

THEORY AND MEASUREMENT OF VISUAL MECHANISMS

XII. ON VISUAL DUPLEXITY

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I

That the visual performance of vertebrates in general involves the separable functioning of two essentially different, morphologically distinguishable classes of retinal sensory units is a doctrine, the duplexity theory, which has developed from the suggestion of Schultze (1866). In outline, the proposition that retinal rods are concerned with visual responses at lower illuminations, cones with excitation at higher intensities,¹ is based upon correlations between retinal structure and the ethology of various animals, their nocturnal or diurnal activities; as well as upon the properties of photic excitability in different parts of the human retina.² These and developing related considerations, taken as a whole, led to the current very general view that retinal rods and their associated visual purple are connected with indistinct, colorless, scotopic vision, cones with distinct, colored, photopic vision. Thus, despite the sometimes considerable difficulty in the way of histological classification of photoreceptor units into two essential categories, even in a single retina, and certainly of regarding these as invariable, exclusive types in the vertebrate series,³ the

¹ von Kries, J., Zur Theorie des Tages- und Dämmerungssehens, in 1929, Handbuch der normalen und pathologischen Physiologie, (A. Bethe, G. von Bergmann, G. Embden, and A. Ellinger, editors), Berlin, Julius Springer, **12**, pt. 1, 678. Arey, L. B., in 1932, Special cytology, (E. V. Cowdry, editor), New York, Paul B. Hoeber, Inc., 2nd edition, **3**, 1213. Granit, R., 1936, Die Elektrophysiologie der Netzhaut. . . ., Copenhagen. Hecht, S., 1937, *Physiol. Rev.*, **17**, 239. von Studnitz, G., 1940, Physiologie des Sehens Probleme der Biologie, Leipzig, Akademische Verlagsgesellschaft, **3**. Polyak, S., 1941, The retina, Chicago, University of Chicago Press. Walls, G. L., 1942, The vertebrate eye and its adaptive radiation, *Cranbrook Inst. Sc., Bull.*, **19**, Bloomfield Hills, Michigan. Detwiler, S. R., 1943, Vertebrate photoreceptors, Experimental Biology Monographs, New York, Macmillan.

² Cf. Hecht, S., 1937, *Physiol. Rev.*, **17**, 239; Crozier, W. J., and Wolf, E., 1941-42, *J. Gen. Physiol.*, **25**, 369.

³ Cf. Tschermak, A., in 1929, Handbuch der normalen und pathologischen Physiologie, (A. Bethe, G. von Bergmann, G. Embden, and A. Ellinger, editors), Berlin, Julius Springer, **12**, pt. 1, 295. Menner, E., 1928, *Z. vergleich. Physiol.*, **8**, 761. Walls, G. L., 1934, *Am. J. Ophth.*, **17**, 892. Verrier, M.-L., 1935, *Bull. biol. France et Belgique*, **20**, suppl.; 1937, *Bull. biol. France et Belgique*, **71**, 238; 1938, **78**, 355.

ordinary assumption has come to be that the high-intensity and the low-intensity segments of duplex curves of visual performance represent respectively the quantitative properties of cones and of rods.

Despite the occurrence, in many forms, of more than simply two structural types of retinal receptor units, only in one case has the probable occurrence of three distinguishable parts to the visual performance contour been recognized.⁴ The phenomena of their photomechanical and otherwise experimentally induced movements,⁵ and of "spontaneous" movements,⁶ frequently serve additionally to separate the photoreceptor units into two distinct morphological categories, the histological types labelled rods and cones. In each such instance that has also been examined functionally a duplex performance contour (flicker; white light) has been found.⁷ Whereas, within the fovea of man and in forms with simplex retinas, only simplex performance contours (flicker) have been found.⁸ New illustrations are given in the present paper. In this sense, a basic feature of the duplexity rule is shown to be valid; that is, a retina obviously not simplex is correlated with a duplex (flicker) performance contour.⁹

We must be careful, however, not to proceed to the mistake of assuming that the quantitative properties of the scotopic and photopic portions of duplex contours are directly those of rods and of cones respectively. Even if they are determined at the retina, or are in simple proportion to retinal properties, the performance data represent at best properties of complex assemblages of units, as their analytical discussion demonstrates. Nor does it follow that any given criterion (*e.g.*, even color perception¹⁰) will necessarily be diagnostic of rod or

Walls, G. L., 1942, The vertebrate eye and its adaptive radiation, *Cranbrook Inst. Sc., Bull.*, **19**, Bloomfield Hills, Michigan. Walls, G. L., 1942, The visual cells and their history, in *Visual mechanisms*, (H. Klüver, editor). Biological symposia, **7**, Lancaster, The Jaques Cattell Press, 203.

⁴ Crozier, W. J., and Wolf, E., 1939-40, *J. Gen. Physiol.*, **23**, 667.

⁵ *E.g.* Laurens, H., and Detwiler, S. R., 1921, *J. Exp. Zool.*, **32**, 207; Verrier, M.-L., 1935, *Bull. Soc. zool. France*, **15**, 193.

⁶ Welsh, J. H., and Osborn, C. M., 1937, *J. Comp. Neurol.*, **66**, 349. Arey, L. B., and Mundt, G. H., 1941, *Anat. Rec.*, **79**, suppl. 2, 5.

⁷ Wolf, E., and Zerrahn-Wolf, G., 1935-36, *J. Gen. Physiol.*, **19**, 495; Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., 1936-37, *J. Gen. Physiol.*, **20**, 211, 411; 1937-38, **21**, 17, 203, 313; 1938-39, **22**, 463; Crozier, W. J., and Wolf, E., 1939-40, **23**, 229, 667; 1943-44, **27**, 315.

⁸ Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., 1938, *Proc. Nat. Acad. Sc.*, **24**, 125, 216; Crozier, W. J., and Wolf, E., 1938, *Proc. Nat. Acad. Sc.*, **24**, 538; Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., 1938-39, *J. Gen. Physiol.*, **22**, 311, 555; 1939-40, **23**, 531; 1940-41, **24**, 317, 625; 1941-42, **25**, 369, 381; 1943-44, **27**, 119, 287.

⁹ 1938, *Proc. Nat. Acad. Sc.*, **24**, 125.

