# INTENSITY DISCRIMINATION IN THE HUMAN EYE\*

# II. The Relation between $\Delta I/I$ and Intensity for Different Parts of the Spectrum

BY SELIG HECHT, JAMES C. PESKIN, AND MARJORIE PATT (From the Laboratory of Biophysics, Columbia University, New York)

(Accepted for publication, April 26, 1938)

### I

# Purpose of This Research

When I and  $I + \Delta I$  are two light intensities which can just barely be recognized as different, then the fraction  $\Delta I/I$  is considered the measure of intensity discrimination. The value of this fraction and its relation to the intensity I have been the subject of many researches, and these have established that as the intensity I increases, the fraction  $\Delta I/I$  decreases, tending toward a minimum value at the highest intensities. This is true not only for the human eye, but for all other organisms thus far studied, namely, *Drosophila*, the bee, and *Mya* (for a summary, see Hecht, 1937 a).

Besides the general relation of  $\Delta I/I$  to *I*, the human eye shows an additional phenomenon due to the duality of its retinal structure. There seem to be two relations of  $\Delta I/I$  to *I*, one at the lower intensities representing rod function, and the other at high intensities representing cone function. This rod-cone dichotomy is apparent in nearly all the published measurements from the earliest by Aubert (1865) to the most recent of Steinhardt (1936). In addition, Steinhardt showed that the double function appears only in measurements with central visual fields larger than 2°, while the single function appears with fields smaller than 2°, and this corresponds to the presence of rods and cones in the larger fields, and to the complete absence of rods in the smaller fields. Moreover, the extent of the low intensity rod section increases with the size of the field because of the increasing number of rods present in comparison with the number of cones.

\*The first paper in this series is by Steinhardt (1936).

7

The rods and the cones possess different sensibility distributions in the spectrum, and this has been used to separate the two systems in measurements of dark adaptation (Kohlrausch, 1931), intermittent stimulation (Hecht and Shlaer, 1936), visual acuity (Koenig, 1897; Hecht, 1937 a), and instantaneous threshold (Blanchard, 1918; Hecht, 1937 b). For intensity discrimination this would mean that in measurements made with extreme red light, the relationship between  $\Delta I/I$  and I would be a single high intensity function even when the field is large; while with other parts of the spectrum more and more of the low intensity section should appear as the wavelength of the light moves toward the blue. The data of Koenig and Brodhun (compare Hecht, 1935) show precisely this for red, orange, yellow, and green lights. However, their data (Koenig and Brodhun, 1888; 1889) with blue, violet, and even white lights show no break between the higher and the lower intensities; instead the points form a flat continuous function which corresponds neither to their own measurements with the other colors, nor with those of Blanchard, of Aubert, and of Steinhardt with white light. We have therefore investigated the situation anew, making measurements not only with different parts of the spectrum, but with white light as well, in order to establish the relation definitively, and to confirm the identification of the two sections of the function.

### II

# Apparatus

We started with the actual materials of Steinhardt's original apparatus B, and rebuilt them into a new instrument.<sup>1</sup> Steinhardt used two light sources, one for I, and the other for  $\Delta I$ . This introduces obvious difficulties in control. Our apparatus therefore uses only one light source. A diagram of the optical system is shown in Fig. 1.

The light source S, which is a glowing ball of tungsten in an arc furnished by a Punktlicht, is at the principal focus of the two lenses L and L'. These two lenses then start completely symmetrical optical paths. The light emerging from the lenses L' and L is reflected by the prisms  $P_1$  and  $P_2$  respectively, and is brought to a focus at  $S_1$  on a half-silvered mirror by means of the lens pair  $L_1$ and  $L_2$ , and the corresponding  $L_1'$  and  $L_2'$ . At  $S_1$  the two images of the source

<sup>&</sup>lt;sup>1</sup>In doing this we had the help and advice of Dr. Simon Shlaer, to whom we gratefully acknowledge our indebtedness.

overlap. The reflected light of one and the transmitted light of the other then traverse a common path to the ocular, O, which focuses an image of  $S_1$  at  $S_2$  in the plane of the pupil of the eye. The size of the image  $S_2$  is about  $1 \times 1.5$  mm. This image becomes an artificial pupil, since its size remains constant at all intensities, and it is smaller than any pupil size achieved even by the most intense illumination.

