THE VISUAL FUNCTIONS OF THE COMPLETE COLORBLIND*

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(Received for publication, February 13, 1948)

I

INTRODUCTION

The purpose of studying the various visual functions of a completely colorblind individual is to secure information about the process in the normal eye. Earlier studies of the completely colorblind have shown them to be of two distinct types. The first of these possesses a low intensity mechanism and a high intensity mechanism much like the normal eye, corresponding most probably to rod vision and cone vision respectively. Visual acuity is high like the normal, and sensory distribution in the spectrum shows a different location for the low intensity and the high intensity mechanisms. Evidently in such cases something has gone wrong with the properties of the three cone mechanism, and color vision is absent although the cones are still active. A second type of complete colorblindness is one in which there is only one visibility curve, and that corresponds to the low intensity spectrum distribution in the normal. Visual acuity also is low, and there may or may not be a central blind spot. In all likelihood, in these cases, the cones either do not exist or are completely non-functional. It is a case of this sort on which we wish to report.

* The work reported in this paper was performed in 1937–38 and was first reported at a meeting of the American Physiological Society in April, 1938, (Hecht, Shlaer, Smith, Haig, and Peskin, 1938). It is unfortunate that the circumstances of the past years, and the premature death of Selig Hecht, have delayed publication for so long a time. Fortunately, Professor Hecht had made an outline which indicated the manner in which he intended to present this work. The main responsibility in preparing the final form of this paper has fallen to one of us (E. L. S.), and he must bear the responsibility for it.

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In previous descriptions of such cases, one, or at most two visual functions have been described by either the visibility curve or the relation of visual acuity to illumination (Uhthoff, 1886; Koenig, 1897). The particular significance of our present contribution is that we have studied several of the functions in some detail and have compared them with the behavior of normal eyes with the same apparatus and under similar circumstances.

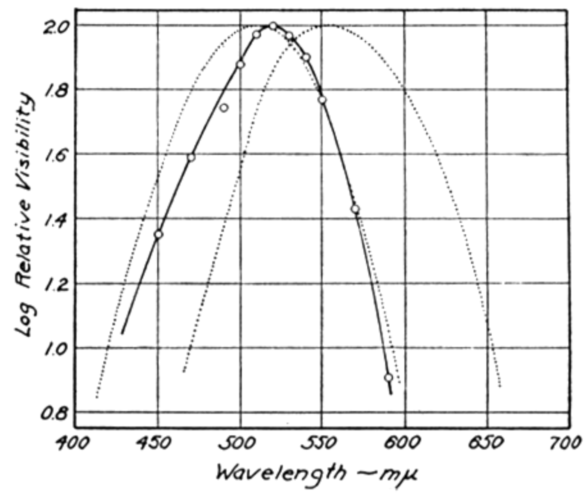

FIG. 1. Brightness distribution in the spectrum. The data for the normal eye are shown by the dotted curves: the one on the left for low intensity (rods) and on the right for high intensity (cones). The points and solid curve are for the complete colorblind.

II

Spectral Brightness Distribution

The measurements were made with the Helmholtz color mixer using the procedure and calibrations already described (Hecht and Shlaer, 1936). Fig. 1 shows the relative sensibility of our subject's eye in the spectrum at an ordinary high brightness; the data are given in Table I. Such a comparison is easy to make because the problem of heterochromic matching does not enter. A field of 1° was first tried, but the measurements were finally made with a 3° field because the subject was able to make more consistent brightness comparisons with a larger field. Included in the figure are first, the relative visibility curve for the human eye at low brightness as measured by Hecht and Williams (1922), and confirmed by Weaver (1937), and second, the bright visibility curve from the data of Gibson and Tyndall (1923). It is apparent that though made at a brightness which in the normal eye would yield the right-hand high visibility curve, our subject shows a sensibility distribution in the spectrum corresponding to that found for rod vision at dim illuminations only.

