

# FLICKER RESPONSE CONTOURS FOR THE SPARROW, AND THE THEORY OF THE AVIAN PECTEN

BY W. J. CROZIER AND ERNST WOLF

(From the Biological Laboratories, Harvard University, Cambridge)

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## I

For image-forming animals generally it has been found that reduction of the light-time fraction in the light/dark cycle results in enlargement of the  $F$ -log  $I$  contour for response to flicker and in movement of the curve to lower flash intensities.<sup>1</sup> The asymptotic maximum of the curve is directly proportional to the percentage dark-time, and the abscissa of inflection ( $\tau'$ ) of the  $F$ -log  $I$  probability integral is inversely proportional to this quantity; so that  $\tau'$  and  $F_{max}$  are related rectilinearly. With man, reduction of image area reduces the effect of the light-time fraction on  $F_{max}$ , but does not greatly change the dependence of  $\tau'$  on  $t_L$ , if area, wave-length composition, and retinal location are constant. The theoretical bases for these findings have been discussed.<sup>1</sup> This general description applies to the properties of simplex flicker contours and of the photopic ("cone") portions of duplex contours. The scotopic ("rod") segments of duplex contours are the resultants of interaction between "cone" and "rod" neural effects, and the properties of the "rod"  $F_{max}$  as a function of  $t_L$  are therefore complex.<sup>1</sup>

In birds one has typically to do with a visual system in which there is cast upon the retina the serrated shadow of a large and complexly developed pecten.<sup>2</sup> Correlated with this we have shown<sup>3</sup> that, using the rotating striped cylinder technic,<sup>1</sup> there arises in a bird a novel effect of the light-time fraction upon the form and position of the flicker contour. That the correlation is a causal one is indicated by the fact that homologous changes are induced in the human  $F$ -log  $I$  contours when, with the same method of producing flicker, an artificial "pecten shadow" is placed on the retina.<sup>3</sup> The unique feature of these cases is in the fact that, for bird and man ("cone" curve), the increase of  $t_L$  to 0.75–0.90 makes the curve much steeper, increases its  $F_{max}$ , and greatly reduces  $\tau'$  with respect to the values these parameters would have if there were no "pecten effect." The nature of these changes is such as to assist materially in the analytical understanding of the flicker contours, and the effect itself can be shown to have a number of consequences in other directions as well.

<sup>1</sup> *J. Gen. Physiol.*, 1936–37, **20**, 393, 411; 1938–39, **22**, 311, 795; 1939–40, **23**, 531; 1940–41, **24**, 635; 1941–42, **25**, 369.

<sup>2</sup> Cf. Menner, E., *Zool. Jahrb., Abt. Zool. Physiol.* 1938, **58**, 481.

<sup>3</sup> *J. Gen. Physiol.*, 1943–44, **27**, 287.

The diurnal bird used for these particular observations,<sup>3</sup> the Australian zebra finch *Taeniopygia*, has in the retina receptor cells of only one general class, histologically. In the tests with human observers the presence of a "pecten shadow" subdividing the illuminated area by several intersecting opaque cross-bars produced no specific effect on the "rod" visual contribution to the flicker contour. The changes found in the "rod" segment of the curves were quantitatively accounted for<sup>3</sup> by the neural interactions of rod and cone effects when the cone curve was altered by the "pecten." This gives a further test of the physiological distinctness of the two groups of neural effects in the usually duplex contour for vertebrate visual performance. Physiologically, the simple zebra finch contours have properties homologous with those of the human "cone" curves. Thus, when low light-time fractions are used, where the "pecten effect" does not introduce complications, the relations of the zebra finch flicker contours to wave-length of light are of the same character, qualitatively, as those found for the normal human "cone" curve.<sup>4</sup> The interesting question thus arises as to whether in general the "rod" curve could be influenced by the "pecten effect;" and if not, why not. It has several further consequences for visual theory, of which we need refer here only to its significance for the analysis of what has often been termed "retinal summation."<sup>5</sup>

The status of certain of these points would be logically more secure if it could be found whether in a bird also the "pecten effect" is one which does not specifically involve the presumptively rod-determined segment of a flicker contour, even when it is naturally apparent in the "cone" segment. Obviously, it is also desirable to determine whether the "pecten effect" is demonstrable at all in more than one kind of bird, even though for purely technical reasons only smaller birds can be used at present for adequate experiments. Data secured in the examination of this point can also be serviceable for theoretical analysis of the visual significance of the difference between (1) "excitable units" and (2) the "elements of neural effect" produced by them, as well as of the neural integration of sensory effects due to excitation of rods and of cones.

