intensity at various levels of $F$. For each observer the mean value of $P.E. I/I_m$ is independent of $t_L$, but the breadth of the scatter band of $P.E.'s$ tends to be greater at $t_L = 0.50$. The mean values of $P.E. I/I_m$ (and of its scatter) run consistently a little higher for E.W. than for W.J.C. This has been noted in certain other experiments as well. The average precision of the measurements as plotted may be given as $\sigma_m = 1.3$ per cent of $I_m$. This value is lower by half than that obtained in our earlier and less homogeneous series with this instrument (Crozier, Wolf, and Zerrahn-Wolf, 1937-38 b). In Figs. 9 and 10 no attempt is made to take account of the slight tendency of the upper points to "drop off"; the highest point tends to be low because of the manipulative procedure involved at the highest intensities with this apparatus.

The "cone" curves drawn in Figs. 7 and 8 are the upper portions of probability integrals, shown rectified in Figs. 11 and 12. In these latter plots the curves have been arbitrarily separated for clearness; their correct relations to one another are given in Figs. 13 a and b. The maximum ordinate to which these curves have been computed are shown in Fig. 14 as a function of $t_L$. The relations shown, and for $\tau'$ as well (Fig. 15), are not the same as found in the bird data (Figs. 4 and 5). It is apparent that instead of declining rectilinearly with increase of $t_L$, $F_{\text{max}}$, here tends to rise slightly, then sinks rapidly. This is taken to mean that, in the human case, even at light-time fractions less than 0.50, the presence of the "pecten" shadow used tends to increase the production of elements of neural effect; since $\sigma'_{\text{log } t}$ does not change appreciably (only for E.W. is it slightly diminished at $t_L = 0.50$), this is held to indicate that with increase of $t_L$ up to 0.50 and possibly beyond there occurs a more effective "summation" of excitations from the several illuminated patches (Fig. 6). With further increase of $t_L$ beyond 0.50 the significant location of the end-point flicker, subjectively, is predominantly along the edges of the crossed bars, and the number of active cone units is correspondingly enhanced, with consequent reduction of $\sigma'_{\text{log } t}$. The same considerations account for the behavior of $\tau'$. From this standpoint the properties of the sets of curves in Figs. 7 and 8 are complicated by a phenomenon not encountered in the bird data, namely the "summation" effect. This is not surprising, since the bird's pecten shadow
does not isolate patches of illumination, but merely provides a serrated shadow outline.

Fig. 11. The upper segments of the curves in Fig. 7 shown on a probability grid, the several curves separated laterally for clearness.

Fig. 12. The upper segments of the curves in Fig. 8 shown on a probability grid, separated for clearness.

We must note here that the present evidence for invoking summation on the basis of flicker end-points is not at all of the kind urged by Granit (1930) as arguing for (extrafoveal) retinal summation. In Granit's observations it
was found that the fusion frequency for four small patches in the periphery was a little higher than that for one patch, at the same flash intensity. This result is almost inevitable, even if there were no question of the involvement of scattering of light in the eye, because the total area covered by the four spots is greater than that covered by one of them. It is well known (Granit and Harper, 1930, etc.) that increasing the size of the test image produces just this effect. A proper examination of the question of "retinal integration," which Granit's experiment does not give, requires a more elaborate investigation of the flicker response contour when the area effect per se can be ruled out, and with due attention to the possibility of distinguishing between monocular and...
binocular integration effects (cf. Crozier and Wolf, 1940-41 c). This we propose to undertake elsewhere.

![Graph](image1)

**Fig. 14 a**

![Graph](image2)

**Fig. 14 b**

Fig. 14 a and b. Behavior of $F_{\text{max}}$ as a function of $t_L$ for the data of Figs. 11 and 12. See text.

The influence of light scattered in the eye can be ignored in the present case, we suspect. If it were a significant factor one could scarcely expect to have the symmetrical curves of Figs. 1, 7, and 8.
We have now to consider the lower, “rod,” sections of the duplex curves in Figs. 7 and 8. In doing so it will be shown that the data using the fragmented field of light provide a significant verification of the method we have used for separating the “rod” and “cone” contributions to the duplex contour. The procedure is to extrapolate the “cone” probability integral back toward \( F = 0 \). The difference between this and the observed curve is taken to represent the “rod” contribution.