Certain points are to be noted. The maximum of the standard scotopic visibility curve is at about 511 mμ. The maximum of our subject is more nearly at 520 mμ. Examination of the figure shows that the long wavelength portions of the two curves coincide almost perfectly, whereas they deviate on the short wave side. There are several factors which may explain this situation. The standard curve is an average of 48 individuals, and since these may vary somewhat in the precise location of the maximum, the average curve is slightly wider than that of any single individual. A more important factor

TABLE I

Brightness Distribution in Spectrum

The maximum is placed at 100. The measurements are the average of two runs made on successive days.

Wavelength	Relative brightness
mμ	
450	0.225
470	0.389
490	0.555
500	0.759
510	0.940
520	1.000
530	0.929
540	0.800
550	0.589
570	0.270
590	0.080

is the relative amount of pigment which absorbs light in the short wave portion of the spectrum. Keilin and Smith (1939) found two diffuse absorption bands at about 495 mμ and 455 mμ which were visible to the eye in a small dispersion spectrum. They also deduced the presence of pigment in the optical path of the eye from an examination of the visibility data for the normal and for the colorblind eye. These data reveal two distinct depressions in the cone visibility curves at the same wavelengths where the absorption bands can be seen directly. The visibility data of our complete colorblind also show a depression in the curve at 490 mμ. Since the measurements with our subject were made with central fixation, it is quite likely that the narrow shape of the curve of the colorblind is due in part to the yellow pigment of the macula lutea. The rod visibility curve of the normal individual is measured in the periphery of the eye, therefore, the macular pigment would not influence the curve. Wald (1945) has recently extracted the macular pigment of the human eye and found that it possessed an absorption spectrum similar to leaf xanthophyll. He has also shown that the difference in spectral sensitivity between peripheral and central cones is due to the presence of the macular pigment in the center of the eye. Still another factor may also influence the shape of the visibility curve and that is the absorption by yellow pigment in the lens and ocular media of the eye (Ludwigh and McCarthy, 1938).

Whatever the exact meaning of the minor deviations, it is reasonably clear that our colorblind subject has elements in the retina which correspond fairly well with our rods, and not at all with our cones.

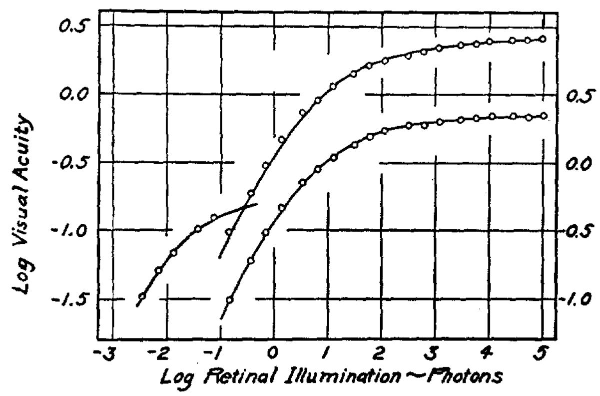

FIG. 2. Visual acuity for the normal eye. The upper curve shows two sections, the one at low intensities made with the periphery of the eye, and the one at higher intensities made with the rod-free center. The lower curve shows the data obtained with the center of the eye at all intensities (ordinate on the right).

III

Visual Acuity

Koenig (1897) once measured visual acuity as a function of intensity with a completely colorblind person and found that the relationship between these two variables was much like that found for the normal eye at low illuminations, although it extended beyond the normal rod region. Our meaning will be clear from examination of Fig. 2 which shows this relationship for the normal eye from the work of Shlaer (1937). The upper curve shows clearly that there are two sections to the relationship between visual acuity and illumination, one at low intensities which is measured with the periphery of the eye, and one at higher intensities for which the measurements are made with the rod-free center. The lower curve of Fig. 2 shows the data obtained with the rod-free center of the eye, even at the lowest intensities visible.