What the eye E sees may be made out in terms of the dashed construction shown in the figure. A point on the lens  $L_1$ , which is at the focal distance of the



FIG. 1. Diagrammatic top view of the apparatus. S is the light source, and  $S_1$  and  $S_2$  are its two double, superimposed images formed by the two trains of lenses  $L, L_1 \ldots$  and  $L', L'_1 \ldots$ , and the ocular O.  $P_1$  and  $P_2$  are right angled prisms; Sh is a shutter; D a diaphragm; W is a neutral wedge and B its balancer; M is a half-silvered mirror;  $F_1$  to  $F_5$  are neutral filters; MF is a monochromatic filter. The actual appearance of the field to the eye E is shown in the lower right corner.

lens  $L_2$ , produces a parallel beam which is reflected or transmitted at the mirror and forms an image by means of the lens  $L_3$  in the front face of the ocular O. In other words, the eye, looking through the ocular, sees an image of either the lens  $L_1$ or the lens  $L_1'$  or of both superimposed, and the two may be brought sharply into focus. The lens  $L_1$  furnishes the intensity I, and  $L_1'$  the added intensity  $\Delta I$ . The appearance of the luminous surface of the lens  $L_1$  may be varied by means of diaphragm D to form any chosen pattern. We have found it convenient to have the diaphragm represent two half circles subtending a visual angle of 12° and separated by an opaque bar 3° in width. The appearance of the field is shown in the inset, where the larger circle represents the prevailing intensity I, and subtends an angle of about 40° at the eye. The stippled half circles represent the pattern of the intensity  $\Delta I$  superimposed upon this field of view.

In the path of the  $\Delta I$  beam are a shutter Sh so that the duration of exposure of  $\Delta I$  may be controlled, and a neutral wedge and balancer W and B, having a range of 1:100 for the purpose of gradually varying the intensity of the  $\Delta I$  beam. In addition, the neutral filter  $F_1$ , which has a density of 1 may be inserted to decrease the intensity of the  $\Delta I$  beam by 1/10 when this is necessary. This is useful when the value of  $\Delta I/I$  is very small. On the other hand, when  $\Delta I/I$ is large, it may be necessary to insert the neutral filter  $F_2$  into the path of the Ibeam. Filter  $F_2$  also transmits 1/10, and is useful as well in making a comparison of the absolute brightness between the I and  $\Delta I$  beams.

The combined I and  $\Delta I$  beams pass through the monochromatic filters, MF, which are the Wratten monochromatic series 70-76 plus the Corning 428 already used (cf. Hecht and Shlaer, 1936) for isolating different parts of the spectrum. In addition, both beams pass through a series of three neutral step filters,  $F_3$ ,  $F_4$ , and  $F_5$ . Filter  $F_3$  has two steps whose densities are respectively 0 and 4.  $F_4$  has five steps whose densities are respectively 0, 1, 2, 3, and 4. Filter  $F_5$  is in three steps whose densities are 0, 0.3, and 0.6. Thus, with the three filters in the position of 0 density the brightness is maximal. The brightness may then be reduced in steps of 0.3 log unit down to a total density of 8.6, which easily covers the whole range of intensities over which the measurements need to be made.

The lenses, prisms, and filters, as well as the wedge, mirror, lamp, etc. are properly set and housed in metal mounts so that no stray light is visible. However, in order to avoid the stray reflections from the lamp for reading the wedge and ammeter, the observer sits in a cubicle open at the back, into which projects the ocular arm of the apparatus.