The basis for doing this, and its results, have been described in a number of reports of which some are already cited in this paper. Various lines of evidence have been held to justify the conception that “rod” contributions are progressively inhibited as, with rising \( F \), “cone” effects are increased (cf. Crozier and Wolf, 1938-39 a, 1940-41 d, 1941-42 a, etc.). Under most conditions of observation the overlapping of the human “rod” and “cone” curves is complete, so that the measurements in the lower section of the duplex graph represent a summation of “cone” plus uninhibited “rod” effects. Consequently the raw “rod” data do not fall upon a normal probability integral curve. In connection with other visual functions the suggestion has, of course, been made before that at lower intensities one may well be dealing with a combination of rod and cone effects (cf. Parsons, 1927). Recently this has been emphasized by Lythgoe (1940). But no attempt seems to have been made to use the idea quantitatively or otherwise than speculatively, except in our analyses of duplex flicker contours.

Figs. 16 and 17 exhibit the calculated extrapolations of the “cone” curves in Figs. 7 and 8 (and Figs. 11 and 12), together with the “difference curves” presumed to depict the “rod” contribution. It is seen that in terms of this analysis the “rod” measurements for \( t_L = 0.90 \) are almost completely free from
"cone" complication, those at \( t_s = 0.75 \) only a little less so. For the first time, then, we can be reasonably sure that we are able to deal directly with "rod" flicker observations freed from the inhibitive effects of cone excitation (Crozier and Wolf, 1941-42 c). These measurements as taken directly do adhere well to the probability integral formulation, as shown in Figs. 18 and 19; the others do not.

The rising and the falling branches of the "rod" curves obtained by difference
are shown in Figs. 18 and 19 to adhere very well to probability integrals. The slopes of the rising branches for \( t_L = 0.10, 0.25, \) and \( 0.50 \) are the same. This is what has already been shown for the ordinary data at all values of \( t_L \) in the absence of the “pecten” (Crozier and Wolf, 1940–41 d). The inhibitive effect of cone excitations must therefore be concerned in these instances with the inhibition of elements of neural effect due to excitation of rods, and not to the suppression or complete side-tracking of different numbers of rod units. The almost complete elimination of overlap at \( t_L = 0.75 \) and especially at 0.90 shows that the “rod” \( \sigma'_{\log t} \) then becomes quite distinctly greater, and the \( P_{\text{max}} \) increases. We know from other lines of evidence that the rod and cone populations of units behave differently with respect to the consequences of an increase in numbers (area): the “cone” \( \sigma'_{\log t} \) decreases, the “rod” \( \sigma'_{\log t} \) increases when the respective numbers of units are made much larger, regardless of changes in the total number of elements of effect produced, as induced by

![Graph showing the rising and declining curves of the rod contributions to the duplex curves of Fig. 7 (as shown in Fig. 16) are here put on a probability grid. Note that for \( t_L = 0.75 \) and 0.90 the observations are taken directly (solid lines). The other points plotted are read from the dotted lines in Fig. 16.]
changing \( t_L \). We may conclude that when overlapping of the "rod" and "cone" curves is relatively complete a certain number of rod units are forced out of the picture so far as concerns contributing to the discrimination of flicker, while others have their effective contributions reduced.

The declining branches of the "rod" curves have slopes which depend, as in other cases, merely on the degree of separation of the "rod" and "cone" popu-

![Graph](image)

**Fig. 19.** The rising and declining curves of the rod contributions to the duplex curves of Fig. 8 (as shown in Fig. 17) are here put on a probability grid. Note that for \( t_L = 0.75 \) and 0.90 the observations are taken directly (solid lines). The other points plotted are read from the dotted lines in Fig. 17.

lations of effects on the log \( I \) axis and on the steepness of the "cone" curves (Crozier and Wolf, 1938–39 a, 1940–41 d).

It is of some formal consequence that the analysis in Figs. 16 to 19 leads to concordant principles with two sets of curves differing in details of shape and of scale.

