

THE FLICKER RESPONSE CONTOUR FOR THE GECKO (ROD RETINA)

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I

By cytological criteria the retina of the gecko is devoid of cones. The visual cells are structurally rods,¹ and are associated with a visual purple.² Determinations were made of the interdependence of flash frequency and flash illumination for threshold response to visual flicker, using the species *Sphaerodactylus inaguae* Noble. These measurements give a flicker response contour for flash cycles with equal light and dark times, at a particular temperature. The comparison of this function with that obtained for the turtle *Pseudemys*,³ with pure cone retina, provides material for critically evaluating certain aspects of the duplexity doctrine of visual performance in vertebrates.

The duplexity doctrine⁴ has endeavored to bring together the proof of the composite character of the curves of visual performance as seen in most vertebrates, the known presence in these animals of at least two chief histological types of receptor elements, the relations of these to the ethological types of predominantly diurnal or nocturnal activity, and the spatial distribution of excitability in the (human) retina. Retinal rods are held to be connected with scotopic, indistinct, colorless vision, cones with photopic vision, distinctness, and

¹ Rochon-Duvigneaud, A., *Ann. d'oculist*, November, 1917, 16. Detwiler, S. R., *J. Comp. Neurol.*, 1923, **36**, 125. Verrier, M. L., *Bull. biol. France et Belgique*, suppl. **20**, 1935, 140 pp.; 1937, **71**, 238.

² Detwiler, S. R., *J. Comp. Neurol.*, 1923, **36**, 125.

³ *Proc. Nat. Acad. Sc.*, 1938, **24**, 125, 216. *J. Gen. Physiol.*, 1938-39, **22**, 311.

⁴ Cf. citations in *Proc. Nat. Acad. Sc.*, 1938, **24**, 125; 1939, **25**, in press.

color. The measurement of the flicker response contour affords a precise estimate of important features of visual performance, since it depends upon a limiting case of intensity discrimination.⁵ The data³ on the turtle *Pseudemys*, with pure cone retina, gave an unequivocal instance of the direct correlation of one class of retinal elements with one class of excitation elements. The $F - \log I$ curve is here a simple probability integral over its whole extent, whereas for vertebrates having both rods and cones it is a duplex affair.⁶ This curve has the general properties ($F_{max.}$, position on the intensity scale, and standard deviation of the first derivative) characteristic of the so called cone section of the duplex $F - \log I$ curve for typical vertebrates. It is of considerable interest to discover if a known purely rod retina will provide a similar comparison with the so called rod segment of the duplex curves.

It could be expected that if this should be the case the $F - \log I$ contour for the gecko would be a single probability integral, not duplex, rising to a comparatively low maximum, having a comparatively large $\sigma'_{\log I}$ and a low value of the abscissa of inflection (τ'). In expecting a single simple curve we, of course, ignore possible effects associated with the occurrence of both single and double rods,² since in *Pseudemys*³ no complications are introduced by the existence of double cones.⁷ The maximum F expected (under the same conditions of experimentation) could well be higher than for the "rod" segment in duplex curves; this could be due simply to the presence of a relatively larger number of excitation elements. Conditions experimentally known to elevate $F_{max.}$ are increase of retinal area⁸ and decrease of the light time fraction in the flash cycle;⁹ these procedures also, and in the same proportion, lower τ' ; hence increase of $F_{max.}$ should in the gecko case be expected to tend to lower τ' , and thus to

⁵ *J. Gen. Physiol.*, 1935-36, **19**, 503; 1936-37, **20**, 393; 1937-38, **21**, 313.

⁶ *J. Gen. Physiol.*, 1935-36, **19**, 495; 1937-38, **21**, 17, 203, etc.

⁷ That such effects are not impossible (although certainly not demonstrated) was suggested by the tripartite character of the $F - \log I$ contour for the newt *Triturus* (*Proc. Nat. Acad. Sc.*, 1938, **24**, 125. *J. Exp. Zool.*, 1939, in press).

⁸ *J. Gen. Physiol.*, 1937-38, **21**, 223.