If our subject possesses elements which have the characteristics of rods, the high intensity section of Fig. 2 should not be present, but the low intensity curve should extend into the high illumination region without much increase in visual acuity. Fig. 3 presents the measurements made with our subject; the

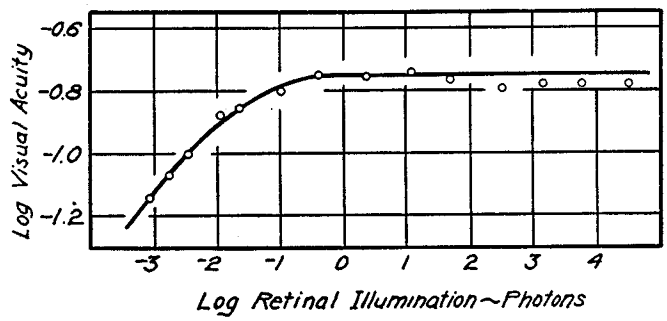

FIG. 3. Visual acuity for the complete colorblind eye. Only a single curve is found and this corresponds to rod function. The maximal visual acuity is only about one-tenth that found for cone vision in the normal eye.

TABLE II

The measurements were made with a 3 mm. pupil using blue light obtained with Wratten filter No. 75 and Corning filter No. 428; the dominant wavelength is 490 mμ. The log I values are from Table II of Shlaer, Smith, and Chase (1942), and have been corrected for the change in pupil size and the absence of the Stiles and Crawford effect for rod vision.

Log I in photons	Log visual acuity
−3.040	−1.142
−2.732	−1.067
−2.433	−1.000
−1.917	−0.875
−1.609	−0.853
−0.965	−0.797
−0.358	−0.747
0.387	−0.751
1.111	−0.737
1.719	−0.762
2.543	−0.789
3.187	−0.776
3.794	−0.776
4.539	−0.778

data are given in Table II. It is apparent that there is only one relationship between visual acuity and illumination and that this corresponds very clearly to the rod function of the normal eye. The measurements were made using the apparatus described by Shlaer (1937), employing as a test object a grating of alternate opaque and transparent bars of equal width.

IV

Dark Adaptation

The two functions of the colorblind eye just enumerated conform precisely to what is to be expected from previous knowledge and theory of normal vision. The next measurements show that there are some additional complexities, and

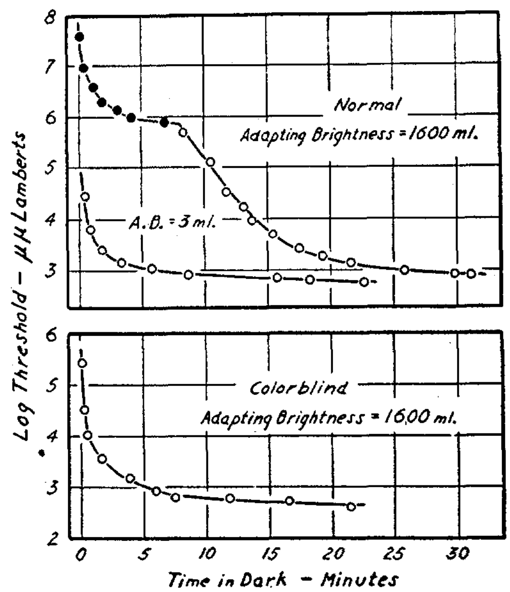

FIG. 4. Dark adaptation for the normal individual and for the complete colorblind. After adaptation to 1600 millilamberts, the normal shows a rapid cone adaptation (solid circles) followed by a slow rod adaptation (open circles). The colorblind shows only a rod curve of the rapid type. The threshold measurements were made with violet light (450 mμ) using a 3° field, 7° off-center (nasal) after preadaptation for 4 minutes. The data are averages of three runs made with the adaptometer described by Hecht and Shlaer (1938).

