THE INFLUENCE OF LIGHT ADAPTATION ON SUBSEQUENT DARK ADAPTATION OF THE EYE*

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I

Rod and Cone Adaptation

Human dark adaptation, though described by Aubert in 1865 and first measured by Piper in 1903, is still inadequately known. The early data of Piper seemed to show that dark adaptation was an exclusive function of the rods. Only after the measurements of foveal cone adaptation had been made (Hecht, 1921) was the reason for this apparent: cone adaptation is so fast that Piper missed it completely. The confirmation and extension of these results by Kohlrausch (1922) emphasized the existence of both cone and rod dark adaptation, and showed that the two are to a certain extent sharply separated in time.

Following adaptation to ordinarily bright lights, dark adaptation occurs in two parts. The first begins at once; it is rapid, and is due to cone function. The second part shows up somewhat later; it is slow, and is due to rod function. Under these circumstances, cone adaptation is over in 3 or 4 minutes, whereas rod adaptation takes at least 30 minutes. The intensity range covered by the rods and by the cones during dark adaptation depends on the color of the measuring light (Kohlrausch, 1922; 1931), on its area and retinal location (Hecht, Haig, and Wald, 1935), and on the duration and intensity of the preceding light adaptation (Müller, 1931; Wald and Clark, 1936; Winsor and Clark, 1936; Hecht and Haig, 1936).

* A preliminary account of these measurements was presented to the Optical Society of America in February, 1936 (*J. Opt. Soc. America*, 1936, **26,** 304), and to the American Physiological Society in March, 1936 (*Am. J. Physiol.*, 1936, **116,** 72).

In this paper we shall describe in detail the effects of the intensity of light adaptation on the dark adaptation which follows it, and show what bearing this information has on other data of visual function.

II

Apparatus and Method

There are five special points in our arrangements for making the measurements. First, the eye is light adapted with the observer in place so that measurements of dark adaptation can begin immediately. Second, the optical system gives a constant pupil size without the inconvenience of an artificial pupil. Third, violet light is used for measurement to secure the largest range of rod adaptation; and red light to secure the smallest. Fourth, each exposure to the measuring light is a flash of 0.2 second. Fifth, the measurements represent not quite the threshold of vision but a brightness about 3 times as high, secured by using the appearance of a black cross as criterion.

The data obtained in this way are only slightly more accurate than those usually made with a diffuse threshold criterion, indefinite time for determining the threshold, an artificial pupil as ordinarily used, and even without an artificial pupil at all. However, the arrangements make the work easier for the observer, and give him a feeling of certainty in making the measurements.

The observer sits in a dark box in a dark room, with his head fixed in a chin and head rest, facing a fixation point which is so circumscribed by diaphragms as to place his eye with precision at a given spot in space. This spot is at the focus of two lenses, one for light adaptation and the other for dark adaptation.

The source for light adaptation is a 3.8 volt flash-light bulb running on 0.3 amp., and placed 9 cm. from a pair of 11 diopter lenses 5 cm. in diameter each. The arrangement is shown in the lower right of Fig. 1. The eye is placed at the conjugate focus at an equal distance on the other side of the lenses, and sees the nearer lens evenly illuminated as a large field 30° in diameter. Its brightness is 400,000 photons, as determined by a binocular photometric match. In front of the lens, filters may be inserted to reduce the brightness. To save space a mirror is introduced between the lamp and the lens. In these experiments light adaptation is always with whole (white) light.

The light adaptation arrangement is mounted on a small board sliding on rails, and can be moved into the dotted position shown in Fig. 1 in front of the eye. At the close of light adaptation, it can be instantly slid out of the way so as to permit view of the second lens which focusses the measuring light on the same spot just inside the cornea of the eye at the pupil.

The light for measuring dark adaptation is a 3.8 volt flash-light lamp, carefully maintained at 0.28 amp., and placed 31 cm. from a 6.5 diopter lens, 3.6 cm. in diameter. The pupil of the eye is at the conjugate focus, at an equal distance on the other side of the lens, so that the lens appears as an evenly illuminated field. The image of the filament produced by the lens is less than 1 sq. mm., and therefore falls entirely within even the smallest dimensions assumed by the pupil of the eye. This arrangement avoids the necessity for an artificial pupil to keep