⁹ *J. Gen. Physiol.*, 1937-38, **21**, 313, 463.

assist rather than interfere in the analogy with rod properties in other vertebrates if the comparison is really appropriate.

For reasons which may be relevant and partly valid in the long run, it was suggested¹⁰ as a result of the analytical dissection of the duplex $F - \log I$ contour for fishes that the rod contribution might be found to decline at higher intensities, if it could be separately examined in isolation. It naturally does not necessarily follow that (in terms of the duplicity theory) the flicker curve (whatever it may prove to be) for a completely color-blind human being should exhibit this behavior; in the nature of the situation, one cannot very well demand to examine the retina in point under the microscope. From the standpoint of elementary logic a considerable fraction of the argumentation and interpretation involving the duplexity theory has been of an eminently circular character. Aside from all this, however, there is now a basis for the suggestion¹¹ that the decline of the rod curve may, in a duplex flicker contour, be the result of inhibitory influences due to the excitation of "cone"-connected elements.

II

A supply of the small nocturnal gecko *Sphaerodactylus inaguae* Noble was collected for us at Matthew Town, Great Inagua, Bahama Islands, by Mr. R. A. McLean in the summer of 1938. We are very grateful to him for this assistance, and for his bringing them to us. We are indebted to Dr. Thomas Barbour, Director of the Museum of Comparative Zoology, for his identification of the species.

The animals were kept in insectary cages, provided with pieces of broken flower pots giving dark recesses, and periodically supplied with living *Drosophila*. Over half the geckoes lived upwards of 3 weeks after arrival in Cambridge, at room temperature 26–27.5°.

The apparatus used for tests involving response to visual flicker¹² is such as to require that the animals tested be rather small (not over about 12 cm. long). The specimens of *Sphaerodactylus* were not over 7 cm. in length. With a terrestrial reptile one cannot maintain the same control of temperature as is possible with the small aquatic forms we have used hitherto. The mean temperature was reasonably constant, however, at 26.7°, with a P.E. of the dispersion of the readings on various days = 0.206°; the extreme deviations were at 26.4° and 27.1°.

¹⁰ *J. Gen. Physiol.*, 1936–37, **20**, 411; 1937–38, **21**, 17.

¹¹ *J. Gen. Physiol.*, 1938–39, **22**, 463. *Proc. Nat. Acad. Sc.*, 1938, **24**, 542.

¹² *J. Gen. Physiol.*, 1935–36, **19**, 495; 1936–37, **20**, 211.

The temperature of lizards is likely to be a little below that of the environment¹³ (due to evaporation of water), but probably by not more than 0.2°.

Sphaerodactylus is not particularly active in the daytime. There appeared to be no definite indication of periodicity in this respect, day or night. Individuals were taken at random, a group of 10 being used for each test. On each of these three observations were taken. The average of the individual means (I_1 or F_1) is recorded as I_m or F_m .¹⁴ The data are thus not homogeneous, since at the different points (Fig. 1) the individuals used are not the same group. The comparative general form of the $F - \log I$ contour was the primary objective. Each set of readings was preceded by 45 minutes dark adaptation. When tested by exposure to gradually increased flash intensities, or to gradually reduced flash frequencies with fixed intensities,¹⁵ the animal is usually motionless until at a certain level of I (or F) there occurs a bending of the head against the direction of movement of the revolving stripes, with head nystagmus. This is the threshold response.¹⁶ In some cases the gecko bends the head ventrally, and makes slight rotating motions with it. The critical readings were not based on this response, as it is difficult to see at low intensities. Head nystagmus occurs regardless of the position of the gecko in its jar, whether radially oriented with reference to the striped cylinder or parallel to the cylinder facing with or against the stripe motion. The response is inhibited by stereotropic effects if there is contact with the wall of the containing cylinder. The clearest threshold responses are obtained when the gecko is facing in the direction of rotation of the striped cylinder, but not parallel with the wall. The animals are so quiescent that they may be put in this position before observation is begun. Adaptation during the observations is not a factor; a series of as many as twelve readings taken in succession shows no trend in the critical intensity over some 10 minutes.