these may be introduced by examining the dark adaptation of normal eyes and of our subject's eye. The upper half of Fig. 4 shows normal dark adaptation under two conditions. The upper curve records what happens after light adaptation to 1600 millilamberts, and the lower one to 3 millilamberts. The dark adaptation following preadaptation to high brightness shows two sections; the first is cone adaptation and the second is rod adaptation. Following preadaptation to a low intensity, one finds in the normal eye only rod adaptation. Its shape, however, is different from the rod adaptation which follows high preadaptation because it is much faster, and instead of gradually leaving the intensity axis, it does so sharply (Wald and Clark, 1937; Hecht, Haig, and Chase, 1937).

We had supposed that with our colorblind subject, following adaptation to high brightness, we should not find the preliminary cone adaptation but should

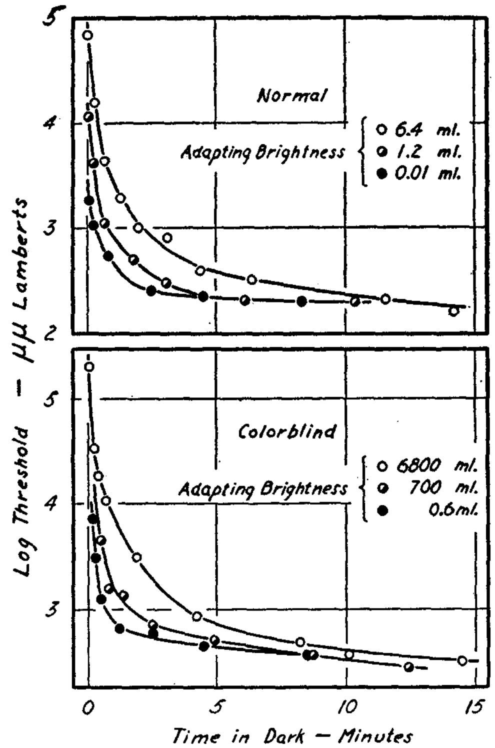

FIG. 5. Dark adaptation for normal and for the colorblind after different adapting brightnesses. The colorblind shows only rapid rod adaptation regardless of the intensity of the preadaptation. The measurements were made under the same conditions as those described in Fig. 4. However, similar results for the colorblind were also obtained using a 5° central field (violet) and a 3° central field (red).

immediately go to the subsequent rod adaptation, and thus secure information about that part of the rod adaptation curve which one can never obtain in normal eyes because of the speed and dominance of cone adaptation. The lower half of Fig. 4 shows the results secured with the colorblind subject. Although adapted to 1600 millilamberts, her eye showed a dark adaptation curve much more similar to the normal following low preadaptation than to the normal following high preadaptation. This situation is brought out more clearly in Fig. 5. The precise shape of the dark adaptation curve may be varied by the intensity of preadaptation. The upper half of Fig. 5 shows for the normal eye the dark adaptation following three low intensity preadaptations; the lower half shows results with the colorblind. Approximately the same results as those with the normal are secured with intensities very much higher. In other words, under all circumstances, a completely colorblind subject shows only the fast type of rod dark adaptation.

Precisely what this means is hard to say at the moment because the nature and kinetics of even normal dark adaptation are not completely clear. The type of curve secured resembles more nearly what is to be expected in terms of a simple equilibrium between visual purple and its photoproducts, and the regeneration from them in the dark.

Table III gives the data for the threshold of the colorblind eye for different retinal positions. The data show that the threshold is about 1 log unit higher in the center of the eye than it is in the periphery. Haig and Haig (1947) have recently reported that for the normal eye, under identical conditions of measurement the difference in threshold between the rod-free center and the periphery is about 3 log units, while the difference in threshold between 2° off-center and the periphery is about 1 log unit. Thus the rod picture in our colorblind subject is the same as in the normal except for the presence in the center of rods having the same threshold as those 2° off-center.