The house sparrow, *Passer domesticus* L., is a form taxonomically rather closely near to *Taeniopygia* and has a prominent pecten. Its retina, however, is duplex, containing a fair and easily recognizable proportion of rods.<sup>6</sup> In keeping with the essential requirements of the duplexity doctrine<sup>7</sup> we now find that the sparrow's flicker contour is likewise duplex. The curves obtained for *Passer* with different light-time fractions in the flash cycle (white light) are recorded and discussed in the present paper.

<sup>4</sup> *J. Gen. Physiol.*, 1941-42, **25**, 381.

<sup>5</sup> Several following papers.

<sup>6</sup> Slonaker, J. R., *J. Morphol.*, 1918, **31**, 351; cf. Menner, E., *Z. vergleich. Physiol.*, 1929, **8**, 761; Verrier, M.-L., *Bull. biol. France et Belgique*, 1936, **70**, 197.

<sup>7</sup> *Proc. Nat. Acad. Sc.*, 1938, **24**, 125, 538; 1939, **25**, 171; *J. Gen. Physiol.*, 1938-39, **22**, 311, 555; 1940-41, **24**, 317, 625.

## II

Our sparrows were obtained through the kindness of Dr. F. A. Beach of the American Museum of Natural History, New York City. They had been in captivity for a considerable time, and were the survivors of a large group; mortality of captive sparrows is said to be in excess of 80 per cent. The birds were held for about 4 months before the observations began. From a group of fourteen, six were chosen—three males and three females. They were kept apart from the others, and identified by leg bands; Nos. 1, 5, and 6 were females. They are difficult to catch. Unless the cage is covered with black cloth they fly swiftly against the walls. They did not become tamer with prolonged handling. For each sparrow an observation jar was provided. This was a glass cylinder 5 inches in diameter and 4.5 inches high. The top is a celluloid plate, perforated for ventilation. The bottom is of perforated sheet metal, and on it the bird stands. Sparrows will not sit on a perch in the cylinder (as zebra finches do).

After being put in the cylinders the birds are kept in darkness for at least 2 hours before being tested. This long period in darkness is important to permit the excitement due to handling to subside; without this period of quiescence definite responses to flicker cannot be recognized with any certainty. The procedure was that already described in our experiments with other forms.<sup>3</sup> After they had quieted down in darkness the sparrows in their cages could be handled without inducing excitement. The cage cylinder is placed within a striped cylinder, which is then rotated at a known, desired speed giving a particular  $F$ . The observer being properly dark adapted, the diaphragm admitting light is slowly opened. A sparrow then usually "straightens up" and makes a few head motions as soon as any light is admitted. These motions are easily distinguished from the directed nystagmic motions which ultimately appear as the intensity is increased. If the initial low intensity is maintained briefly, the undirected motions quickly cease and the bird becomes quiescent. When the intensity is increased the end-point for response to flicker is signalized by a typical head nystagmus. This involves turning of the head in a direction following the motion of the stripes on the rotated cylinder, and then a quick return motion. The occurrence of two successive movements of this kind was taken to give the flash intensity  $I_c$  critical for response to flicker. This was necessary because after having made several such movements the birds are liable to intermingle them with undirected motions which could be difficult to evaluate. At lower flash frequencies (and thus at lower intensities) this is not a source of complication; the critical responses are then sharp and simple. Above  $F = 25$  the sparrows are more restless; Nos. 3 and 5, and occasionally No. 2, gave responses by hopping around the wall of the cage, following the moving stripes, while the others often stretched out the neck and the whole body as the head showed the typical nystagmus. The forced response to the stripes can be so extreme as to cause mechanical unbalance, so that fast stepping is required to prevent toppling over. The quality of these responses was not changed by altering the light-time ratio, although the decisiveness of the responses, and thus the observer's quickness and certainty in recognizing them, was greater with the decrease of the dark-time

<sup>3</sup> Cf. *J. Gen. Physiol.*, 1939-40, 23, 531.

fraction. It should be noted that there is no reflection of this in the variability of the determinations of the mean critical intensities (§ III).