III

Table I contains the results of determinations of critical flash frequency at fixed flash intensities, and of critical illumination at fixed flash frequencies. The flash cycle was of equally long light and dark intervals. The slit iris in the gecko is highly active. A plot of the measurements in Table I, given in Fig. 1, shows that below flash intensities *ca.* 0.0002 millilambert the critical intensity at given flash frequency is abnormally lowered. This implies that at these lower

¹³ Cf. Hoagland, H., 1927-28, *J. Gen. Physiol.*, **11**, 715.

¹⁴ *Proc. Nat. Acad. Sc.*, 1936, **22**, 17; 1937, **23**, 23. *J. Gen. Physiol.*, 1936-37, **20**, 211, *etc.*

¹⁵ *J. Gen. Physiol.*, 1936-37, **20**, 211, 363.

¹⁶ Loeb, J., *Arch. ges. Physiol.*, 1891, **49**, 175. Ehrenhardt, H., *Z. vergleich. Physiol.*, 1937, **24**, 248. Öhm, J., *Arch. Ophth.*, Leipsic, 1931, **126**, 547.

TABLE I

Mean critical flash frequencies (F per sec.) at fixed flash intensities (milli-lamberts) for the gecko *Sphaerodactylus*. Flash cycle with light time (t_L) equal to dark time (t_D). Temperature = $26.7^\circ \pm 0.06^\circ$. At each point three observations were taken on each of 10 individuals, but not the same 10 individuals; the data are thus not truly homogeneous; in three instances ($\log I = 2.5, 1.5, 1.5$) the differences between the means from duplicate tests exceed expectation. P.E. $_{1F_1}$ is the P.E. of the dispersion from which F_m is computed (see text).

$\log I$	F_m	P.E. $_{1F_1}$
$\bar{6}.50$	1.74	0.0988
	1.79	0.0454
$\bar{5}.00$	2.62	0.0249
$\bar{5}.50$	3.45	0.137
	3.46	0.0231
$\bar{4}.00$	4.30	0.0695
$\bar{4}.50$	5.33	0.153
$\bar{3}.00$	6.94	0.102
$\bar{3}.50$	8.89	0.124
$\bar{2}.00$	11.22	0.0570
$\bar{2}.50$	13.29	0.142
	13.93	0.118
$\bar{1}.00$	15.60	0.453
$\bar{1}.50$	17.47	0.530
	17.10	0.440
0.00	19.90	0.719
0.50	22.28	0.209
	21.70	0.168
1.00	23.16	0.447
1.50	24.20	0.642
	24.04	0.395
2.25	25.09	0.177

Mean critical flash intensities at fixed flash frequencies; conditions otherwise the same as in the converse tests.

F	$\log I_m$	$\log P.E._{1F_1}$
2.0	$\bar{6}.7475$	$\bar{7}.1430$
4.0	$\bar{5}.7561$	$\bar{6}.0398$
6.0	$\bar{4}.7137$	$\bar{5}.0708$
8.0	$\bar{3}.3043$	$\bar{5}.6486$
10.0	$\bar{3}.7523$	$\bar{4}.0233$
12.5	$\bar{2}.2353$	$\bar{4}.6856$
15.0	$\bar{2}.7898$	$\bar{4}.7343$
18.0	$\bar{1}.5032$	$\bar{3}.6329$
21.0	0.3646	$\bar{2}.6701$
24.0	1.4839	0.1038

flash intensities the iris opens. This interpretation agrees with direct inspection, and can be checked by the closing of the iris with pilocarpine (Table II); this raises the critical intensity, in this region of the distortion of the graph, to a level which is theoretically predictable (see below). On the other hand, attempting to increase the disten-