All the filters were calibrated with a Martens polarization photometer, using the method described by Hecht, Shlaer, and Verrijp (1933). They were calibrated for each of the monochromatic filters separately, as well as for the white light. The neutral wedge and balancer were also calibrated with the Martens photometer for white light and for each of the monochromatic filters.

In order to compare the  $\Delta I$  and I beams, a diaphragm is inserted near  $L_1$ and near  $L_1'$ ; these diaphragms cut off symmetrical halves of the respective fields. With filter  $F_2$  in position and filter  $F_1$  out, the wedge is moved until the two half fields match. Knowing the transmission of the  $F_2$  filter, and the brightness of the I beam, we secure the brightness of the  $\Delta I$  beam at that position of the wedge. From the calibration curve of the wedge, one can then compute the value of  $\Delta I/I$ for any position of the wedge and any combination of  $F_1$  and  $F_2$  filters.

The maximum brightness achieved with white light is about 1,000,000 photons. This was determined by making a binocular match with a semicircular field formed on an opal glass illuminated with a lamp whose distance was variable. The right eye looked at a half field in the ocular, while the left eye looked at the variable

10

comparison field through an artificial pupil. When the fields were matched, the outside field was measured with the Macbeth illuminometer.

### $\mathbf{m}$

### Procedure

The observer was dark adapted for 15 or 20 minutes before any measurements were made. He then started with the lowest illuminations and worked up to the highest. The observer sat properly shielded with his chin in a rest and his eye placed near the ocular, and looked centrally at the large field of intensity Ifor at least a minute until he was adapted to it. The wedge was then placed at such a position that an exposure of the  $\Delta I$  beam for 1/25 of a second by means of the shutter Sh produced an increase in brightness which was below the threshold. The wedge was then moved to increase the value of  $\Delta I$ , and an exposure made again. This was continued at 20 or 30 second intervals until the position of the wedge was found at which the eye could just clearly distinguish the pattern produced by the flash of the  $\Delta I$  beam. The wedge was reset below the threshold and the observation repeated. If the two readings were very near each other, no third reading was made; otherwise, a third setting of the wedge was made and an average taken.

The intensity was then increased 0.3 log unit, and the whole procedure repeated. This was continued with increasing intensities until the complete function was established. Such a run took between  $1\frac{1}{2}$  to 2 hours. We made three runs each for five portions of the spectrum and for white light. Before each run the match point of the *I* and  $\Delta I$  beams was determined, but this varied only slightly over a year.

### IV

### Measurements

Measurements were made with our own eyes; J. C. P. and M. P. served as subjects for the whole series of runs, while S. H. made the preliminary measurements as well as an occasional run which proved so similar to those of the other two observers that he did not complete the series. The data are given in Table I.

The measurements with white light are shown graphically in Fig. 2, where the points for M. P. have been lowered 0.5 log unit for convenience. They are plotted as the logarithm of  $\Delta I/I$  against the logarithm of the intensity *I*, because only in this way can the nature of the results be realized in view of the enormous range of intensities covered and the rather large range of the fraction  $\Delta I/I$ . By plotting the data in logarithmic form the percentage error occupies the same

# TABLE I Relation between $\Delta I/I$ and I for Different Parts of Spectrum

Central test field is 12° in diameter with 40° surround. Exposure of  $\Delta I$  is for 0.04 second