¹⁰ *Cf.* Wald, G., 1941, *J. Opt. Soc. America*, **31**, 461. Lewis, S. D., and Mandelbaum, J., 1943, *Arch. Ophthalm.*, **30**, 225.

cone functioning. What one is required to say is that, in duplex performance curves we have to do with the occurrence of two populations of neural effects in the constitution of the response contour.¹¹ This might well be found to occur in cases where only "cones" or only "rods" are revealed by ordinary histological inspection, but where either might really include more than one functional type. Reciprocally, it might easily happen that a structurally duplex retina should be associated with a simplex performance curve, but this we have not thusfar found. It is true that even within the fovea certain kinds of effects, involving intensity, image area, exposure-time, and wave-length, are not exactly "simplex";¹² but these questions are of a different sort. We may also put to one side the details of interrelationships between "rod" effects and "cone" effects, in recognition of flicker for example,¹³ as revealed by the analytical dissection of compound contours, although it is to be noted that a proof is obtained that two independently modifiable groups of neural effects are represented in duplex contours. This is, however, an important part of the question as to the extent to which the "raw" data of performance as a function of intensity can be taken as a direct description of the properties of assemblages of neural units. The analytical form of the separated "rod" and "cone" performance contours is found to be of the same kind as when "rod" and "cone" properties can be dealt with quite independently, in the same retina¹⁴ or in different kinds of animals,¹⁵ and also in cases involving threshold discriminations where no integration of the two sets of effects may occur.¹⁶ These contours reflect, in their form and in the properties of their implicit parameters, the statistical attributes of effects due to assemblages of neural units.¹⁷ These properties are unequivocally not consistent with the view¹⁸ that the shapes of the performance contours as function of intensity reveal the organization of the physicochemical systems in rods and in cones which make excitation possible.¹⁹ Moreover, there is specific, quantitative evidence demonstrating that differ-

¹¹ 1938, *Proc. Nat. Acad. Sc.*, **24**, 538; 1938-39, *J. Gen. Physiol.*, **22**, 555.

¹² Cf. 1943-44, *J. Gen. Physiol.*, **27**, 119 (p. 122); Walters, H. V., and Wright, W. D., 1943, *Proc. Roy. Soc. London, Series B*, **131**, 340.

¹³ Cf. 1937-38, *J. Gen. Physiol.*, **21**, 17, 203, 313; 1938-39, **22**, 463; 1939-40, **23**, 229, 667, 677; 1940-41, **24**, 505, 635; 1941-42, **25**, 89, 293, 369; 1943-44, **27**, 287, 315, 401.

¹⁴ 1941-42, *J. Gen. Physiol.*, **25**, 369.

¹⁵ 1938, *Proc. Nat. Acad. Sc.*, **24**, 125, 538; 1938-39, *J. Gen. Physiol.*, **22**, 311, 451, 555; 1940-41, **24**, 317, 625; 1941-42, **25**, 381.

¹⁶ 1940, *Proc. Nat. Acad. Sc.*, **26**, 334, 382.

¹⁷ Cf. 1943-44, *J. Gen. Physiol.*, **27**, 119, 287, 401.

¹⁸ Hecht, S., 1937, *Physiol. Rev.*, **17**, 239; *Harvey Lectures*, 1937-38, **33**, 35.

¹⁹ 1937-38, *J. Gen. Physiol.*, **21**, 313, 463; 1938-39, **22**, 311, 487, 795; 1939, *Proc. Nat. Acad. Sc.*, **25**, 171; 1939-40, *J. Gen. Physiol.*, **23**, 143, 531; 1940-41, **24**, 505, 635; 1941-42, **25**, 89, 293, 369; 1943-44, **27**, 119, 287, 315.

ences in the shapes of "rod" and "cone" contours cannot be taken to signify differences in the physicochemical basis of excitation: the τ' constants (= abscissæ of inflection) of "rod" and "cone" components of duplex flicker contours in particular kinds of vertebrates are affected to the same extent by changes of temperature and of light-time fraction in the flash cycle.²⁰ Conversely, there is reasonable indication that differences in the forms of simplex contours, in a single animal, as a function of wave-length of light, cannot be taken to indicate differences in the photochemical basis of excitation.²¹ Nevertheless it is perfectly clear that the two groups of neural effects distinguishable in flicker contours for visually duplex vertebrates are organically distinct, although integratively related. They are separately modifiable by change of wave-length composition,²² retinal location,²³ subdivision of the image,²⁴ and by the introduction of the "pecten effect".²⁵ Their common quantitative dependence upon such variables as light-time fraction and temperature, already referred to, the quantitative character of the variation of performance in flicker recognition,²⁶ the properties of binocular simultaneous flicker,²⁷ all these are consistent with the conception that, although organically separable, the "rod" and "cone" populations of neural effects are intimately related in particular ways at the same general central nervous locus. Although the mass of this evidence is derived from the use of the only convenient method for testing visual performance quantitatively in a considerable variety of animals, there is no good reason either to ignore its import or to suppose that in general other modes of visual response would really be likely to give evidence of a very different meaning.

Thus while the parameters of the flicker contour have reproducible, specific significance in terms of the organization of the animals tested,²⁸ and must be understood to be determined by the statistical organization of the neural systems producing them, it does not follow that for quite different animals performance contours will necessarily be diagnostic of the type of peripheral receptors in the retina. Nor ought it be expected that there should be found a simple correlation between behavior, in general, and retinal histology. It is well known that while such a correlation is sometimes quite striking, it is often

²⁰ 1936-37, *J. Gen. Physiol.*, **20**, 411; 1940-41, **24**, 635.

²¹ 1943-44, *J. Gen. Physiol.*, **27**, 119.

²² 1941-42, *J. Gen. Physiol.*, **25**, 293; 1943-44, **27**, 119.

²³ 1941-42, *J. Gen. Physiol.*, **25**, 293; paper XIV, data to be published.

²⁴ 1943-44, *J. Gen. Physiol.*, **27**, 401.

²⁵ 1943-44, *J. Gen. Physiol.*, **27**, 287, 315.

²⁶ 1940-41, *J. Gen. Physiol.*, **24**, 505, 635; 1941-42, **25**, 293; 1943-44, **27**, 119.

²⁷ 1940-41, *J. Gen. Physiol.*, **24**, 505.