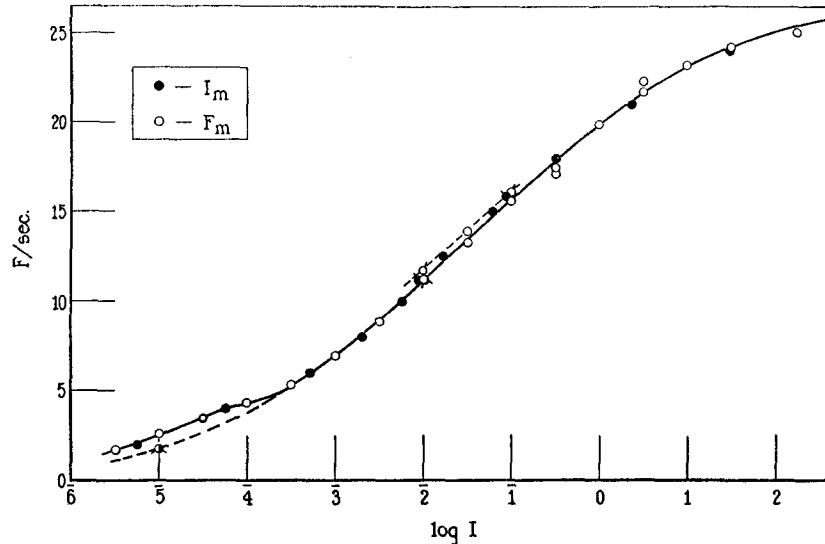


FIG. 1. Data in Tables I and II. The flicker response contour for the gecko *Sphaerodactylus*; temperature 26.7° , light time fraction in the flash cycle = 50 per cent. Below flash intensity = antilog *ca.* $\bar{4}.3$, the expansion of the iris opening increases the effective intensity (see text); points obtained with iris constricted by pilocarpine (Table II) are distinguished by lower tags; this effect is checked by the action of atropine, ineffective in modifying the curve below $\log I = \bar{4}.3$, but increasing the critical flash frequency at higher intensities where pilocarpine is without effect; points obtained after instillation of atropine bear upper tags. Open circlets, F_m ; solid circlets, I_m . The curve is obtained (*cf.* Fig. 4) as described in the text; it is a probability integral.

tion of the iris opening by instilling atropine solution (Table II) in this part of the graph produces no real effect on the critical intensity. In the upper portion of the graph (*cf.* Table II and Fig. 1), conversely, pilocarpine is without effect; but the opening of the iris under atropine lowers the critical intensity and raises the critical flash frequency.

The variation of I_1 follows the rule uniformly found¹⁷ in other cases: P.E. _{I_1} is directly proportional to I_m (Fig. 2), and the proportionality constant is of the same order of magnitude as in other animals. There is no break in the plot of log P.E. _{I} vs. log I_m , as in various other instances in which we deal with a single rather than a duplex population of elements of excitation.¹⁸

The variation of F_1 (Fig. 3), in correlation¹⁸ with the low slope of the $F - \log I$ curve (Fig. 1), is low. It clearly tends to pass through a maximum, just beyond the inflection of F vs. log I ,¹⁸ as in other cases. The relative scatter of P.E. _{F_1} is probably constant, as larger numbers of observations would make clearer. The

TABLE II

The effect of dilatation of the pupil of the gecko by *atropine* is to lower the critical intensity I_m for response to flicker at a fixed flash frequency F , or to raise the critical flash frequency F_m at a fixed flash intensity I . The normal values of F_m are taken from Table I, of I_m from the curve in Fig. 1. I_m and F_m were obtained from sets of three observations on each of 3 individuals (see text); the P.E.'s are for the dispersions. See Fig. 1.

log I	F_m	F	log I_m	log P.E. _{I_1}
2.00	11.74 ± 0.108 11.22 ± 0.0570	11.2	3̄.9437 2̄.00	4̄.6551
1.00	16.10 ± 0.211 15.60 ± 0.453	15.8	2̄.9426 1̄.03	3̄.5611

The result of constricting the pupil by *pilocarpine* is the reverse of the above, and is more pronounced at the lower end of the F -log I curve:

5.00	1.781 ± 0.115 2.62 ± 0.0249	1.8	5̄.0082 5̄.500	7̄.4701
2.00	11.13 ± 0.147 11.22 ± 0.0570	11.2	2̄.0107 2̄.00	4̄.5430

extent of this scatter is influenced by the fact that the 10 individuals used were not the same for the different tests. This probably also accounts for the fact that the F_m points (Fig. 1) do not clearly fall above^{15, 18} the curve for I_m , as theoretically required and found for homogeneous data. In the analysis (Fig. 4) of the F_m and I_m curves, however, it is clearly necessary to assign a slightly higher maximum F for the F_m data, as theory¹⁷ requires.