	White		(Filte	450 mµ srs 76 and	1 428)		535 m# Filter 74)			575 mu Filter 73.			605 mu Filter 72)		Ŭ	670 mµ Filter 70	
log I	Ā	1/1	log I	4	11	log I	A	1	log I	4	1/	log I	<u>مر</u>	1	log I	3	П.
tons	J.C.P.	M.P.	tons	J.C.P.	M.P.	tons	J.C.P.	M.P.	tons	J.C.P.	M.P.	tons	J.C.P.	M.P.	tons	J.C.P.	M.P.
4.899	1	9.31	$\bar{3}.001$		5.45	4.853		7.66	$\bar{2}.007$		11.9	$\bar{2}.236$		5.90	$\bar{2}.435$		10.8
3.387	68.1	4.67	<b>3.292</b>	8.97	3.45	$\bar{3}.069$		4.62	2.329	8.09	5.22	$\bar{2}.496$	7.52	3.97	$\bar{2}.693$		6.52
3.712	5.18	2.63	3.550	7.13	2.24	$\bar{3}.336$		3.18	2.565	5.75	3.63	$\bar{2}.913$	5.12	2.11	1.083	5.62	2.66
3.970	3.85	1.92	$\bar{3}.920$	4.93	1.60	3.784	10.4	1.87	2.960	3.66	2.17	1.200	3.14 1	1.39	1.390	3.05	1.31
2.433	2.33	1.23	$\overline{2}.219$	3.54	1.34	$\overline{2}.100$	7.67	1.57	1.264	2.47	1.52	1.459	2.12 (	964	Ī.548	.76	0.929
2.758	1.75	1.08	$\bar{2}.480$	2.84	1.19	$\bar{2}.368$	5.72	1.37	I.519	1.82	1.30	<b>1.886</b>	1.09	0.668	0.133		0.509
1.016	1.38	0.871	$\bar{2}.915$	2.07	1.04	$\bar{2}.749$	4.09	1.01	1.998	0.944	0.912	0.172	0.622(	0.521	0.276	0.545	
1.452	1.02	0.726	Ī.205	1.81	0.900	1.065	3.03	0.986	0.302	0.581	0.610	0.432	0.429		0.4410	.473	0.337
1.777	0.759	0.617	1.466	1.65	0.807	$\bar{1}.332$	2.43	0.834	0.556	0.380		0.850	0.272	0.169	0.541	.348	
0.035(	).564	0.448	$\bar{1}.860$		0.805	$\bar{1}.862$	1.55	0.634	0.960	0.294	0.270	1.132	0.204(	0.166	0.699	0.330	0.247
0.436	0.316	0.267	0.033	0.927		0.178	1.03	0.542	1.263(	0.208	0.153	1.396	0.178(	0.100	1.327	0.160	0.127
0.761	0.202	0.189	0.150		0.575	0.445	0.716	0.398	1.518(	0.166	0.112	1.893	0.1400	0.0618	1.651	0.131	0.0793
1.019(	0.156	0.147	0.323	0.689		0.829	0.478	0.258	1.950	0.132	0.0855	2.179	0.128	0.0528	1.909	0.116	0.0678
1.405	0.114	0.0897	0.411		0.500	1.145	0.381	0.185	2.254(	0.109	0.0798	2.439	0.120	0.0488	2.248(	0.109	0.0546
1.730	0.0955	0.0728	0.584	0.498		1.412	0.300	0.139	2.508(	0.102	0.0740	2.868	0.113	0406	2.573	0.103	0.0530
1.987	0.0816	0.0579	0.978	0.392	0.348	1.897	0.227	0.0911	2.926	0.0973	0.0702	3.154	0.105(	0.0385	2.831	00000	0.0490
2.410	0.0762	0.0500	1.269	0.322	0.248	2.213	0.191	0.0705	3.248	0.0973	0.0661	3.414	0.109(	0.0428	3.274(	9060.0	0.0453
2.735	0.0718	0.0459	1.529	0.267	0.216	2.480	0.173	0.0690	3.439	0.102	0.0635	3.831	<u> </u>	0.0433	3.5990	1.0887	0.0472
2.993(	0.0708	0.0434	1.879	0.218	0.160	2.929	0.170	0.0614	3.879		0.0700	4.117		0.0432	3.857	0.0824	0.0486
3.456	0.0703	0.0439	2.169	0.187	0.128	3.245	0.165	0.0561	4.183		0.0721	4.377		0.0435			
3.781	0040.0	0.0435	2.429	0.165	0.121	3.512	0.160	0.0583	4.437		0.0807						
4.039	0.0678	0.0471	2.806	0.150	0.0968	3.894		0.0568								,	
4.474(	).0644	0.0445	3.096	0.138	0.0826	4.210		0.0594									
4.799(	0.0646		3.357	0.132	0.0798	4.477		0.0638									

12

space at all intensities and all values of  $\Delta I/I$ . Moreover, the form assumed by the results is not changed by the actual numerical values of the fraction or by the units in which the intensity is measured.

