THE SIMPLEX FLICKER THRESHOLD CONTOUR FOR THE ZEBRA FINCH

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I

The quantitation of the visual performance of birds presents a number of theoretically attractive possibilities; it has also presented certain technical difficulties, which undoubtedly have been responsible in part for the fact that little information on this subject has been recorded. Diurnal birds are said to have in the retina a receptor population largely or exclusively of cones (*cf.* Menner, 1929), just as such typically nocturnal birds as the owls exhibit a considerable or exclusive preponderance of retinal rods (Rochon-Du Vigneaud, 1919; *cf.* Verrier, 1939). In our examination of responses to visual flicker we have been anxious to deal with the behavior of certain possibly typical birds. The reasons for this have not been entirely, or even decisively, determined by the requirements of the doctrine of visual duplexity in vertebrates generally. We have already pointed out in other connections (Crozier and Wolf, 1938, 1939) that when a duplex curve of visual performance is found to be associated with the presence of a retinal population containing both rods and cones one is constrained to describe the two branches of the duplex performance contour by means of the parameters of their descriptive functions, rather than to associate them with intrinsic properties of "rods" and of "cones" as causative categories; this position is confirmed by the examination of the visual performance of vertebrates possessing only one general histological class of photoreceptor cells (Crozier, Wolf, and Zerrahn-Wolf, 1938; 1938–39 *a*; Crozier and Wolf, 1938–39, 1940–41).

In another direction the occurrence of simplex performance contours, when not complicated by purely accessory structural conditions, permits a test of the nature of the analytical function really usable for the description of such data (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1938–39 *a*, *b*; Crozier and Wolf, 1938–39 *b*, 1940–41). In most vertebrates the occurrence of visual duplexity restricts the usable range of the data for any really significant test by curve-fitting. This is due to the overlapping of the two

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populations of sensory effects customarily attributed to the activation of rods and of cones respectively, and to the nature of the interaction between these (Crozier and Wolf, 1939–40; 1940–41 b). The discovery of additional cases in which a simplex visual performance curve can be demonstrated has thus a number of theoretically useful aspects.

Furthermore, since the visual acuity of birds is in general notably high one could expect that the performance contour would in general be pitched at a comparatively low intensity. This should make possible certain extensions of investigations otherwise hampered by the fact that, ordinarily, high intensities of illumination are difficult to manipulate precisely for the reasonably complete measurement of reaction contours, and if required to be monochromatic such intensities are difficult or even impossible to obtain for experiments of this kind.

The most generally applicable procedure for the investigation of visual capacity in diverse animals is unquestionably that based upon response to flicker. The great majority of animals with image-forming eyes give forced reactions to moving patterns in the visual field, provided the rate of the movement and the luminous intensities of the parts of the pattern are suitably adjusted. Most birds, with the possible exception of owls (cf. Bartels, 1931), exhibit eye nystagmus to moving patterns. The head nystagmus in doves and pigeons is well known (cf. Visser and Rademaker, 1934; Mowrer, 1936). For the quantitation of this performance the procedure we have used with various other animals (cf. Crozier and Wolf, 1940–41 a) requires a sufficiently small, reactive bird. We have used the Australian zebra finch (Taeniopygia castanotis (Gould)). The retina of passerine birds, for example the sparrows, is usually described as either exclusively of cones, or quite predominantly so constituted (cf. Menner, 1929; Slonaker, 1918). Our study of the zebra finch retina shows it to be devoid of rods. The eye has a pecten of good size. The possible significance of the pecten will be considered in connection with other experiments.

<center>II</center>

The zebra finches used for the observations were obtained from Dr. Roy M. Whelden of this Laboratory, who has raised several generations of this stock. Four males were employed throughout. They proved to be a decidedly homogeneous group, reactively. When surrounded by a revolving striped cylinder head nystagmus is easily recognizable. The head turns in the direction of the stripe motion, often through more than 180°, then rapidly returns to the initial direction; so long as the rotation speed is low enough, or the illumination high enough, these motions are regularly repeated. With sufficiently high cylinder speeds, or low enough illumination, no nystagmus is seen.

Each bird was put for observation into a thin glass cylinder, mounted on a bottom and lower part of wide mesh wire netting; the top is a plate of celluloid, cemented to the glass, with many circular holes punched in it. Adequate air circulation is essential. These cylinders fit neatly inside the striped cylinder of the apparatus producing flicker (*cf.* Crozier and.Wolf, 1939–40 *b*), and are large enough to permit free movement of the bird. At an appropriate height in the glass cylinder a wood cross-bar is fastened as a perch.