²⁸ 1937, *Proc. Nat. Acad. Sc.*, **23**, 516; 1938, **24**, 221; 1939, **25**, 171, 176, etc.

decidedly blurred.²⁹ We have already pointed out³⁰ that in essential respects (intensity range, slope constant) the flicker response contour for a nocturnal gecko (exclusively rod retina) can be practically identical with that for a sun-seeking turtle (with exclusively cone retina).³¹

We have sought to examine, in relation to these questions, flicker response contours from additional animal forms, several of which are here considered, with particular reference to the problem of correlations between visual performance and retinal organization. There are two chief points: (1) Is visual duplexity correlated with a retinally duplex structure, and (2) can quantitative performance properties in general be correlated with "rod" and "cone" categories of visual excitability? The examination of relevant data shows that the answer to (1) is, Yes; to (2), for an interestingly complex reason, the answer is, No.

II

Flicker contours were determined, by the method already described in detail,³² for the Florida "chameleon" *Anolis carolinensis* and for a soft-shelled turtle, *Trionyx (Amyda) emoryi* (Agassiz).³³ After completion of the observations, made in October and November, eyes of each were sectioned³⁴ and examined microscopically. The prediction from the nature of the flicker curves was that *Anolis* might have a simplex retina, *Trionyx* a duplex one;³⁵ this was found.

Anolis was studied after 45 minutes dark adaptation, using vigorously reactive individuals at air temperature $23.5^\circ \pm 1^\circ$. The responses to rotating stripes at the critical intensity involve a head motion up to 120° of turning in the direction of the movement of the stripes, then a quick "return." At $t_L = 0.10$ and 0.25 the response is less sharp than at higher values of t_L , particularly at lower intensities. At higher intensities the critical responses tend to be of smaller amplitude, and may even be

²⁹ Verrier, M.-L., 1932a, *Arch. zool. exp.*, **84**, 305; 1932b, *Compt. rend. Acad. sc.*, **195**, 1333; 1933c, *Bull. biol. France et Belgique*, **67**, 350. Detwiler, S. R.,¹ chapter V.

³⁰ 1938, *Proc. Nat. Acad. Sc.*, **24**, 538; 1938-39, *J. Gen. Physiol.*, **22**, 555.

³¹ For some reason which we do not understand Walls¹ speaks repeatedly of "the nocturnal *Pseudemys*;" statements about the retinas of such forms may be correct, but do not accord with the structural picture in our sections of the individuals we have used, nor with the habitual behavior we have described.

³² 1935-36, *J. Gen. Physiol.*, **19**, 495; 1936-37, **20**, 211; 1939-40, **23**, 531.

³³ We are obliged to Mr. A. Loveridge, of the Museum of Comparative Zoology, Harvard University, for the identification.

³⁴ Mr. D. M. Easton, to whom we are grateful, prepared these sections.

³⁵ Gillett, W. G., 1925, *Am. J. Physiol. Opt.*, **6**, 592, reported "only cones" in the retina of an *Amyda*.

reduced to a flickering movement of the eyeballs if the lizard has become comparatively rigid in posture; temporary reduction of I generally induced relaxation and freer responses under these conditions. The tests were made with three values of light-time fraction, $t_L = 0.10, 0.50, 0.90$.

TABLE I

Critical flash intensities (I_m) for response to flicker as a function of flash frequency F , at three values of the light-time fraction t_L , with *Anolis* ($22.8^\circ \pm 1^\circ$).

F per sec.	$t_L = 0.10$		$t_L = 0.50$		$t_L = 0.90$	
	$\log I_m$	$\log P.E._1$	$\log I_m$	$\log P.E._1$	$\log I_m$	$\log P.E._1$
1					$\bar{2}.4655$	$\bar{3}.5222$
2			$\bar{3}.9429$	$\bar{4}.9821$	$\bar{2}.6959$	$\bar{3}.3039$
			$\bar{3}.9417$	$\bar{4}.1521$		
3			$\bar{2}.1538$	$\bar{4}.9364$		
			$\bar{2}.1644$	$\bar{4}.8206$		
5			$\bar{2}.3777$	$\bar{3}.0827$	$\bar{1}.1075$	$\bar{3}.8796$
					$\bar{1}.1137$	$\bar{2}.0231$
7			$\bar{2}.5501$	$\bar{3}.2579$	$\bar{1}.2749$	$\bar{3}.9239$
10	$\bar{2}.0515$	$\bar{4}.9714$	$\bar{2}.8617$	$\bar{3}.6556$	$\bar{1}.4291$	$\bar{3}.8316$
					$\bar{1}.4918$	$\bar{3}.9090$
15	$\bar{2}.3906$	$\bar{4}.8728$	$\bar{1}.0993$	$\bar{3}.5145$	$\bar{1}.8067$	$\bar{3}.5598$
20	$\bar{2}.6387$	$\bar{3}.1181$	$\bar{1}.2781$	$\bar{3}.6306$	0.0037	$\bar{2}.3935$
			$\bar{1}.2983$	$\bar{3}.8080$		
25	$\bar{2}.8857$	$\bar{3}.7382$	$\bar{1}.5183$	$\bar{2}.2085$	0.2477	$\bar{2}.7734$
30	$\bar{1}.0535$	$\bar{3}.7068$	$\bar{1}.7392$	$\bar{2}.0000$	0.4713	$\bar{2}.8093$
35	$\bar{1}.2054$	$\bar{3}.4550$	$\bar{1}.8958$	$\bar{2}.5120$	0.6172	$\bar{1}.0496$
40	$\bar{1}.4031$	$\bar{2}.1803$	0.1127	$\bar{2}.4913$	0.8389	$\bar{1}.1839$
43			0.3092	$\bar{2}.9763$		
45	$\bar{1}.7143$	$\bar{3}.8674$			1.1790	$\bar{1}.8796$
47			0.6145	$\bar{1}.1013$		
48	$\bar{1}.8893$	$\bar{2}.1495$			1.4584	0.3514
50	0.2151	$\bar{2}.3206$	0.9652	$\bar{1}.3636$	1.8731	0.1736
	0.1644	$\bar{2}.8153$				
52			1.1440	$\bar{1}.3734$	2.0734	0.2633
53	0.5591	$\bar{1}.1534$	1.2987	$\bar{1}.8796$		
	0.4465	$\bar{1}.0039$				
54			1.5290	$\bar{1}.8517$		
55	1.2100	$\bar{1}.9612$	1.9777	0.3132		
	0.8157	$\bar{1}.7814$				
57	1.9848	$\bar{1}.8887$				