V

Critical Fusion Frequency and Intensity Discrimination

The most striking thing which appeared in the measurements with our colorblind subject is in the data of flicker and of intensity discrimination. Fig. 6 shows the data secured for the relationship between intensity and the critical fusion frequency.[1] We used a large field and a small field but the results are much the same. For the normal eye, there is a marked increase in the rod curve when a large field is used as compared with a small one (Hecht and Smith, 1936). With the colorblind eye, there is no effect of field size. There seem to be two types of sensory systems in this eye, one functional at low illuminations, and the other at high illuminations. Naturally, one would immediately suspect that the high intensity sections represent cone function of perhaps a rudimentary kind. This, however, is not the case because the

[1] The intensity scale used for the different colors is that derived by heterochromic comparison with white light for the cone vision of the normal eye. Obviously, this has no real meaning for the colorblind eye which possesses a different sensibility distribution in the spectrum. The data have been left in this form for comparison with the normal eye. Logically, one should use the intensity comparison made by the colorblind. When this is done, the three curves of Fig. 6 show a transition between the two different functions at the identical intensity. This is also found for the intensity discrimination data of Fig. 8.

sensibility distribution of the high intensity elements is identical with that of the low intensity elements, as can be seen from Fig. 6 where the measurements

TABLE III

Threshold and Retinal Position

The measurements were made after complete dark adaptation with a 1° field using the light transmitted by Wratten filter No. 76 and Corning filter No. 428 (the color is violet with the dominant wavelength 450 mμ).

Distance from fovea	Log *I* in micromicrolamberts
degrees	
0	3.65
2.0	3.63
5.0	3.15
7.0	2.78
10.0	2.78
12.5	2.60
15.0	2.73
20.0	2.63

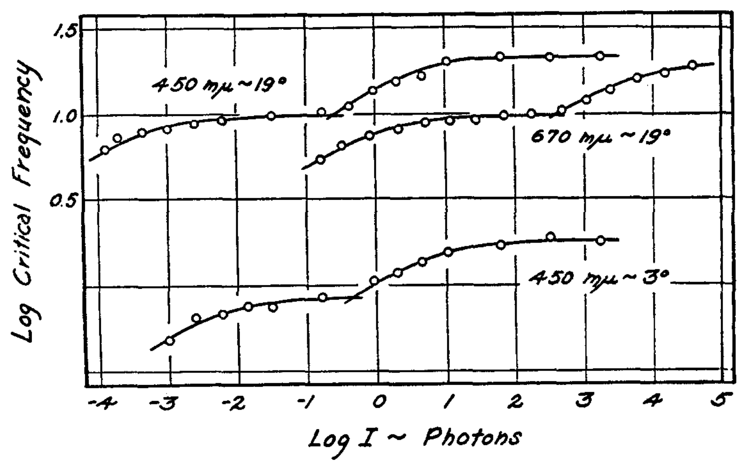

FIG. 6. Critical fusion frequency and intensity for the colorblind. Low intensity and high intensity functions are present but these are not influenced by the size of the field or the color.

are made with extreme violet and extreme red light. What may be expected when the two elements have different sensibility distributions in the spectrum is shown in Fig. 7 which records the behavior of the normal eye under similar circumstances (Hecht and Shlaer, 1936). Because the rods and cones have such different sensibilities in the spectrum, the measurements with red light show only cone function and not a trace of rod function, while with blue light the measurements show a very large rod function because of the relatively greater sensibility of the rods in the blue. No such difference between red and blue is apparent in Fig. 6 which records the data of the colorblind. The measurements with the colorblind were made with the apparatus previously described (Hecht and Shlaer, 1936). The data are recorded in Table IV.