Before the tests the birds are dark-adapted for at least 45 minutes. Then, with a fixed rotation speed of the striped cylinder, the light intensity is slowly increased until the characteristic response to the moving stripes can be noticed. At low critical intensities (and low levels of flash frequency F) the bird may turn completely around on its perch. At higher levels they are seen to be "restless" before arrival at the intensities critical for nystagmus. There is no difficulty, however, in recognizing the onset of the typical repeated head motions; the twisting of the neck so characteristic of many birds when viewing an object often appears, and finally the crouching and the opening of the beak. In darkness these birds are always quiet, but in contrast to frogs or horned toads (Crozier and Wolf, 1939–40 *a*, 1940–41 *a*) they are always "on the alert" as soon as the least light reaches them. The proper dark adaptation of the observer is of course essential.

III

The observations are summarized in Table I. The three measurements made on each individual are averaged to give I_1, and the mean of the four values of I_1 is given for each F. The P.E.₁'s are for the dispersion of I_1; they would be larger if suitably corrected for the small number of cases, but we are concerned simply with the form of the law for P.E.₁ as a function of I_m and with the criteria of internal homogeneity in the measurements. The curve shown in Fig. 1 is not changed if the plotted values of I_m are obtained by simply averaging the twelve readings at each F; the four birds used are essentially equivalent. The first series of measurements, at $F = 20$, gave the result bracketed in Table I and plotted as an open circlet in the figures; although I_m was a little high, it does not really depart by a significant amount from the value obtained at $F = 20$ at the conclusion of the whole series, as Fig. 2 demonstrates. The observations were arranged to show any influence of training during the repeated tests, but no effect of this sort can be detected.

The log I_m data of Table I are plotted in Fig. 1. To them has been adjusted a normal probability integral (*cf.* also Fig. 2). The description by this curve must be regarded as excellent, particularly in view of the comparatively small number of observations at each point. The flicker response contour for the finch may therefore be placed with those of *Pseudemys* (turtle), *Sphaerodactylus* (gecko), *Phrynosoma* (lizard), and *Asellus* (isopod) as example of a simplex performance curve; each of these (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1938, 1938–39 *a*, *b*; Crozier and Wolf,

1938, 1938–39, 1940–41 a) is also well described by the probability integral. In keeping with the simplex character of the curve in Fig. 1, the ratio of P.E.$_{1_{I_1}}$ to I_m is statistically constant (Fig. 3) over the whole range (cf. Crozier, Wolf, and Zerrahn-Wolf, 1938–39 a; Crozier and Wolf, 1939–40 a, etc.). The band in Fig. 3 is divided arithmetically in half on the ordinate; the equality of distribution of the points in the two halves is a test of the homo-

TABLE I

Flicker response critical flash intensities for the zebra finch (*Taeniopygia castanotis* (Gould)) at fixed flash frequencies F per second, with equality of light and dark time; log I_m (millilamberts) gives the mean intensities from three observations on each of the same four male individuals at all points. (The figures in parentheses are from an initial set of exploratory measurements.) The dispersions of the individual means are given under log P.E.$_{1_{I_1}}$; these are not corrected for the small sample size.

F	log I_m	log P.E.$_{1_{I_1}}$
2	$\bar{6}.7087$	$\bar{7}.1683$
4	$\bar{5}.3677$	$\bar{7}.7801$
6	$\bar{5}.6354$	$\bar{6}.0096$
10	$\bar{4}.1268$	$\bar{6}.5777$
15	$\bar{4}.6408$	$\bar{6}.5366$
20	$(\bar{3}.3477$	$\bar{4}.3065)$
	$\bar{3}.1389$	$\bar{6}.7853$
25	$\bar{3}.6245$	$\bar{4}.0811$
	$\bar{3}.5594$	$\bar{4}.0623$
30	$\bar{3}.8919$	$\bar{4}.1854$
35	$\bar{2}.2463$	$\bar{4}.9473$
40	$\bar{2}.7037$	$\bar{3}.3724$
	$\bar{2}.6431$	$\bar{3}.1410$
45	$\bar{1}.1086$	$\bar{3}.4946$
48	$\bar{1}.5168$	$\bar{3}.8106$
50	$\bar{1}.9530$	$\bar{2}.4428$
52	0.4344	$\bar{2}.6329$
53	0.8868	$\bar{1}.5568$
54	1.2785	$\bar{1}.1034$
55	2.0302	$\bar{1}.8498$
	2.0370	$\bar{1}.6884$

geneity of the sets of measurements (cf. Crozier and Holway, 1938, 1939–40; Holway and Crozier, 1937).