The first series of final measurements was made at  $t_L = 0.50$ , with 0.90, 0.10, 0.75, and 0.25 following in that order. Of the six individuals used throughout, No. 5 was consistently the most sensitive and No. 6 the least sensitive. The mean rank-order positions of the others fluctuated at random, although No. 1 was often close to No. 6 (all three of these are females). The difference between Nos. 5 and 6 was relatively a little greater for the higher values of  $t_L$ , even then amounting to a difference of only  $0.04 \pm 0.01$  log unit but consistent at all values of  $F$ . It is curious that this small difference should be detected repeatedly. The order in which the six sparrows were tested was purposely rotated in such a way as to prevent the origin of such differences through systematic errors of observation. Differences of this sort between individuals have been found in other cases (*cf.* footnote 1); where they occur, the averaged data are of course not strictly homogeneous.

### III

The data of the present experiment are collected in Table I. The measurements are given as  $\log I_m$  for each  $F$  and each  $t_L$ , together with  $\log P.E._I$  for the dispersion of the individual mean determinations ( $I_1$ ) of the critical flash intensity for the nystagmus end-point.

The scatter of  $I_1$  has been found in all earlier cases<sup>9</sup> to be such that  $I_m$  and  $\sigma_I$  are related rectilinearly, the dispersion of  $\sigma_I$  itself being a constant fraction of mean  $\sigma_I$  at all levels of  $I_m$ . It has also been found that with *homogeneous* data<sup>10</sup> the scatter of  $\sigma_I$  for flicker is<sup>11</sup> a function of  $t_L$ , although the mean values of  $\sigma_I$  are not. With *Taeniopygia*<sup>3</sup> it was observed that this effect was not so apparent. This is correlated with the nature of the "pecten effect," which raises  $F_{max.}$  at the higher values of  $t_L$ , and is found also in the "pecten" experiments with man.<sup>11</sup> In the present case  $F_{max.}$  changes very little from  $t_L = 0.10$  to 0.90, and the character of the inhomogeneity of the data averaged tends to make the scatter of  $\sigma_I$  reverse the usual order since that at  $t_L = 0.10$  is greatest (Fig. 1). The mean value of  $\sigma_I/I_m$  is exactly the same as for *Taeniopygia*.<sup>4</sup>

The flicker contours for the sparrow are shown in Fig. 2. It is apparent that they are of the same general form as seen in all tested visually duplex vertebrates.<sup>7</sup> It is also clear that, as with the zebra finch,<sup>3</sup> the shape of the upper (cone) portions of the curves is not independent of the light-time fraction.

The upper parts of the curves in Fig. 2 are shown in Fig. 3 on a probability grid. The lines in Fig. 3 are extended toward  $F = 0$  in Fig. 2. By ordinate

<sup>9</sup> *J. Gen. Physiol.*, 1935-36, **19**, 503; 1936-37, **20**, 211, 363; 1937-38, **21**, 17; 1940-41, **24**, 505, 635; 1941-42, **25**, 89, 293.

<sup>10</sup> *J. Gen. Physiol.*, 1935-36, **19**, 503; *Proc. Nat. Acad. Sc.*, 1937, **23**, 23; 1938, **24**, 130.

<sup>11</sup> *J. Gen. Physiol.*, 1940-41, **24**, 635; 1941-42, **25**, 89; 1943-44, **27**, 287.

differences from the curves given by the data at the lower ends the flicker response contributions specifically due to rod excitation are obtained<sup>12, 13</sup> (dashed lines) in the low intensity region (Fig. 2).

TABLE I

Log  $I_m$  and log P.E.<sub>1</sub> for appearance of response to flicker, using white light and light-time fractions 0.10 to 0.90, as a function of flash frequency  $F$ , for the sparrow *Passer domesticus*.

Six individuals, the same throughout, for all measurements; three observations on each at every  $F$  (i.e.,  $n = 18$ ; see text). Plotted in Figs. 1 and 2.