As Fig. 8 shows, the same phenomenon appears when we measure the intensity discrimination of the colorblind. Here also, there seem to be two systems, one functional at low intensities, and the other at high intensities. However, here too the measurements with blue light and red light show exactly

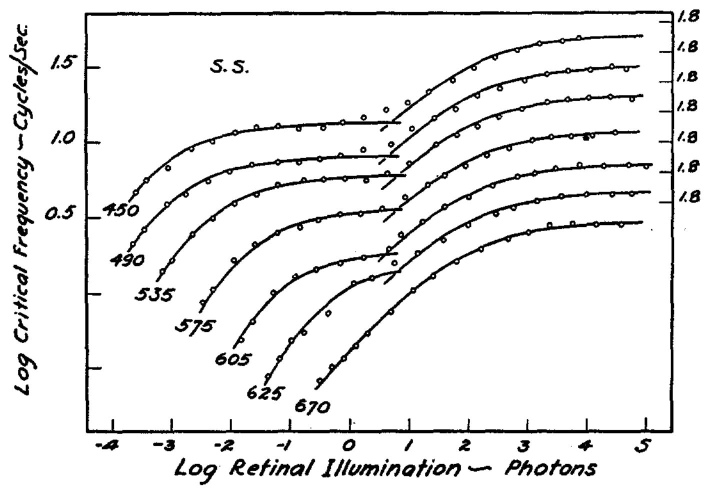

FIG. 7. Critical fusion frequency and intensity for different spectral regions for the normal eye. The measurements with red light show only cone function; those with other colors show both rod and cone function.

the same amounts of the two functions. Fig. 9 (Hecht, Peskin, and Patt, 1938) illustrates what happens in the normal eye under similar circumstances. It can be seen that with blue light there is a large rod section which is completely missing from the measurements made with red light.

It is noteworthy that the best intensity discrimination of the colorblind is very nearly the same as for the normal eye. This is in contrast to the data for critical fusion where the frequency for the normal is about 55 cycles per second as compared to 20 for the colorblind.

We must therefore conclude from the measurements of critical fusion frequency and intensity discrimination that although the colorblind eye possesses two systems functioning in different parts of the intensity range, these two systems possess sensibility distributions in the spectrum which are identical. It thus appears as though there are two kinds of rods present in the eye of our colorblind. Although they possess the same sensitive material, namely visual purple, they have different intensity thresholds. We may account for this by supposing that the concentrations of visual purple are different in the two systems. Those rods which have the usual concentration of visual purple behave like ordinary rods, and are sensitive to the very lowest intensities as in the normal eye. Those rods, however, which contain visual purple in much lower concentrations would then have a threshold very much higher and would

TABLE IV

Critical Fusion Frequency and Illumination

Each set of data is the average of three identical runs. The measurements were made with central fixation.

Blue light (λ = 450 mμ)			Red light (λ = 670 mμ)	
Log I in photons	Cycles per sec.		Log I in photons	Cycles per sec. 19° field
	3° field	19° field		
−3.88		6.17	−0.79	5.41
−3.71		6.84	−0.48	6.46
−3.35		7.76	−0.08	7.31
−2.99	4.60	8.07	0.33	8.00
−2.61	6.49	8.69	0.72	8.79
−2.22	6.84	9.00	1.08	8.85
−1.85	7.55	—	1.44	9.06
−1.50	7.48	9.62	1.84	9.57
−0.77	8.51	10.1	2.25	9.84
−0.38	—	10.9	2.68	10.3
−0.03	10.6	13.5	3.04	11.7
0.31	11.7	15.2	3.39	13.5
0.67	13.7	16.4	3.78	15.6
1.03	15.4	19.8	4.18	16.7
1.80	17.1	21.0	4.59	18.5
2.52	18.8	20.8		
3.25	17.7	21.0		

thus function at the higher intensities since in order to produce a given amount of photoproduct, the intensity required varies inversely as the concentration of photosensitive material.