The averages of critical flash intensities entered in Table I are derived from three measurements with each of the same five individuals throughout. As shown in Fig. 1, each contour is accurately described by a probability summation. The curve moves to higher intensities as t_L is increased, in the usual way, and $F_{max.}$ is lowered. Fig. 2 shows that the parameter $\sigma'_{\log I}$ is constant, since on the probability grid the lines through the data are parallel. These

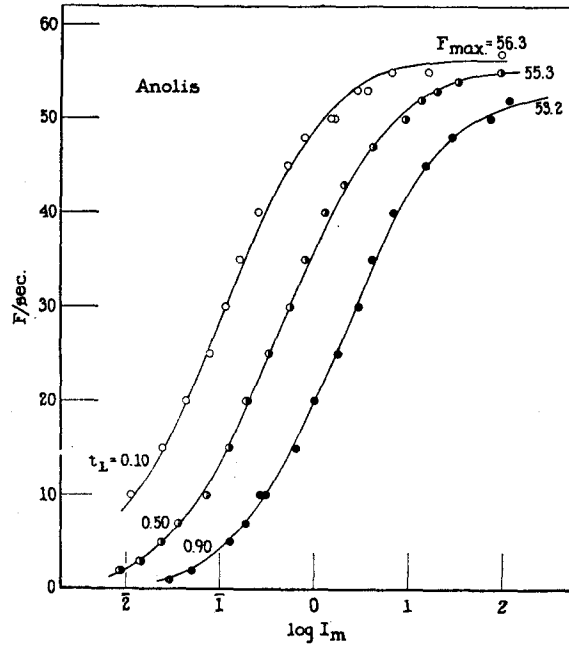


FIG. 1. Flicker contours for *Anolis*, with three light-time fractions. Data in Table I. The curves are probability integrals (cf. Fig. 2), calculated to the asymptotic maxima indicated.

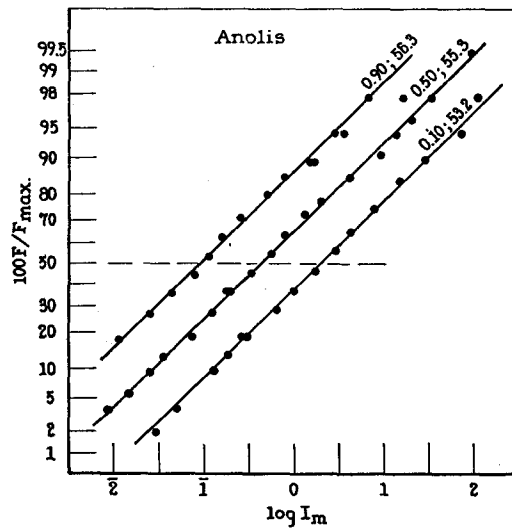


FIG. 2. Flicker response data for *Anolis* (Fig. 1) shown on a probability grid. The slopes for the three light-time fractions, and hence $\sigma'_{\log I}$, are the same.

relations are those found in other cases examined.²⁰ The relation of F_{max} and of τ' , the abscissa of inflection, to t_L is rectilinear, as shown in Figs. 4 and 5.

The statistically constant relative variation of I_1 in the *Anolis* data is a little higher (N is smaller) than in our series with fishes,³⁶ gecko,³⁰ crayfish,³⁷ *Anax*,³⁸ about the same as that with *Pseudemys*,³⁹ but lower than for *Phrynosoma*;⁴⁰ the mean value of P.E.₁/ I_m is 0.0316. The internal correlation of the meas-

TABLE II

Critical flash intensities (I_m) for response to flicker as a function of flash frequency F , at three values of the light-time fraction t_L , with *Trionyx* ($22.6^\circ \pm 1^\circ$).

F per sec.	$t_L = 0.10$		$t_L = 0.50$		$t_L = 0.90$	
	$\log I_m$	$\log P.E._1$	$\log I_m$	$\log P.E._1$	$\log I_m$	$\log P.E._1$
2	$\bar{4}.8844$	$\bar{5}.5831$	$\bar{3}.6083$	$\bar{4}.2887$	$\bar{2}.2720$	$\bar{4}.8907$
3	$\bar{3}.2417$	$\bar{5}.8061$	$\bar{2}.0241$	$\bar{4}.6254$	$\bar{2}.7162$	$\bar{3}.0648$
4	$\bar{3}.4352$	$\bar{4}.0172$				
5	$\bar{3}.6501$	$\bar{4}.2936$	$\bar{2}.4355$	$\bar{4}.8949$	$\bar{1}.1473$	$\bar{3}.5463$
8	$\bar{2}.0675$	$\bar{4}.2587$	$\bar{2}.8074$	$\bar{3}.0857$	$\bar{1}.5519$	$\bar{3}.3946$
10	$\bar{2}.2900$	$\bar{4}.9139$	$\bar{1}.0103$	$\bar{3}.6247$	$\bar{1}.7358$	$\bar{3}.6079$
15	$\bar{2}.5898$	$\bar{4}.7084$	$\bar{1}.2983$	$\bar{3}.6729$	0.0342	$\bar{2}.3467$
20	$\bar{2}.7747$	$\bar{3}.1361$	$\bar{1}.4946$	$\bar{2}.0188$	0.2274	$\bar{2}.5485$
25	$\bar{1}.0174$	$\bar{3}.5856$	$\bar{1}.7448$	$\bar{2}.2618$	0.4729	$\bar{2}.8739$
30	$\bar{1}.2475$	$\bar{3}.3167$	$\bar{1}.9566$	$\bar{2}.2294$	0.6710	$\bar{2}.9050$
35	$\bar{1}.4480$	$\bar{2}.0457$	0.1626	$\bar{2}.7938$	0.8818	$\bar{1}.3046$
40	$\bar{1}.7483$	$\bar{2}.0696$	0.4630	$\bar{2}.4198$	1.1903	$\bar{1}.7475$
45	0.0799	$\bar{2}.6477$	0.8257	$\bar{1}.2708$	1.6036	$\bar{1}.7672$
	(0.1377)	$\bar{2}.7329)$				
48	0.3109	$\bar{2}.3394$	1.2001	$\bar{1}.3320$	1.9931	0.2065
	(0.4866)	$\bar{2}.8552)$				
50	0.6974	$\bar{1}.2820$	1.5469	$\bar{1}.8507$		
	(0.9245)	$\bar{1}.5461)$				
51	1.1418	$\bar{1}.4465$				
	(1.4544)	$\bar{1}.7699)$				

urements²⁴ (among the *individuals*, here) is not too low (0.568 to 0.738) and τ is maximum at $t_L = 0.50$, as found for other instances.²⁴

The data on *Trionyx* are given in Table II.