$F$ per sec.	0.10		0.25		0.50		0.75		0.90	
	log $I_m$	log P.E. <sub>1</sub>	log $I_m$	log P.E. <sub>1</sub>	log $I_m$	log P.E. <sub>1</sub>	log $I_m$	log P.E. <sub>1</sub>	log $I_m$	log P.E. <sub>1</sub>
2							6.4016	8.5207	6.8000	7.1530
4					6.1338	8.4555	6.5979	8.9807	6.0017	7.9751
6					6.2725	8.3497	6.7572	8.7692	6.9993	7.5538
8			6.1326	8.3615	6.5009	8.5914	6.9748	7.2399	6.1749	7.6477
10	7.9923	8.4711	6.3646	8.6783	6.7381	8.8686	6.9748	7.2399	6.3804	7.9643
12	6.2240	8.5667					5.2177	7.5268	5.6050	7.9419
13			6.7913	8.9547	6.1798	7.6276	6.6567	7.6323	4.0454	6.2887
14	6.5999	8.6401								
15			5.1929	7.5612	5.5708	6.1737	4.0286	6.5862	4.4150	6.8984
16	5.0111	7.4228			6.5542	7.6726				
17			5.6656	7.8011	4.0481	6.2136	4.4972	6.8539	4.9050	6.9326
18	5.5097	7.5064	5.9208	6.1544	4.2936	6.7446	4.6907	6.8405	3.0910	5.5594
20	5.8316	6.2107	4.2615	6.8967	4.6233	6.9924	4.9435	5.2613	3.3214	5.9334
	5.8398	6.0691			4.6214	5.2613			3.2991	4.0968
25	4.2415	6.7299	4.6698	5.1074	3.0378	5.4288	3.3286	5.8668	3.5947	4.0522
30	4.5667	6.9968	4.9889	5.4293	3.3657	4.1058	3.5718	4.0202	3.7893	4.2301
35	4.9126	5.3867	3.3379	5.5862	3.6973	4.7401	3.8094	4.1651	3.9548	4.3792
					3.7252	5.8959				
40	3.3185	5.8011	3.7332	4.1115	2.0846	4.1521	2.0257	4.2817	2.1159	3.0703
45	3.7728	4.0708	2.1711	4.6416	2.5013	4.9271	2.2485	4.6683	2.3383	4.7397
									2.3731	3.0393
47					2.7483	4.7646				
50	2.4420	4.6880	2.8561	3.3238	1.2953	3.5612	2.7017	3.1042	2.8047	3.3196
53	1.0888	3.5931	1.5620	2.1273	1.9483	2.2074	1.2036	3.6115	1.2918	3.9736
54									1.5020	2.0012
55	0.1670	2.5775	0.5488	1.2463	0.9516	1.1421	0.2512	2.7133	1.7884	2.2140
									0.3460	1.0564

We have pointed out<sup>3</sup> that the changed shape of the  $F$ -log  $I$  ("cone") curve at  $t_L = 0.75$  and  $0.90$  can be understood as due to the activation of a larger

<sup>12</sup> *J. Gen. Physiol.*, 1936-37, 20, 203; 1940-41, 24, 635; etc.

<sup>13</sup> *J. Gen. Physiol.*, 1941-42, 25, 293, 369.

number of cone units than would be concerned in critical recognition of flicker if the pecten shadow were not present. At the same time (since  $F_{max}$  does