There is evidence in the studies with the normal eye that makes one believe in the existence of these high intensity rods even in the normal eye. Examination of Figs. 7 and 9 shows that with blue and violet light, there always are some points which fit neither on the cone nor the rod curves. These points do not appear when light of green or longer wavelengths is used. It is possible that these points represent the function of the high intensity rods because they come off the rod curve in the normal eye at about the place on the flat maximum

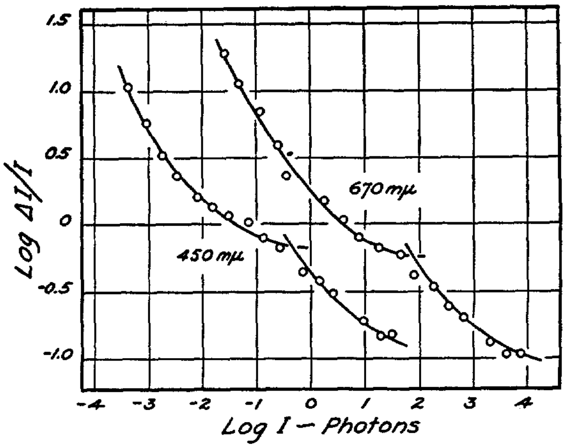

FIG. 8. Intensity discrimination for the colorblind eye. Two functions are present; these are the same with extreme red or violet light.

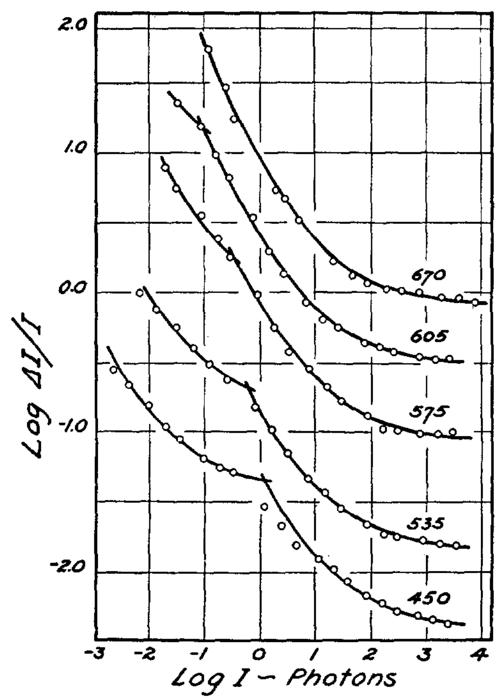

FIG. 9. Intensity discrimination for different spectral regions for the normal eye. Rod function is absent with red light but appears with the other colors. The ordinates apply to the data for yellow light in the middle; those for orange and red have been raised 0.5 and 1.0 log units respectively, and those for green and blue have been lowered 0.5 and 1.0 units respectively.

portion where they appear in the data of the colorblind. Obviously, the moment we use light in which the rod curve becomes less extensive so that these high intensity points fall beyond the rod-cone intersection point, they would no longer become evident in the normal data, and that indeed is the case.

SUMMARY

1. The visual functions of a completely colorblind individual are compared with those of the normal. The sensibility distribution in the spectrum has a maximum at 520 mμ at all brightnesses and thus corresponds to rod vision alone. This is confirmed by studies of dark adaptation which show final thresholds like those usually found for rod vision. Dark adaptation, measured both centrally and peripherally in the retina, is a single continuous function, and regardless of the brightness of the preceding light adaptation, is of the rapid type only, such as that found for the normal following low light adaptation. Visual acuity also shows a single continuous function like that for rod vision.

2. Both critical fusion frequency and intensity discrimination show two sections, one at low and the other at high intensities with a sharp transition from one to the other. Intensity discrimination is as good as for the normal eye, and covers much the same range. The maximal critical fusion frequency is only about 20 cycles per second as compared to 55 cycles for the normal.

3. The two sections shown by the colorblind eye for intensity discrimination and fusion frequency possess the spectral sensitivity of rod vision since the relative positions on the intensity scale are not influenced by using different parts of the spectrum.

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