The experimental separation of the "rod" and "cone" processes by the use of the grid shadow gives a new kind of proof for the reality of visual duplexity, while emphasizing again the fact that the performance contours do not describe
the physicochemical nature of the primary process of peripheral excitation (cf. Crozier and Wolf, 1939-40 a, 1940). It is of interest here, and in relation to the summative overlapping of rod and cone effects, to comment upon the character of the subjective end-points. In the measurements of Table III (Fig. 7) the end-point fields at fusion, that is with the flash intensity just below that critical for the appearance of flicker, appear smooth, not granular or "frosted," down to a flash frequency which varies with \( t_r \); at \( t_r = 0.10 \), this point is at about \( F = 26 \); at \( t_r = 0.90 \), it is at 16. Below these flash frequencies the field is granular down to a low and variable \( F \), below that blue-gray. The grid pattern is clearly visible at \( F = 18 \) (at \( t_r = 0.10 \)) and down to \( F = ca. 1 \) (at \( t_r = 0.90 \)). As with the measurements employing colored lights (Crozier and Wolf, 1941-42 a, b) there is no simple correlation between the subjective character of the end-point fields and the location of singular points on the \( F \log I \) contour, such as the sharp bend.

We are obliged to Dr. Gertrud Zerrahn-Wolf for her assistance during the course of the experiments.

VI

SUMMARY

1. When there is projected on the retina (man, monocularly) the shadow of a grid which forms a visual field in several distinct pieces (not including the fovea in the present tests), the ordinary properties of the flicker recognition contour (\( F \) vs. \( \log I \)) as a function of the light-time cycle fraction (\( t_r \)) can be markedly disturbed. In the present experiments flicker was produced by the rotation of a cylinder with opaque vertical stripes. In the absence of such a grid shadow the "cone" segments of the contours form a set in which \( F_{\text{max.}} \) and the abscissa of inflection are opposite but rectilinear functions of \( t_r \), while the third parameter of the probability integral (\( \sigma_{\log I} \)) remains constant. This is the case also with diverse other animals tested.

In the data with the grid, however, analysis shows that even for low values of \( t_r \) (up to 0.50) there occurs an enhancement of the production of elements of neural effect, so that \( F_{\text{max.}} \) rises rather than falls as ordinarily with increase of \( t_r \), although \( \sigma_{\log I} \) stays constant and hence the total number of acting units is presumed not to change. This constitutes valid evidence for neural integration of effects due to the illumination of separated retinal patches. Beginning at \( t_r = 0.75 \), and at 0.90, the slope of the "cone" curve is sharply increased, and the maximum \( F \) is far above its position in the absence of the grid. The decrease of \( \sigma_{\log I} \) (the slope constant) signifies, in terms of other information, an increase in the number of acting cone units. The abscissa of inflection is also much lowered, relatively, whereas without the grid it increases as \( t_r \) is made larger. These effects correspond subjectively to the fact that at the end-
point flicker is most pronounced, on the "cone" curve, along the edges of the grid shadow where contrast is particularly evident with the longer light-times.

The "rod" portion of the $F - \log I$ contour is not specifically affected by the presence of the grid shadow. Its form is obtainable at $t_L = 0.90$ free from the influence of summing "cone" contributions, because then almost no overlapping occurs. Analysis shows that when overlapping does occur a certain number of rod units are inhibited by concurrent cone excitation, and that the mean contribution of elements of neural action from each of the non-inhibited units is also reduced to an extent depending on the degree of overlap. The isolated "rod" curve at $t_L = 0.90$ is quite accurately in the form of a probability integral. The data thus give a new experimental proof of the occurrence of two distinct but interlocking populations of visual effects, and experimentally justify the analytical procedures which have been used to separate them.

2. The changing form of the $F - \log I$ contour as a function of $t_L$, produced in man when the illuminated field is divided into parts by a shadow pattern, is normally found with the bird Taeniopygia castenotis (Gould), the zebra finch. The retina has elements of one general structural type (cones), and the $F - \log I$ contour is a simplex symmetrical probability integral. The eye of this bird has a large, complex, and darkly pigmented pecten, which casts a foliated shadow on the retina. The change in form of the $F - \log I$ curve occurs with $t_L$ above 0.50, and at $t_L = 0.90$ is quite extreme. It is more pronounced than the one that is secured in the human data with the particular grid we have used, but there is no doubt that it could be mimicked completely by the use of other grids. The increase of flicker acuity due to the pecten shadow is considerable, when the dark spaces are brief relative to the light. The evidence thus confirms the suggestion (Menner) drawn from comparative natural history that the visual significance of the avian pecten might be to increase the sensory effect of small moving images. It is theoretically important that (as in the human experiment) this may be brought about by an actual decrease of effective retinal area illuminated. It is also significant theoretically that despite the presence of shadows of pecten or of grid, and of the sensory influences thus introduced, the probability integral formulation remains effective.

CITATIONS