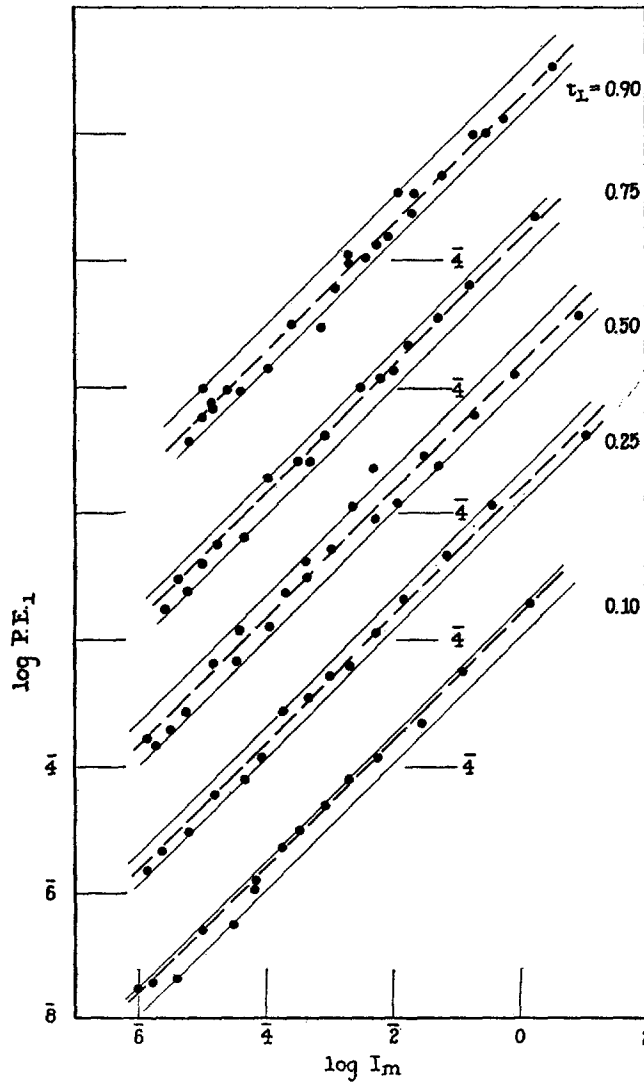


FIG. 1. Variation of critical intensities for response to flicker at different light-time fractions; data in Table I. The mean proportionality constants are the same for the different light-time fractions, the curves being separated arbitrarily for convenience.

not greatly change) the average number of elements of neural effect derived from each cone unit must be reduced. When no "pecten effect" is involved,

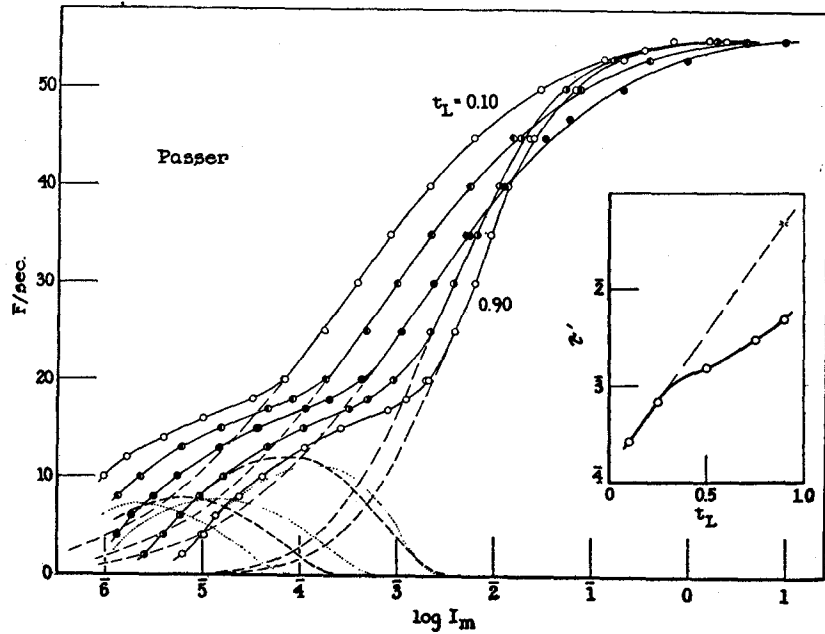


FIG. 2. Flicker response contours for the house sparrow. Data in Table I. The photopic curves are the probability integrals shown in Fig. 3. The analyses of the lower, scotopic sections are discussed in the text: the ascending and descending "rod" curves here shown dashed are shown on a probability grid in Fig. 4. The inset shows the actual relationship between abscissa of inflection of the "cone" curves ( $r'$ ) as a function of  $t_L$ , the extrapolation indicating the expected course of this relationship were there no effect due to the pecten; see text.