¹⁷ *J. Gen. Physiol.*, 1935-36, **19**, 503; 1937-38, **21**, 313, etc.

¹⁸ *J. Gen. Physiol.*, 1938-39, **22**, 311, 451; 1936-37, **20**, 363; 1938-39, **22**, in press.

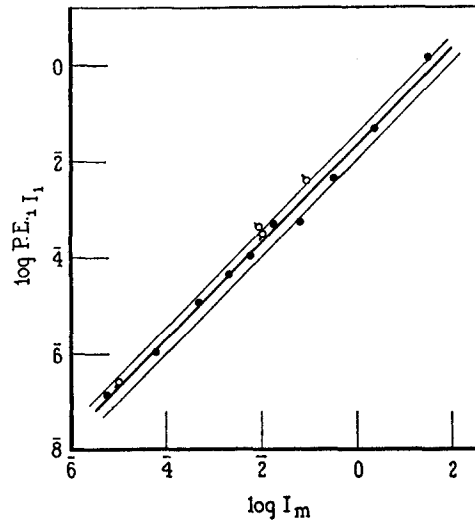


FIG. 2. $\log P.E._1 I_1$ vs. $\log I_m$. The proportionality of the variation of critical intensity to mean critical intensity is simple and direct (the slope of the line—band—is unity). Data in Tables I and II; symbols as in Fig. 1.

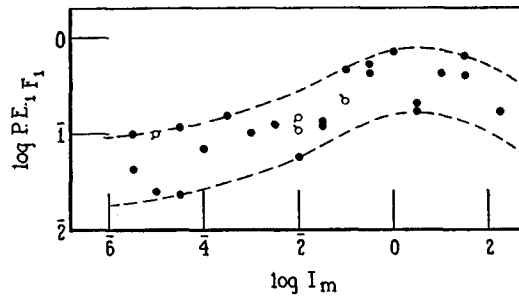


FIG. 3. $P.E._1 I_1$ as a function of $\log I$. $P.E._1 I_1$ is plotted on a logarithmic scale, since $\sigma_{P.E.}$ is proportional to P.E. if the material is sufficiently homogeneous, and the vertical spread of the band in this plot should therefore be constant.

IV

Taking into account the correction for the activity of the iris, considering that below $\log I = 4.3$ the opening of the iris mechanically distorts the plot (Fig. 1) by altering the intensity scale, we may test

the application¹⁹ of the probability integral by means of the graph in Fig. 4. For the F_m data (Table I), $F_{max.}$ is taken as 26.79; for the I_m measurements, $F_{max.} = 26.51$. The position of the points with iris constricted by pilocarpine is also indicated in Fig. 4. The description of the data is clearly adequate. The curve drawn in Figs. 1 and 5