The measurements with white light corroborate the work of Aubert, of Blanchard, and of Steinhardt in showing a sharp transition between the low intensity section and the high intensity section. It is hard to understand why the measurements of Koenig and Brodhun show



FIG. 2. Intensity discrimination for white light where *I* is a field 40° in diameter, and  $\Delta I$  is 12° in diameter exposed for 0.04 sec. The points for M. P. have been lowered 0.5 log unit for convenience in keeping the two observers apart. Note the two sections in each set of data; note also that at high intensities  $\Delta I/I$  reaches a constant minimum. The curves are all from the equation  $\Delta I/I = c[1 + 1/(KI)^{1/2}]^2$  derived on theoretical grounds.

no break, especially since their data with orange, yellow, and green lights do show it. With us the break has always shown up under the appropriate conditions, though it may be added that when Steinhardt first found a break in his measurements, it was unexpected because of our reliance on the data of Koenig and Brodhun. When the observer is tired and his fixation and attention are poor, he occasionally gives results which, like those of Koenig and Brodhun, show no clear break. This may have been the case also with the data of Holway (1937). Another significant point about the measurements in Fig. 2 is that the value of  $\Delta I/I$  does not rise at high intensities, but reaches a minimum at which it remains no matter how high the brightness. This also contradicts the measurements of Koenig and Brodhun who reported a rise in  $\Delta I/I$  at high values of *I*. However, this aspect of the matter is understood; the rise does not occur when adequate adaptation is allowed and when an adequately large field surrounds the test field. The rise also fails to appear in intensity discrimination measurements with *Drosophila* (Hecht and Wald, 1934) and with the honey bee (Wolf, 1933).

The data for the five selected portions of the spectrum are shown graphically in Fig. 3. The intensity scale on the abscissa is the same for all the colors, and is in Troland's photon units (Troland, 1916). We obtained these brightness values in two ways. One was by the heterochromic matching of the monochromatic filters among themselves and against white, while the other was by the superposition of the high intensity cone portions of the data for the different colors, which assumes that a given brightness produces a given value of  $\Delta I/I$  regardless of color. The differences between the two methods were so small that, knowing the errors of heterochromic photometry, we have actually used the superposition method in presenting the data. The scale on the ordinates applies only to yellow (575 m $\mu$ ); the orange (605 m $\mu$ ) and red (670 m $\mu$ ) measurements have been moved up by 0.5 and 1.0 log units respectively, while the green (535  $m\mu$ ) and blue (450 m $\mu$ ) measurements have been moved down 0.5 and 1.0 log units respectively. The data in Fig. 3 are those of J. C. P. only because those of M. P. are essentially the same.

Judging by the measurements in Table I, it might seem that the lowest  $\Delta I/I$  values achieved differ for the different spectrum portions. This is an artifact due to the circumstance that the measurements were made over the course of many months at odd times and in no special order. During this time the observers varied to a certain extent, but what is more important, the shutter in the apparatus varied because the apparatus was demonstrated frequently and this involved resetting the shutter. When this long period variation became evident, we deliberately tested the minimum  $\Delta I/I$  at high intensities for the different colors at one sitting. The measurements

were made on the eye of J. C. P. and the  $\Delta I/I$  values secured were 0.138, 0.125, 0.116, 0.114, 0.129 for blue, green, yellow, orange, and red respectively; this gives a maximum variation of about 10 per cent from the mean, and is probably of no importance.