IV

The smoothly symmetrical character of the F—log I_m graph in Fig. 1 indicates the absence of special effects, with $t_L = t_D$, due to movements of the iris, or to the presence of a pecten (cf. Menner, 1938). In this respect the curve is similar to that for *Phrynosoma* (Crozier and Wolf, 1940–41 a), although situated at a much lower intensity level, the abscissa of inflection r' ($\bar{3}.73$) being 2.90 log units less. The slope is also much lower for the

finch curve, being only a little greater than that for *Pseudemys* (Crozier, Wolf, and Zerrahn-Wolf, 1938–39 *a*); by extrapolating the data for the dependence of the *Pseudemys* τ' on temperature, for flash cycles with $t_L = t_D$ (Crozier, Wolf, and Zerrahn-Wolf, 1938–39 *a*; Crozier and Wolf, 1939–40 *b*), τ' at 42°C. would be about $\bar{3}.8$. This indicates a fairly close parallelism between the cone curves for *Pseudemys* and the finch, as the values of $F_{max.}$ are also fairly close together (52.6 and 55.25), although the slope of the finch
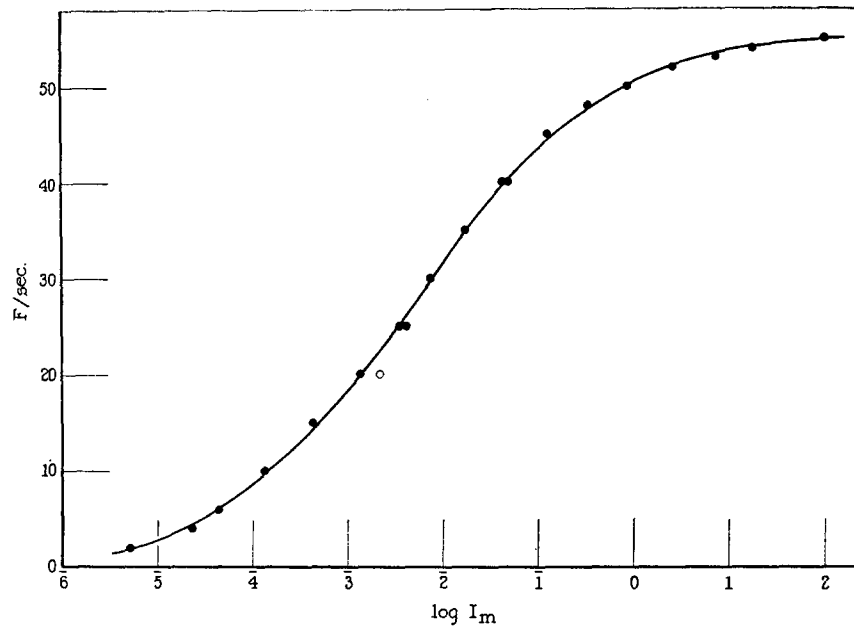

FIG. 1. The relation between flash frequency F and log mean critical flash intensity (I_m), with the light-time fraction = 0.5, for the zebra finch (*Taeniopygia castanotis* (Gould)) (cone retina). Data in Table I. The simplex curve is a normal probability integral.

curve is greater. In thus comparing the flicker acuity of the finch with that of other forms, even when correction is made for body temperature, it should be remembered, however, that we are here discussing data in which $t_L = t_D$ and the opaque moving bars cover the whole visual field. With the presence of the pecten, the sensory effects produced by a single moving image might be of quite a different order. An indication in this direction might well be given by tests in which t_L/t_D is varied systematically; certainly we have reason to know that the quantitative dependences of the two parameters of the curve sensitive to this variable, namely $F_{max.}$ and τ', are different in different animals (*cf.* Crozier and Wolf, 1939–40 *c*, 1940–41 *b*).