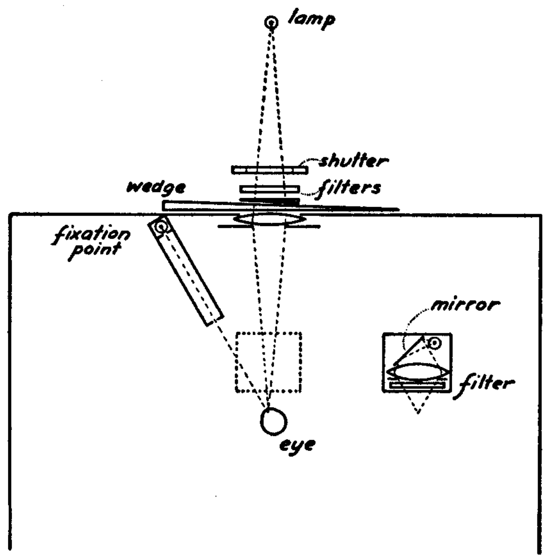

FIG. 1. Arrangement for adapting the eye to different intensities of light, and for measuring the course of the subsequent dark adaptation. In the set-up for light adaptation in the lower right, only one lens has been drawn in; actually there are two.

constant the area of the beam as it enters the eye. A circular diaphragm cuts the lens to form a field whose diameter is 5° visual angle. Extending over the entire field is an opaque cross, the width of whose arms occupies a visual angle of 30′ and thus corresponds to a visual acuity of 0.033, which is perceptible almost at the threshold of vision. The intensity of the measuring light is controlled by decimal neutral filters manipulated by the recorder, and by a neutral wedge moved by the observer. The color is secured either with a violet filter (Corning No. 511) which transmits light below 480 mμ only, or with a red filter (Wratten No. 88) which transmits light above 690 mμ only. The exposure is made with a photographic shutter by a cable in the hands of the observer. The arrangements are shown diagrammatically in Fig. 1.

The center of the light-adapting field and that of the measuring field are at 30° nasally on the retina. Note that the light-adapted area is 36 times the size of the measuring area. The fixation point is central, of course. Its intensity is varied by a rheostat controlled by the observer so as to be adequate for fixation but not too bright.

Light adaptation is for precisely 2 minutes. It is always preceded by a 10 to 15 minute stay in the dim light of the dark room in order to remove the effects of the variable conditions to which the observer has been exposed. Measurements are made at definite intervals after light adaptation, the observer determining the minimum brightness at which he can just see the black cross silhouetted against the field. He does this by moving the wedge to a position below the threshold, then turning it up in steps, and testing at each step by a flash until he can see the cross. The observer allows at least 20 seconds and frequently more between flashes in making a determination. In the first 2 minutes after light adaptation, dark adaptation is so rapid that a slightly different procedure is required. The wedge is brought to a given position which is maintained until the observer, who tests for its visibility at 10 or 15 second intervals, announces that he can see the field.

III

Measurements with Violet Light

Our measurements were made with the right eye only, and we three served as observers. S. H. and A. M. C. are emmetropes; C. H. is a myope, and used a minus 6 diopter lens in front of his eye as a correction. Five intensities of light adaptation were chosen after preliminary trials in order to cover the main range of the phenomenon. Each observer made two runs for each light adaptation and for each color. The data in Table I are the averages of the two runs using violet light for measurement. The intensities are in microphotons, that is, millionths of a photon. A photon is the retinal illumination produced when the eye looks through a 1 sq. mm. pupil at a surface whose brightness is $\pi/10$ millilamberts. The individual runs are nearly as regular and precise as the averages, but we use the averages because of day to day variations in threshold; the data are thus more homogeneous as a whole. The measurements for S. H. are shown graphically in Fig. 2. The data for the other two observers are the same in all essentials, and Fig. 2 will serve as a description for them as well.

TABLE I

Dark adaptation measured with violet light following adaptation to different intensities of white light. Time is in minutes; intensity in microphotons. The heavy values show color at the threshold.