FIG. 3. Intensity discrimination for the red, orange, yellow, and blue parts of the spectrum. The ordinates apply to the yellow data in the middle; those for orange and red have been raised 0.5 and 1.0 log units respectively, and those for green and blue have been lowered 0.5 and 1.0 log units respectively. Note the increasing size of the low intensity section with decreasing wavelength corresponding to the increasing sensibility of the rods in the short-wave part of the spectrum. The curves through the data are all from the equation used for Fig. 2.

The form which the data assume follows expectation. The measurements with red light show only a single continuous intensitydiscrimination function. The data with orange light, however, already show a slight break quite comparable to that shown by Koenig and Brodhun's measurements, and the same is true of measurements with yellow light (cf. Fig. 7 in Hecht, 1935). The data as a whole show that the extent of the low intensity section steadily increases as the spectrum goes from red to blue, and this is in conformity with the Duplicity theory as implemented by the spectrum sensibility curves of rods and cones.

# v

# Photochemical Theory

In addition to their relation to the Duplicity theory, these measurements, in their quantitative implications, are consonant with the theory developed for intensity discrimination in vision and photoreception (Hecht, 1935). Essentially, this theory supposes that in order to discriminate between an intensity I, and another just perceptibly brighter intensity,  $I + \Delta I$ , a constant increment in the photochemical decomposition must take place in a given time when the photosensory system in the receptor is exposed to the added intensity  $\Delta I$ . Since the exposure to  $\Delta I$  is constant in these measurements, this is equivalent to saying that a constant initial photochemical change must be produced by  $\Delta I$ , in order that its addition to I will be just perceptibly recognized.

Of the equations deduced in terms of such an interpretation, the one which fits the cones best by far is

## $\Delta I/I = c[1 + 1/(KI)^{1/2}]^2$

and it is actually the curve for this equation which is drawn through all the cone data in Figs. 2 and 3. This is the equation which originally (Hecht, 1935) was found to fit Blanchard's data, those of Steinhardt, of Koenig and Brodhun, and has since been found to describe the more recent data of Smith (1936) and of Graham and Kemp (1938). Its agreement with the present measurements is obvious.

The same curve has been drawn through the measurements of the rod sections. One cannot be too sure of the rod curves, because the data do not cover a large enough range. Steinhardt's rod sections, as well as our own, are best fitted by this equation; however, this does not exclude a fair agreement with the other equations involving slightly different exponents. The double logarithmic grid on which the data are plotted is useful for comparison with theory, because on such a plot the form of the curve resulting from the equation is invariant. The constants c and K merely fix the position of the curve on the ordinates and abscissas respectively, and comparison between measurements and theory may be made by inspection without computing the numerical values of c and K. The constant c is obviously the asymptotic value of  $\Delta I/I$ at the highest intensities, and K is the reciprocal of the intensity at which  $\Delta I/I$  is four times as large as its minimal value.

It is to be noted that for the data with blue light, three points near the transition are distinctly off the theoretical curve. This phenomenon has already been noted with intermittent stimulation (Hecht and Shlaer, 1936). These aberrant points cannot be attributed to summation of the effects of rods and cones, since such a summation could just as well take place at the transition for white light, for green, and for yellow, but is not evident in any of these functions. There is some evidence that these points may represent the behavior of elements which have the spectrum visibility curve of rods but the threshold of cones, and are comparable to those described in the eye of a completely colorblind individual (Hecht, Shlaer, Smith, Haig, and Peskin, 1938).

### SUMMARY

1. A new apparatus is described for measuring visual intensity discrimination over a large range of intensities, with white light and with selected portions of the spectrum. With it measurements were made of the intensity  $\Delta I$  which is just perceptible when it is added for a short time to a portion of a field of intensity I to which the eye has been adapted.