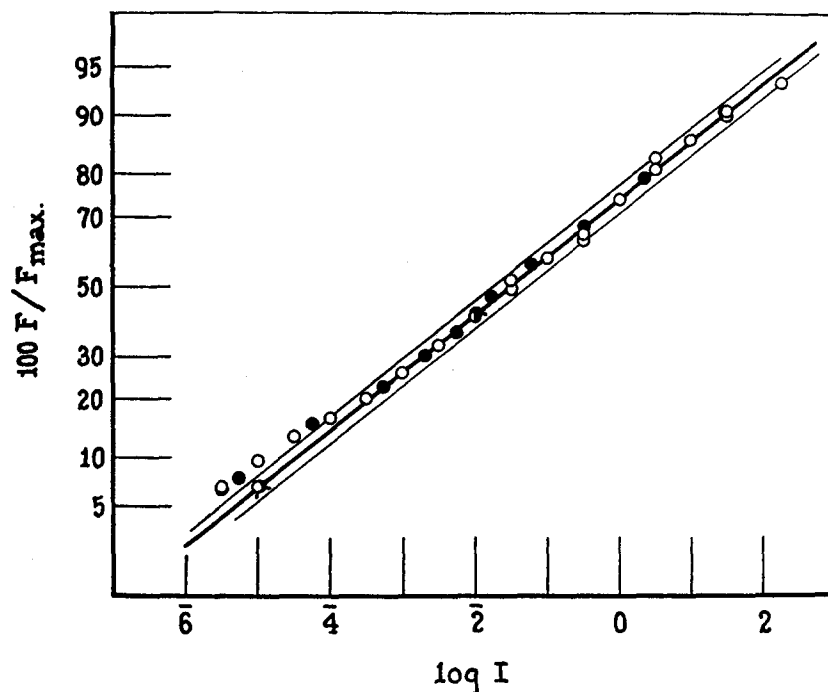


FIG. 4. The data of Table I on a probability grid (see also Fig. 1). Discussed in the text. For I_m , solid dots, $F_{max.} = 26.51$; for F_m , open circles, $F_{max.} = 26.79$; see text. The deviation at the lower end, and the significance of the circles with tags, are discussed in the text and in the legend of Fig. 1.

is the average of the two very slightly different ones shown superimposed in Fig. 4 (*i.e.*, with the slightly different values of $F_{max.}$ each made equal to 100 per cent).

The analytical form of the $F - \log I$ contour for the gecko is there-

¹⁹ *Proc. Nat. Acad. Sc.*, 1937, **23**, 71; 1938, **24**, 125. *J. Gen. Physiol.*, 1937-38, **21**, 17; 1938-39, **22**, 311, 451.

fore the same as for other animals.¹⁹ Particular effort was made to detect any downward swing at the upper end of the curve, but within the limit of intensity afforded by the apparatus it does not materialize.

The value of $F_{max.}$ is lower than any previously found for other dark adapted vertebrates, or for invertebrates. This could result from the small size of the population of sensory units. The inflection point in the curve comes at a level of τ' which corresponds to that for the cone curves of vertebrates in general. Comparison with the flicker contour for the turtle, *Pseudemys*, having purely cone retina,³ is most clearly made by bringing the respective curves to the same value of $F_{max.} = 100$ per cent. This does not change τ' , and allows the comparison of the spread constants ($\sigma'_{\log I}$) since the form of the function is the same in the two cases. The data were obtained by the same procedure and with the same apparatus. Under given conditions (*i.e.*, of light time cycle-fraction, and constancy of retinal area) $F_{max.}$ is specific for the type of animal and is not directly correlated with τ' or $\sigma'_{\log I}$. The comparison of the two curves on this basis is given in Fig. 5.

The gecko's flicker discrimination covers the same range of intensities as does that of the turtle. The temperature differs—for the turtle measurements, 21.5°; for the gecko, 26.7°. Using the temperature characteristic found³ for the turtle, its curve is moved to the left to correspond to temperature 26.7°. The respective abscissae of inflection (τ') with this shift then differ by *ca.* 0.08 unit. The values of $\sigma'_{\log I}$ differ by less than do those for the cone segments of the curves for different kinds of fishes or other vertebrates.^{10, 11}

The largest rod curve we have thus far encountered is in the teleost *Fundulus*.²⁰ In this case the descriptive parameters are $F_{max.} = 9.05$; $\tau' = \bar{5}.06$; $\sigma'_{\log I} = 0.66$. This is the closest approach we have to the curve for the gecko, and the differences (the particularly significant differences involve τ' and $\sigma'_{\log I}$) are in fact huge; the values for *Sphaerodactylus* are $\tau' = \bar{2}.49$, $F_{max.} = 26.5$, $\sigma'_{\log I} = 1.03$.