These animals, young, kept in a shallow tank with sand and gravel, and fed with *Enchytraeus* and lettuce, were observed to be almost constantly buried in the mud

³⁶ 1937-38, *J. Gen. Physiol.*, **21**, 17; 1938-39, **22**, 463, etc.

³⁷ 1939-40, *J. Gen. Physiol.*, **23**, 1.

³⁸ 1936-37, *J. Gen. Physiol.*, **20**, 363, 393; 1937-38, **21**, 223, 463; 1938-39, **22**, 795.

³⁹ 1938-39, *J. Gen. Physiol.*, **22**, 311, 1939-40, **23**, 531.

⁴⁰ 1940-41, *J. Gen. Physiol.*, **24**, 317.

during the daytime. The same five individuals were used throughout, with 45 minutes preliminary dark adaptation. Each turtle was used with just a little water in its cylindrical container, the head protruding into air. The critical end-points were obtained from head nystagmus. In *Trionyx* these movements are less sharp, slower, and less extensive than in (young) *Pseudemys*.

Particular care was taken in the work at lower flash frequencies. The data show at these lower frequencies (Fig. 3) a persistent "bump." This is not

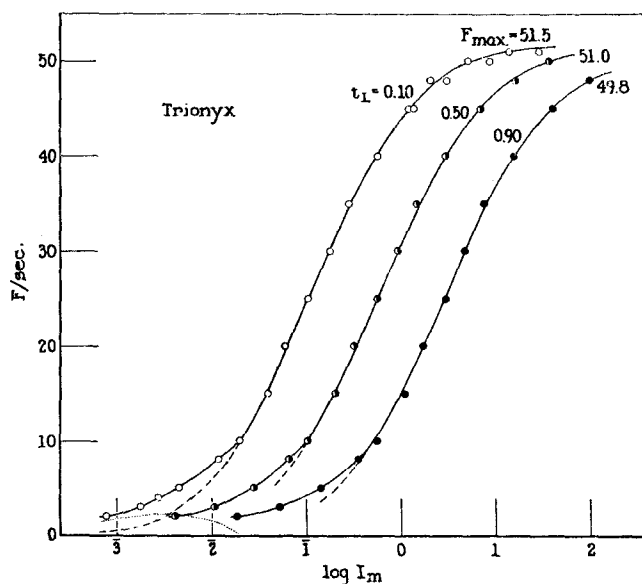


FIG. 3. Flicker contours for *Trionyx*, with three light-time fractions. Data in Table II. Above $F = 10$ the curves drawn are probability integrals calculated to the maxima indicated and with the same $\sigma'_{\log I}$. The departures below $F = 10$ are interpreted as due to a second group of excited neural units ("rods"). For $t_L = 0.10$ the difference curve as obtained in the usual way has been drawn. See text.

similar in shape to that found for the $F - \log I$ curve in the gecko.³⁰ It was not possible to secure responses below $F = 2$, but the behavior of this "tail" at the several light-times shows the "tail" to be not very probably due to iris (as in gecko case). Treated by the method of dissection⁴¹ the presumptive "rod" part is larger the greater t_L is.

As with frog⁴² and *Triturus*,⁴ the presumptive rod contribution to the $F -$

⁴¹ 1937-38, *J. Gen. Physiol.*, **21**, 17; 1938-39, **22**, 463; 1939-40, **23**, 677; 1940-41, **24**, 505, 635; 1941-42, **25**, 293, 369; 1943-44, **27**, 119.

⁴² 1939-40, *J. Gen. Physiol.*, **23**, 229.

log I contour in Fig. 3 is small. Subsequent histological examination of the eyes of these *Trionyx* showed only a comparatively few rod units; but in our frogs, and in certain fishes we have used,³⁶ the "rod" component of the flicker contour is also small although (relative to numbers of cones) the proportion of retinal rods is high.

It should be noticed here that, as we have already mentioned for other cases,⁸ the comparison of visual excitabilities by a chosen technique may lead to essentially meaningless results if a particular set of arbitrary standard conditions is imposed. Suppose, for example, that one desired to compare the capacities of *Anolis* and *Trionyx* to resolve stripe images. It is clear, from Fig. 6 for exam-

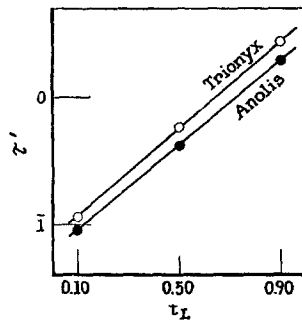


FIG. 4

FIG. 4. For *Trionyx* and for *Anolis* the abscissa of inflection (τ') of the flicker contour is directly proportional to the light-time fraction t_L , and the curves are shifted to essentially the same extent when t_L is changed.

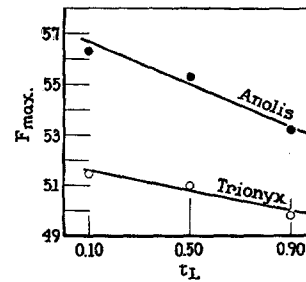


FIG. 5

FIG. 5. F_{max} . (Figs. 1 and 2) declines with t_L for both *Anolis* and *Trionyx*.

ple that the answer would depend upon the intensity level at which one might chose to operate. This type of procedure has been rather extensively used, as it happens,⁴³ and although we have already commented upon the essential point involved³⁶ it is worth re-emphasizing that unambiguous statements of visual properties can be achieved only in terms of properties of formulations of functional dependence.⁴⁴ It is part of the difficulty and fascination of this problem that the achievement of such statements must cope with the multivariate character of visual "thresholds."

Fig. 3 shows that the *Trionyx* "cone" curves are very similar to those for *Anolis* (Fig. 1), although with lower F_{max} . and situated at slightly higher intensities. Fig. 4 indicates that with increase of t_L the abscissa of inflection τ'

⁴³ Cf. Smith, K. U., 1938, *Psychol. Bull.*, **35**, 193; Kalmus, H., 1943, *J. Genetics*, **45**, 206.