2. For white and for all colors the fraction  $\Delta I/I$  decreases as I increases and reaches an asymptotic minimum value at high values of I. In addition, with white light the relation between  $\Delta I/I$  and I shows two sections, one at low intensities and the other at high intensities, the two being separated by an abrupt transition. These findings are contrary to the generally accepted measurements of Koenig and Brodhun; however, they confirm the recent work of Steinhardt, as well as the older work of Blanchard and of Aubert. The abrupt transition is in keeping with the Duplicity theory which

attributes the two sections to the functions of the rods and cones respectively.

3. Measurements with five parts of the spectrum amplify these relationships in terms of the different spectral sensibilities of the rods and cones. With extreme red light the relation of  $\Delta I/I$  to I shows only a high intensity section corresponding to cone function, while with other colors the low intensity rod section appears and increases in extent as the light used moves toward the violet end of the spectrum.

4. Like most of the previously published data from various sources, the present numerical data are all described with precision by the theory which supposes that intensity discrimination is determined by the initial photochemical and chemical events in the rods and cones.

### BIBLIOGRAPHY

Aubert, H., Physiologie der Netzhaut, Breslau, E. Morgenstern, 1865, 394 pp.
Blanchard, J., The brightness sensibility of the retina, *Phys. Rev.*, 1918, 11, 81.
Graham, C. H., and Kemp, E. H., Brightness discrimination as a function of the duration of the increment in intensity, *J. Gen. Physiol.*, 1938, 21, 635.

- Hecht, S., A theory of visual intensity discrimination, J. Gen. Physiol., 1935, 18, 767.
- Hecht, S., Rods, cones, and the chemical basis of vision, *Physiol. Rev.*, 1937*a*, 17, 239.
- Hecht, S., The instantaneous visual threshold after light adaptation, Proc. Nat. Acad. Sc., 1937b, 23, 227.
- Hecht, S., and Shlaer, S., Intermittent stimulation by light. V. The relation between intensity and critical frequency for different parts of the spectrum, J. Gen. Physiol., 1936, 19, 965.
- Hecht, S., Shlaer, S., Smith, E. L., Haig, C., and Peskin, J. C., The visual functions of a completely colorblind person, Am. J. Physiol., 1938, 123, 94.
- Hecht, S., Shlaer, S., and Verrijp, C. D., Intermittent stimulation by light. II. The measurement of critical fusion frequency for the human eye, J. Gen. Physiol., 1933, 17, 237.
- Hecht, S., and Wald, G., The visual acuity and intensity discrimination of Drosophila, J. Gen. Physiol., 1934, 17, 517.
- Holway, A. J., On the precision of photometric observations, J. Opt. Soc. America, 1937, 27, 120.
- Koenig, A., Die Abhängigkeit der Sehschärfe von der Beleuchtungsintensität, Sitzungsber. Akad. Wissensch., Berlin, 1897, 559.
- Koenig, A., and Brodhun, E., Experimentelle Untersuchungen über die psychophysische Fundamentalformel in Bezug auf den Gesichtsinn, Sitzungsber. Akad. Wissensch., Berlin, 1888, 917.

- Koenig, A., and Brodhun, E., Experimentelle Untersuchungen über die psychophysische Fundamentalformel in Bezug auf den Gesichtsinn, Zweite Mittheilung, Sitzungsber. Akad. Wissensch., Berlin, 1889, 641.
- Kohlrausch, A., Tagessehen, Dämmersehen, Adaptation, in Bethe, A., von Bergman, G., Embden, G., Ellinger, A., Handbuch der normalen und pathologischen Physiologie, Berlin, Julius Springer, 1931, **12**, pt. 2, 1499.
- Smith, J. R., Spatial and binocular effects in human intensity discrimination, J. Gen. Psychol., 1936, 14, 318.
- Steinhardt, J., Intensity discrimination in the human eye. I. The relation of  $\Delta I/I$  to intensity, J. Gen. Physiol., 1936, 20, 185.
- Troland, L. T., Apparent brightness; its conditions and properties, Tr. Ill. Eng. Soc., 1916, 947.
- Wolf, E., The visual intensity discrimination of the honey bee, J. Gen. Physiol., 1933, 16, 407.