The closeness of agreement of the parameters τ' and $\sigma'_{\log I}$ for gecko and turtle is, of course, accidental. Data on two kinds of turtles would probably differ more. But it is evident that these observations do not support the idea that a rod retina necessarily functions best

²⁰ *J. Exp. Zool.*, 1939, in press.

at low illuminations, even in a nocturnal animal. Nor is it indicated that a rod retina performs less ably than a cone retina at high illuminations. The danger of associating histological appearance and functional capacity in matters of visual performance is sharply emphasized.

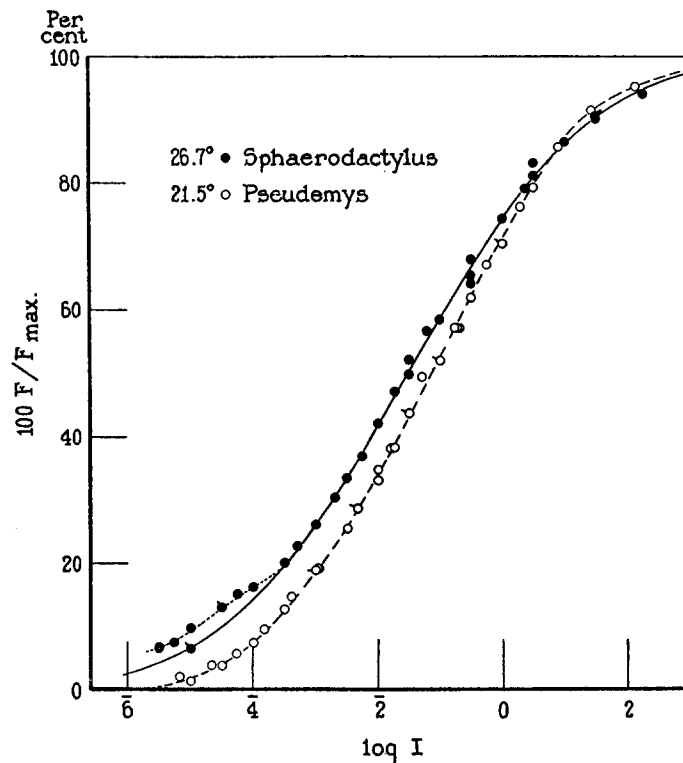


FIG. 5. The flicker response contour for the gecko (*rod* retina, at 26.7°) and for the turtle (*cone* retina), with $F_{max.} = 100$ per cent in each case.

The analysis of various visual functions among vertebrates demonstrates the presence of two constituent populations of sensory effects in many forms. These must be separately dealt with on the basis of their respective quantitative properties. The assumption that these two populations are directly due to the histological and chemical differentiation of the receptive units into rods and cones implies that

the quantitative properties of the data of visual performance in the various types of intensity discrimination are taken to be determined by quantitative properties of the rods and cones respectively. This assumption is arbitrary, unnecessary, and probably wrong.²¹ The histological contribution to the assumption from the side of comparative properties of rods and cones in various animals is manifestly of small significance when the quantitative properties of visual performance in animals with purely rod and purely cone retinas are found to be essentially identical.²²

SUMMARY

The flicker response contour for the gecko *Sphaerodactylus* (retina with only rods) agrees in all essential respects (intensity range, shape) with that for the turtle *Pseudemys* (cone retina), as determined under equivalent conditions with the same apparatus. With experimentally determined correction for the expansion of the iris at the very lowest intensities, the $F - \log I$ contour for the gecko is a simple probability integral. Its maximum F is lower than that for other animals; this means simply a smaller number of available sensory elements. The quantitative parallelism in the magnitudes of the intensities at the inflection of $F - \log I$ and the shape constants for rod and cone animals show that assumptions from comparative histological evidence concerning the properties of rods and cones in relation to visual performance may be quite misleading.

²¹ *J. Gen. Physiol.*, 1938-39, **22**, 341.

²² The difficulties of the situation cannot be escaped, logically, by suggestion that the gecko possesses a peculiar kind of retinal rod; this merely destroys the complex accepted conception of rod with which we started.