⁴⁴ 1938, *Proc. Nat. Acad. Sc.*, **24**, 542; 1939, **25**, 171, 176; 1940-41, *J. Gen. Physiol.*, **25**, 89.

changes at just about the same rate as for *Anolis* (and *Phrynosoma*), although (Fig. 5) F_{max} declines less rapidly.

In line with the sharper quality, on the whole, of its responses at critical intensity, we find that for *Trionyx* the variation of I_I (cf. Table II) is a little less than for *Anolis*, $P.E._1/I_1$ averaging 0.025. The internal correlation evident in the measurements is also higher, since r in the expression $\sigma_\sigma = (\bar{\sigma}/\sqrt{2})(\sqrt{1-r})$ declines only from 0.895 ($t_L = 0.10$) to 0.780 ($t_L = 0.90$).

Sections of the eye of *Anolis* disclose conditions paralleling those apparently to be taken as typical for eyes of lacertilians. Only one kind of retinal unit is recognizable under careful scrutiny, the cone. There is a deep, well marked foveal depression; in this part the density of cones is four to five times as great as in the peripheral retina. There is present a pecten, in the form of a simple, finger-like, protrusion based at the entrance of the optic nerve and extending toward the lens; this structure is deeply pigmented; it is quite unlikely that the foveal region can be covered by the shadow image of this pecten.

The retina of *Trionyx* shows mostly stout cones;³⁵ in the foveal region the number per unit area is slightly higher than elsewhere. Rods are sparsely intermingled with these cones. They are relatively robust and are well extended in dark adapted retinas. In the relatively flat, thinned foveal region and elsewhere in the retina the proportion of rods to cones is at best 1:5, at poorest 1:8.

III

Fig. 6 compares "cone" flicker contours, $t_L = 0.50$, for *Anolis*, *Trionyx*, *Phrynosoma*,⁴⁰ *Pseudemys*,³⁹ *Taeniopygia*,⁴⁵ and *Passer*.⁴⁶ The curves for the two lizards, *Phrynosoma* and *Anolis*, are of a similar steepness despite the difference in maximum F . The curves for the two (closely related) birds are not unlike. The curves for the two turtles, *Pseudemys* and *Trionyx*, are not at all similar. The slight temperature differences obtaining in the data on turtles and lizards we can for present purposes ignore; and since we know⁴⁷ that change of temperature does not affect either F_{max} or the shape constant of the curve ($\sigma'_{\log I}$), at any level of t_L (0.10 to 0.90), we can use the form constants $\sigma'_{\log I}$ as basis for attempted classification of the contours. This is the best invariant measure for the purpose, since the extent of change of F_{max} with t_L ,⁴⁸ and of the abscissa of inflection τ' with t_L ,⁴⁸ is characteristic of the animal; hence no "standard conditions," as regards t_L , can be chosen to give non-arbitrary values

⁴⁵ 1940-41, *J. Gen. Physiol.*, **24**, 625; 1941-42, **25**, 381; 1943-44, **27**, 287.

⁴⁶ 1943-44, *J. Gen. Physiol.*, **27**, 315.

⁴⁷ 1936-37, *J. Gen. Physiol.*, **20**, 393, 411; 1938, *Proc. Nat. Acad. Sc.*, **24**, 216; 1938-39, *J. Gen. Physiol.*, **22**, 311; 1939-40, **23**, 531.

⁴⁸ 1936-37, *J. Gen. Physiol.*, **20**, 393, 411; 1937-38, **21**, 463, 1938-39, **22**, 311, 795.

of F_{max} , or τ' for purposes of classification of the curves. Whereas $\sigma'_{\log I}$, the standard deviation of the first derivative of F vs. $\log I$ with $F_{max} = 100$, is only slightly affected by image area (in a given eye⁴⁹) or by wave-length,⁵⁰ it is independent of t_L and of temperature, although sharply influenced by subdivision of the image⁵¹ and in birds by the influence of the pecten⁵² (for high values of t_L , with the moving stripe technique).

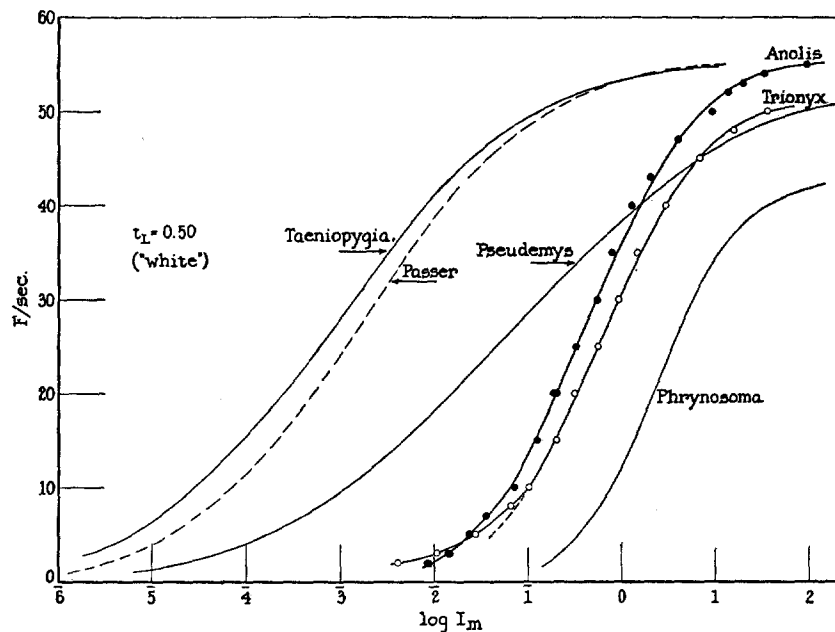


FIG. 6. Flicker contours at $t_L = 0.50$ are shown for the lizard *Anolis* and for the turtle *Trionyx*, together with contours under the same conditions previously obtained for *Phrynosoma* (lizard), *Pseudemys* (turtle), and for the birds *Taeniopygia* and *Passer*; these are all "cone" curves. See text.

On a probability grid (Fig. 7) curves in Fig. 6 have been drawn, together with certain others from earlier reports. All are for $t_L = 0.50$, "white" light, and are "cone" contours except for *Sphaerodactylus* ("rod").¹¹ It is pretty clear that these contours fall into two fairly distinct groups. The curves for *Xiphophorus*,³⁶ hybrids of *Xiphophorus* with *Platypoecilus*,³⁶ *Enneacanthus*,³⁶ *Fundulus*,⁵³ *Rana*,⁴² *Triturus*,⁴ *Sphaerodactylus*,³⁰ *Pseudemys*,³⁹ *Taeniopygia*,⁵²

⁴⁹ 1937-38, *J. Gen. Physiol.*, **21**, 223; and a following paper.