Under the conditions of test the simplex cone curve of the finch runs to lower critical intensities than does that for *Pseudemys*, or for man (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1937–38 *a*; Crozier and Wolf, 1940–41 *b*). A casual commentator might easily venture the thought that in general the
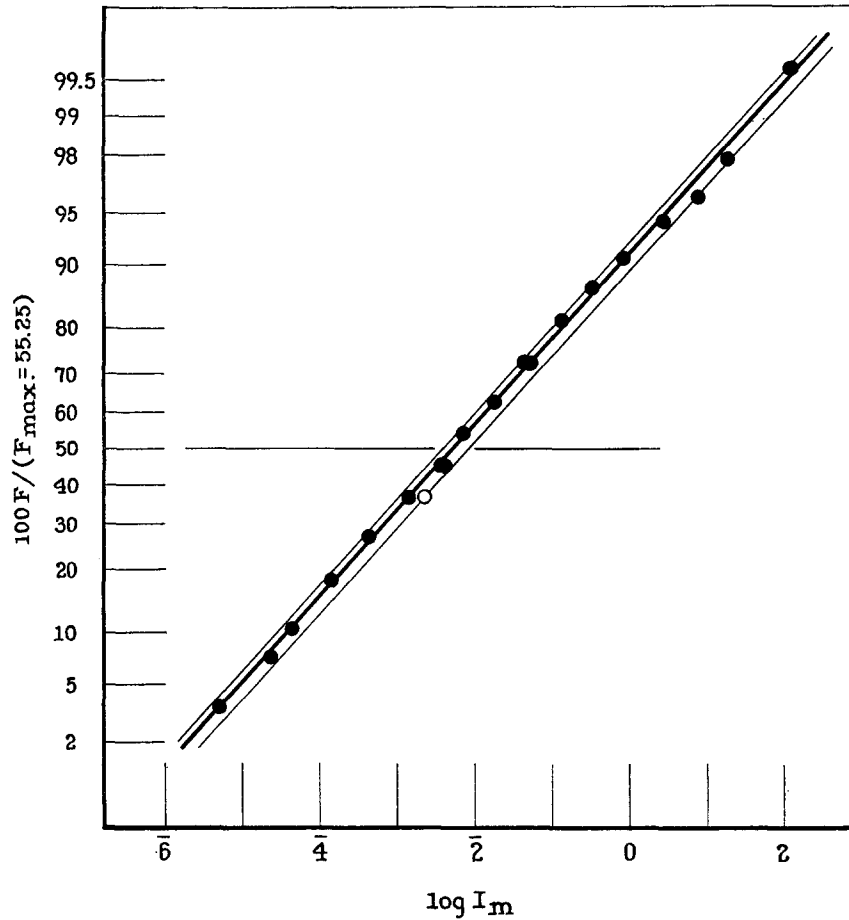

Fig. 2. The graph of Fig. 1 on a probability grid; see text

form of the F — log I curve could be influenced, or even determined, by the "visual acuity" curve of the human observer. The latter is unquestionably a duplex affair (*cf.* Hecht, 1937); consequently, having decent respect for the probability that serious observers are likely to be rationally sophisticated with reference to such a point, it is only necessary to refer to the fact that within the low intensity range concerned the observers find (*a*) specific types of duplexity in the response contours of diverse vertebrates (*cf.* Crozier, Wolf, and Zerrahn-Wolf, 1937–38; Crozier and Wolf, 1938–39,

1939–40 a, b, d, etc.), but also (b) perfectly symmetrical lower ends to the visual response contour, in *Pseudemys*, in the gecko, in *Asellus* (Crozier, Wolf, and Zerrahn-Wolf, 1938–39 b), and in the present data on the finch. The simplex or the duplex character of the various measured curves therefore cannot possibly be regarded as due to the visual limitations of the human observer.

The existence of simplex performance contours for certain vertebrates permits an empirical test of the proposition (Hecht, 1938) that their F — log
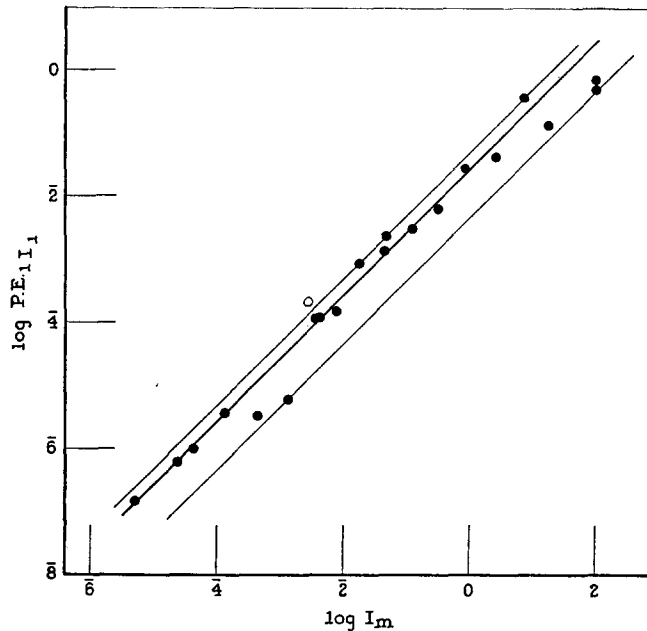

FIG. 3. The observed variation of critical flash intensity (Table I) is randomly distributed in direct proportion to I_m.