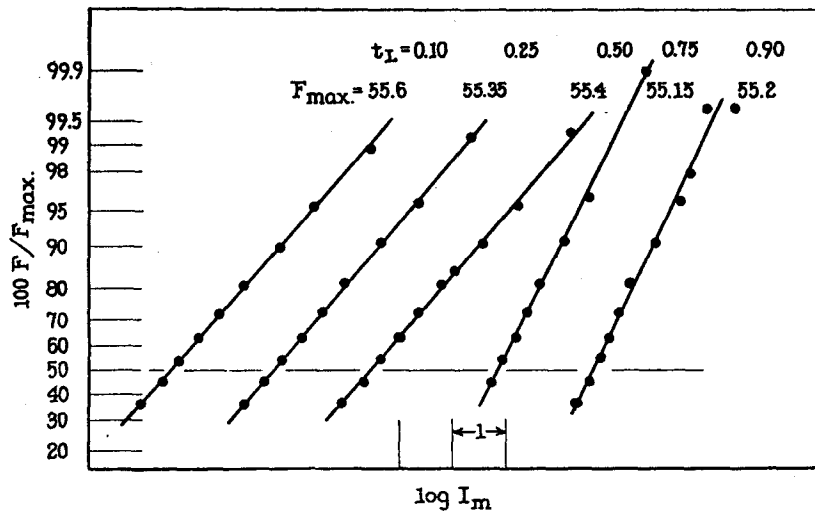


FIG. 3. The data of Fig. 2, photopic segments, shown on a probability grid. The lateral separation of the graphs is arbitrary, for convenience. The maximum  $F$  to which each curve is computed is shown.

with its accentuation of visual contrast at the shadow edges, increasing  $t_L$  does not change the slope constant of the contour ( $\sigma'_{\log I}$ ), but  $F_{max}$  gets lower; in Fig. 3 the slight differences in slope in  $t_L = 0.10, 0.25, 0.50$  are probably not significant, although Fig. 2 (inset) does show that at  $t_L = 0.50$  the "pecten effect" is already detectable. This is taken to mean that the same number of units is concerned, with reduction in the effective contribution from each.<sup>1</sup>

We can gain an idea of the effect due to the presence of the pecten if we try to construct the appearance of the set of flicker contours in Fig. 2 on the basis of expectation if the pecten were not present. In various cases of this kind<sup>1</sup> we know that the abscissa of inflection of the photopic flicker contour ( $\tau'$ ) is a rectilinear function of  $t_L$ ; in *Taeniopygia*<sup>3</sup> this is also true, as in our human tests with a "pecten shadow," up through  $t_L = 0.50$ . With the sparrow the effect is in one sense not so extreme as in the zebra finch (*cf.* footnote 3), but is already apparent at  $t_L = 0.50$ . As the inset in Fig. 2 shows, the rate of increase of  $\tau'$  with increase of  $t_L$  falls off after  $t_L = 0.25$ . Extrapolating to  $t_L = 0.90$ , on the assumption justified by the data on forms without pecten,<sup>1</sup> we would expect  $\tau'$  for the sparrow at  $t_L = 0.90$  to be at about  $\bar{2}.68$ —a whole log unit above its actual value as found. The gain in acuity for the recognition of moving stripes, under these conditions, is thus a little less than found for the zebra finch, and about the same as produced in man by the particular "artificial pecten" used in our experiments.<sup>3</sup>

This gain in acuity is by no means inconsiderable, and is perhaps even more striking because the low  $t_L$  contours for the sparrow, although of just about the same  $F_{max}$  as those for the zebra finch, are situated at flash intensities about  $0.4 \log$  unit lower. In more usual terms it corresponds to a raising of the critical flash frequency, due to the pecten, from 27.5 per second to 49 per second at  $t_L = 0.90$  and  $\log I_m$  (ml.) =  $\bar{2}.68$ . The "pecten effect" has also another consequence. At high flash intensities the acuity for moving dark stripes is made much more nearly the same for all light-time fractions. Instead of covering a span of about  $2.3 \log I$  units, the curves spread only by  $0.85 \log$  unit, and the 0.75 and 0.90 contours approach that for  $t_L = 0.10$ . To what extent this effect is exhibited for *single* moving images we do not as yet know, but qualitatively it is fairly certain that it must exist. The avian pecten is in effect an internal device for producing visual flicker—a moving image, if small enough, moves (as it were) across a fence of opaque pickets.