⁵⁰ 1941-42, *J. Gen. Physiol.*, **25**, 293, 381; 1943-44, **27**, 119.

⁵¹ 1943-44, *J. Gen. Physiol.*, **27**, 401.

⁵² 1943-44, *J. Gen. Physiol.*, **27**, 287, 315.

⁵³ 1939-40, *J. Gen. Physiol.*, **23**, 677.

*Passer*⁵² (cf. Fig. 6), and man, are of lower slope and lower τ' . Those for *Trionyx*, *Phrynosoma*, and *Anolis* are steeper, with higher τ' . It is true that the *Fundulus* slope might be taken as intermediate, but calculation from all available contours shows that, including those (e.g., man,⁵⁴ ape,⁵⁵ bee⁵⁶) obtained by different procedures but with "white" light and large image fields, $\sigma'_{\log I}$ for "cone" sections ranges from 0.72 to 2.3, with definite modes at ca. 0.80 and at

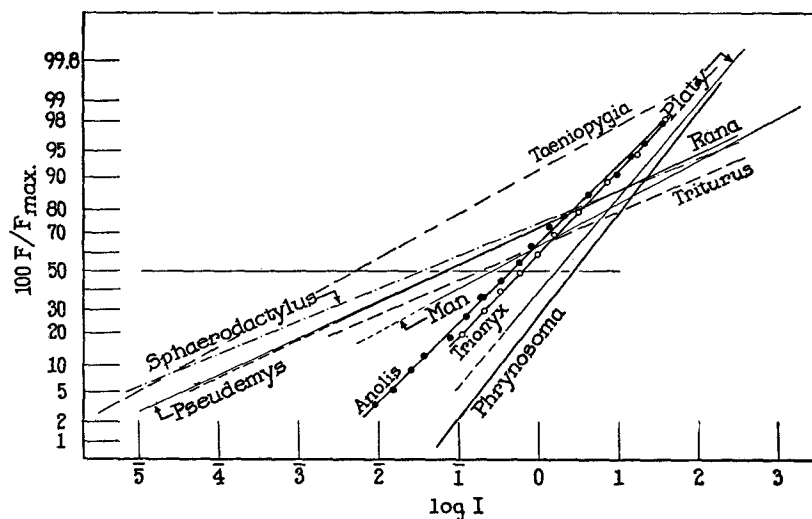


FIG. 7. Flicker contours, $t_L = 50$, white light, rotating cylinder technique, for various animals as indicated; on a probability grid. The data for all but *Anolis* and *Trionyx* are taken from previous papers. For man, *Rana Triturus*, and *Platy* the "cone" curves of duplex contours are given; the other curves are simplex. "Cone" curves for several other fishes are not too dissimilar to that for *Platy*, and the "cone" curve from the duplex curve for the sparrow *Passer* is very similar in slope to that for the finch *Taeniopygia*; these latter are not given, to avoid crowding the figure. It is apparent that these curves fall into two rather sharply contrasted groups; see text.

17.5, no cases at 13.5. This distribution is based on 30 contours and sets of contours, but it is not essentially disturbed if account is taken of other material in the literature¹⁸ and of the effects of image area and retinal position;⁵⁷ 14 cases fall in the steeper group, 16 in the other. While a larger assemblage of vertebrates might show intermediates, this is the state of present information.

It is striking that although the two fringillids go together in this classifica-

⁵⁴ 1937-38, *J. Gen. Physiol.*, **21**, 203; 1940-41, **24**, 505, 635; 1941-42, **25**, 293.

⁵⁵ Cf. Brecher, G. A., 1935, *Z. vergleich. Physiol.*, **22**, 539.

⁵⁶ 1935-36, *J. Gen. Physiol.*, **19**, 503, 1937-38, **21**, 223; 1938-39, **22**, 451.

⁵⁷ Data in a following paper.

tion, as do the two lizards *Anolis* and *Phrynosoma* and the amphibians *Rana* and *Triturus*, and the various fishes, the straight zoological ordering of the curves is plainly impossible: the turtles *Pseudemys* and *Trionyx* are respectively in the less steep and in the steeper groups; the contrast between gecko and lizards is striking; the "rod" curve of the gecko is in the less steep group. We shall point out that all other rod flicker contours known (from visually duplex animals) give slopes agreeing precisely (in mode and range) with those of our steeper cone group, and also that $\sigma'_{\log I}$ for a cone contour, by simple change of conditions, can be caused to shift from one group to the other (man,^{24,52} birds⁵²). The only directly relevant evidence⁵⁸ shows that genetic constitution can determine $\sigma'_{\log I}$ in the absence of such effects. Yet it is to be noted that for such different arthropods as *Apis*, *Anax*, *Asellus*⁵⁹ $\sigma'_{\log I}$ is practically identical (0.96), almost the same as for our modal steep "cone" curves (and our "rod" curves in duplex contours), whereas for *Cambarus*⁶⁰ the value is notably higher (1.41), and for *Uca* also in all probability.⁶¹

If we turn to the "rod" components of duplex contours (Fig. 8) we find them to be of reasonably uniform high slope; 14 examples, from data already published, give a mean $\sigma'_{\log I}$ of 0.814, ranging from 0.50 to 1.104, in fishes, birds, and man. This value is slightly influenced by image area, retinal position, wave-length composition, and subdivision of the image. In man the values for the "rod" segment as isolated by the use of subdivided fields or other arrangements,^{51,52} although increased slightly over their values when cone competition is not present, are not changed markedly,—the highest estimates for $\sigma'_{\log I}$ being 0.75 to 0.96 for these "pure rod" populations.