I curves can be described on the basis of photostationary state equations. We have already pointed out that, so far as concerns this situation in general, the properties of the flicker response contour are in unmistakably fundamental opposition to the idea that its shape permits deductions as to the physicochemical basis of the primary process of receptor excitation by light (cf. Crozier, Wolf, and Zerrahn-Wolf, 1938–39 b; Crozier and Wolf, 1939, 1939–40 a, 1940–41 b). It is of some formal consequence to show, however, that when the uncomplicated rod or cone curve for a vertebrate can be obtained with a known precision over an adequate range, it simply does not follow the course required by the existing photochemical theory of the properties of such data. In discussing this question we have in-

sisted on the significance of two quite different kinds of tests, namely: (1) those connected with the use of objective tests of curve fitting (with, from the classical standpoint, their inevitable limitations arising from the use of homogeneous data); these cannot be used at all, of course, unless the standard deviations of the measurements are known; and (2) those tests, theoretically much more significant, which involve experimentally determined properties of parameters in proposed descriptions.

With respect to tests of the second kind it must be said that the definite results of experiments involving the alteration of temperature, light-time fraction in the flash cycle, and other variables, are fundamentally opposed to the photochemical hypothesis (cf. Crozier, Wolf, and Zerrahn-Wolf, 1938–39 a, etc.; Crozier and Wolf, 1939, 1939–40 a, c, 1940–41 b). Nevertheless it is important to demonstrate that, just as for other simplex response contours obtained (Crozier, Wolf, and Zerrahn-Wolf, 1938–39 a), the curve for the zebra finch, while being entirely consistent with description by a probability integral (Figs. 1 and 2) simply fails to be fitted by the stationary state equation. The demonstration involves two major considerations: (1) in vertebrates to which the photochemical stationary state formulation has been applied only the upper portion of the cone curve is directly exposed for analysis; the portion of this segment which is uncomplicated by the participation of rod effects may be really very small (cf. Crozier and Wolf, 1939–40 d, etc.); and (2), the shape of the low intensity rod segment of the typically duplex curve is commonly, in man for example, the result of a complex interaction with cone effects, as suitable elementary experiments amply demonstrate (e.g., Crozier and Wolf, 1940–41 b, etc.). Consequently, from the standpoint of mere curve-fitting, a primary significance attaches to the precise shape of the simplex contour for flicker recognition by a vertebrate, when this can be ascertained. Under the conditions of the present experiments it can be asserted that each F is effectively constant; we know that for any single measurement of I_c it is within less than 0.1 of the assigned value, while the precision with which I_m is determined is given by the fact that $\sigma_{\log I_m}$ is shown to be effectively constant. It follows that on a plot of $\log I_m$ vs. $\log F$ systematic departures from the stationary state equation have a significance very simple to test. The nature of the function is such that the tails are the most sensitive and significant regions.

In Hecht's (1938) scheme for such phenomena the finch data fall most nearly into line with his equation

$$Ik_1/k_2 = x^n/(a - x)^m,$$

when $n = m = 2$. For $n = m$, with any value, this equation is of course identical with the logistic $F/F_{max.} = 1/(1 + e^{-\rho \log I})$ (cf. Crozier, Wolf, and Zerrahn-Wolf, 1936–37; and Crozier and Wolf, 1939; 1939–40 a).

Consequently a plot of the data on a logistic grid should at once reveal the degree to which this particular formulation is adequate. It is apparent in this plotting that, as for *Pseudemys* and *Asellus* (Crozier, Wolf, and Zerrahn-Wolf, 1938–39 *b*), the deviations are systematic and insuperably great. Therefore on this purely formal ground the photostationary state equation for the flicker response contour is to be rejected. Above $F = 0.2\ F_{max}$. the description might not be regarded as impossibly bad, by criteria of mere inspection; this helps to explain why it has been found acceptable for the cone curves of vertebrates showing visual duplexity, since here the lower end of the curve is of course masked.

V

SUMMARY

The flicker response contour has been determined, with equality of light-dark time ratio, for the diurnal bird the Australian zebra finch. This bird has only cones in the retina. The curve of log critical intensity as a function of flash frequency is simplex, a normal probability integral. In this respect it is like that for other vertebrates not exhibiting visual duplexity. The parameters of the curve most closely approach those for the turtle *Pseudemys* (extrapolated to about the same temperature); it is not improbable that the approximation of these two curves would be less close for other values of the light-time fraction. Some points of interpretive visual theory are discussed in relation to the present measurements.

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