#### IV

We have discussed the "pecten effect" as exhibited in the photopic segment of the duplex sparrow flicker contour. It is of the same kind as that found in the simplex  $F$ - $\log I$  curves for the zebra finch, and for man. We now consider the modifications produced in the scotopic "rod" curves. In our analysis of the "rod" curves for man, with the "artificial pecten," it was pointed out<sup>3</sup> that



the raw "rod" data suffered no such gross changes of slope as found with the "cone" curves. The actual "rod" contributions as dissected out after extrapolation of the "cone" probability integrals<sup>12</sup> gave every evidence of suffering from partial inhibition due to concurrent excitation of cones, rather than being directly influenced by the "pecten" shadow.<sup>3, 13</sup>

The extracted "rod" curves in Fig. 2 are put upon a probability grid in Fig. 4. The properties of this set of curves are qualitatively the same as those of the

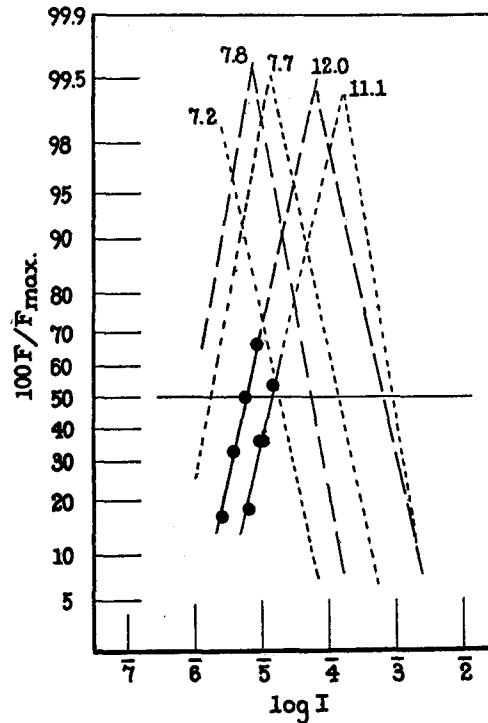


FIG. 4. The computed rising and falling "rod" contribution curves shown in Fig. 2 are here put upon a probability grid. See text.

corresponding sets we have analyzed for human observers.<sup>3</sup> When, for  $t_L = 0.75$  and  $0.90$ , a portion of the curve of observations escapes complication by overlapping cone excitation the data then fall on the probability integral required by the subtraction of the "cone" ordinates for the remainder of the scotopic segment. Again, as shown, the slope constant ( $\sigma'_{\log I}$ ) for these ascending curves is *less* than for those in which the "rod" and "cone" contributions overlap completely (*e.g.*, for  $t_L = 0.25, 0.50$ ). This finding we have already indicated to be the expected one when the number of effective rod units

is increased<sup>8</sup> (*i.e.*, the reverse of the situation with cone units). Since the "rod"  $F_{max}$  also increases sharply, the possibility is not excluded that there may indeed be a true effect of the pecten on the production of action elements from rod units, although we think this unlikely. Even in the absence of a "pecten shadow" the "rod"  $F_{max}$  increases a little (man) with increase of  $t_L$ ,<sup>14</sup> as an automatic consequence of the integration of "rod" and "cone" effects when the "cone"  $\tau'$  is increased faster than the "rod"  $\tau'$  by enlarging  $t_L$ . The inhibition of both "rod" units and elements of effect due to "cone" excitations is sufficient to account for the behavior of the "rod"  $F_{max}$  in Figs. 2 and 4. We therefore concluded that there is no evidence of a direct influence of the pecten on the rod flicker response function.

This question can be investigated more directly with man. We have pointed out<sup>13</sup> that by using lights of limited wave-length composition (*e.g.*, blue) rather than white, image areas and locations can be found in which there is essentially no overlapping of the rising scotopic and the photopic flicker contours. The subdivision of such an image by a "pecten shadow" should permit analysis of the rod curves without admixture of cone effects.

## V

## SUMMARY

The flicker contour for the house sparrow *Passer domesticus* is duplex, corresponding to the presence of both rods and cones in the retina. The presence of the pecten brings about changes in the "cone" part of the contour when the light-time in the flash cycle is varied. These changes are of the same sort as those we have already described for the visually simplex zebra finch, and for man provided with an artificial "pecten shadow." The changes are such as to greatly enhance flicker acuity for small dark-times (moving stripe technique). The form of the scotopic part of the duplex contour (also as in the case with man) gives no evidence that rod excitation is specifically influenced by the presence of the pecten. The changing integration of "rod" and "cone" effects as the light-time fraction is altered provides another means of testing the theory used for the analytical separation of the two components of the duplex flicker contour.

<sup>14</sup> *J. Gen. Physiol.*, 1940-41, **24**, 635.