It might be tempting to argue that one of the "cone" groups corresponds in some significant way to the essential "rod" group, since their modal values of $\sigma'_{\log I}$ are in excellent agreement. "Rod" and "cone" differences not dissimilar appear in the properties of other visual performance contours (man).⁶² But it is a simple matter experimentally to convert a cone curve of the lower slope group into the upper, as by subdivision of the flickered field into several parts a cone contour with $\sigma'_{\log I} = 1.81$ can be made steeper until $\sigma'_{\log I} = 1.25$ or 0.82; in the retinal periphery, using a small image, $\sigma'_{\log I}$ can be changed from 1.85 to 1.11 by shifting from blue light to red.⁶³ Employing the method of rotated stripes with fixed inclined opaque bars in the field ("pecten effect") $\sigma'_{\log I}$ can be reduced from 2.10 (or 1.65) to 0.82 by reducing the dark-time in the flash

⁵⁸ 1937–38, *J. Gen. Physiol.*, **21**, 17; 1938–39, **22**, 463; 1939–40, **23**, 143. 1937, *Proc. Nat. Acad. Sc.*, **23**, 516; 1938, **24**, 221, 542; 1939, **25**, 176.

⁵⁹ 1938–39, *J. Gen. Physiol.*, **22**, 451.

⁶⁰ 1939–40, *J. Gen. Physiol.*, **23**, 1.

⁶¹ 1937–38, *J. Gen. Physiol.*, **21**, 223.

⁶² 1940, *Proc. Nat. Acad. Sc.*, **26**, 334, 382.

⁶³ 1941–42, *J. Gen. Physiol.*, **25**, 293.

cycle. In birds this occurs naturally,⁵² with reduction of $\sigma'_{\log I}$ from 1.65–1.68 to 1.16, and in all probability could be pushed further. In Fig. 7 certain of these effects are illustrated. It should be noted that there is (Figs. 6 and 7) no necessary correlation of $\sigma'_{\log I}$ with the magnitude of τ' .

Thus in the diverse "cone" flicker contours the most nearly invariant index ($\sigma'_{\log I}$) of quantitative performance characteristics falls into two rather distinct

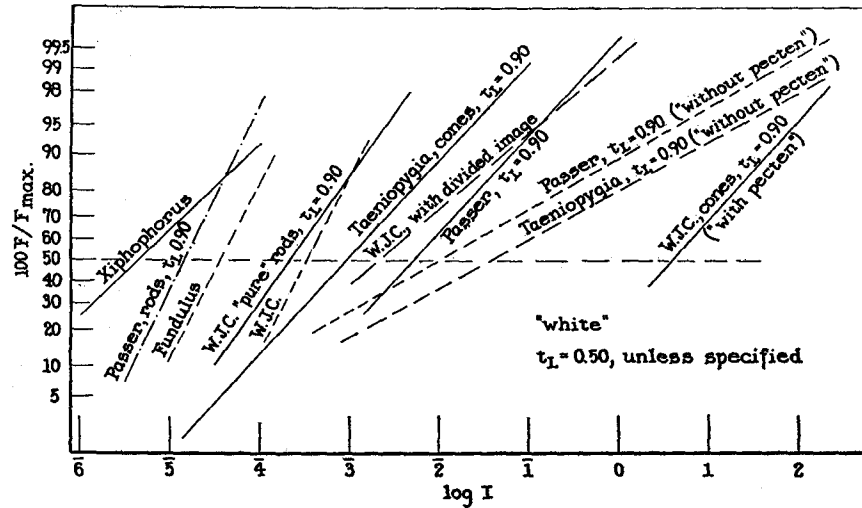


FIG. 8. Various presumptively "rod" flicker contours, white light as obtained with different animals are shown on a probability grid. These include data from *Xiphophorus*, *Fundulus*, *Passer*, and man. The slopes for other "rod" contours are included within the range of slopes illustrated. It is notable that these slopes, even when obtained under such conditions as not to involve cone complication, are of the type found for one of the two groups of cone contours in Fig. 7. The occurrence of the "pecten effect" serves to produce in *Taeniopygia*, *Passer*, and man, a steepening of the "cone" contours, from the slope indicated by the *computed* curves to that characteristic of the "rod" contours in duplex animals (or of the other group of "cone" effects in Fig. 7). See text.

groups, and is only slightly influenced in magnitude by such variables as image area; one of these groups of slope constants agrees precisely with that obtained from "rod" segments of duplex contours; yet a "cone" curve of one group can be caused, by one of several simple methods (subdivision of the image, or change of spectral zone; or, in birds, reduction of the percentage dark-time) to assume the slope constant typical of cone contours in the other group. Hence it cannot be held, in general, that the quantitative characteristics of performance contours are diagnostic of properties intrinsic to retinal rods or cones. The slope constants ($\sigma'_{\log I}$) are the most nearly invariant indices, and despite

their apparent occurrence in two distinct groups no correlations are possible with zoological position or retinal structure, in duplex or in simplex cases.

IV

SUMMARY

Flicker contours from vertebrates (fishes to man) show that the slope parameter $\sigma'_{\log I}$ in the efficiently descriptive probability summation $100 F/F_{max.} = \int_{-\infty}^{\log I} e^{-(\log I/I_i)^2/2(\sigma')^2} \cdot d \log I$ is distributed bimodally (simple fields, "white" light), from 0.60 to 2.3, with well defined peaks at 0.80 and 1.75. This parameter is independent of $F_{max.}$, $\log I_i$, temperature, light-time fraction, and in general not greatly influenced by λ . "Rod" components of known visually duplex contours, without exception, and some "cone" contours, are in the first group; an equal number of "cone" curves are in the second group, together with one simplex "rod" contour; purely cone contours are in each group, as well as cone segments of duplex curves. No firm zoological grouping of the "cone" curves can be made, on present evidence,—although the 5 fishes used give high-slope curves, 2 amphibians low slopes, reptiles (5) either high or low, birds (2) and anthropoids (2) low-slope "cone" curves.

By subdivision of the visual image and by change of wave-length, under certain conditions, in man, and by use of the "pecten effect" in birds (and man), cone contours of the low-slope class can be transformed into curves of the high-slope group. These procedures do not fundamentally change the "rod" slopes.

Consequently, although under simple conditions they are specifically determined, the forms of the $F - \log I$ contour cannot be used as diagnostic for rod or cone functioning. It is reinforced, by new data on *Anolis* (lizard) and *Trionyx* (turtle), that an obviously duplex retina is specifically correlated with a duplex performance contour, a simplex retina with a simplex one. But no support is given to the view that the shapes of these curves are diagnostic of differences in rod or cone fundamental excitabilities, or that they describe properties of these units. In visual duplexity we have to do simply with the fact that two groups of neural effects are available; it is with their properties that we deal in measurements of duplex visual excitability.