Observer	400,000 photons		38,900 photons		19,500 photons		3,800 photons		263 photons	
	Time	Log I	Time	Log I	Time	Log I	Time	Log I	Time	Log I
S. H.	**0.19**	**8.26**	**0.10**	**7.16**	**0.17**	**6.96**	**0.18**	**6.22**	0.14	4.78
	0.52	**7.58**	**0.57**	**6.53**	**0.42**	**6.41**	**0.42**	**5.60**	0.36	4.38
	1.1	**7.07**	**1.0**	**6.11**	**0.97**	**6.11**	**0.67**	**5.25**	0.50	4.12
	1.5	**6.80**	**2.5**	**5.90**	**1.7**	**5.94**	**1.3**	**4.92**	0.90	3.88
	2.2	**6.37**	**3.3**	**5.81**	**2.7**	**5.75**	**2.1**	**4.72**	1.4	3.71
	2.7	**6.19**	**4.1**	**5.76**	**4.1**	**5.59**	**2.9**	**4.64**	2.9	3.57
	3.4	**6.00**	**5.3**	**5.75**	**5.1**	**5.42**	3.8	4.41	4.1	3.45
	4.4	**5.92**	**6.1**	**5.67**	6.3	5.17	4.9	4.15	5.3	3.33
	6.4	**5.80**	**7.1**	**5.61**	7.6	4.81	5.9	3.96	6.2	3.24
	7.7	**5.73**	**7.8**	**5.45**	9.2	4.38	7.7	3.60	7.2	3.07
	9.5	**5.68**	8.9	5.26	10.7	3.98	9.4	3.40	8.9	3.02
	10.7	**5.66**	9.9	4.99	11.9	3.70	10.6	3.16	10.5	2.91
	12.6	5.34	10.8	4.77	13.0	3.50	13.5	2.89	11.5	2.82
	14.3	4.78	12.5	4.28	14.4	3.28	15.0	2.80	13.1	2.80
	16.0	4.28	14.3	3.81	16.1	3.07	16.4	2.77	15.1	2.72
	16.7	4.11	15.4	3.52	17.8	2.92	18.2	2.62	17.3	2.61
	18.0	3.79	16.8	3.29	18.8	2.83	21.9	2.56	19.7	2.58
	19.6	3.55	18.6	3.13	20.0	2.79	23.7	2.49	23.5	2.51
	21.5	3.27	20.5	2.99	21.1	2.78	25.4	2.46	25.8	2.55
	23.0	3.20	22.5	2.92	24.5	2.64	28.8	2.47	27.5	2.51
	24.2	3.13	23.9	2.88	26.1	2.57			29.6	2.53
	25.9	3.08	26.0	2.79	27.7	2.57				
	28.5	2.97	29.3	2.69	29.8	2.58				
	30.8	2.88	32.0	2.55						
	33.4	2.84								
	36.0	2.78								
	38.6	2.72								
C. H.	**0.08**	**8.26**	**0.19**	**7.06**	**0.12**	**6.87**	**0.19**	**6.08**	0.12	4.91
	0.38	**7.12**	**0.66**	**6.47**	**0.42**	**6.26**	**0.64**	**5.28**	0.30	4.45
	0.65	**6.65**	**1.3**	**6.05**	**0.74**	**6.00**	**1.2**	**5.08**	0.74	3.97
	1.2	**6.31**	**1.8**	**5.86**	**1.4**	**5.87**	**2.0**	**4.82**	1.7	3.80
	2.3	**5.99**	**2.8**	**5.76**	**2.3**	**5.75**	2.5	4.70	2.4	3.57
	3.1	**5.78**	**4.3**	**5.59**	**3.2**	**5.66**	3.3	4.59	3.3	3.42
	4.0	**5.64**	**5.4**	**5.57**	**4.3**	**5.54**	4.3	4.45	4.5	3.37
	4.8	**5.57**	**6.3**	**5.54**	5.2	5.40	5.6	4.30	5.6	3.22
	5.7	**5.55**	**7.5**	**5.50**	5.9	5.17	6.8	4.06	7.0	3.11
	7.8	**5.54**	8.1	5.27	6.8	4.98	7.9	3.82	8.1	3.02
	10.5	**5.48**	9.2	5.02	7.9	4.68	9.2	3.67	9.8	2.98
	12.4	**5.46**	10.3	4.64	9.0	4.45	10.4	3.51	10.7	2.93
	13.5	**5.41**	11.7	4.42	11.0	4.05	11.8	3.37	12.2	2.92

TABLE I—*Concluded*

Observer	400,000 photons		38,900 photons		19,500 photons		3,800 photons		263 photons	
	Time	Log *I*	Time	Log *I*	Time	Log *I*	Time	Log *I*	Time	Log *I*
C. H.—*Concluded*	**14.3**	**5.33**	13.4	4.06	11.9	3.88	14.3	3.24	14.1	2.86
	15.1	5.16	15.1	3.82	13.3	3.73	15.9	3.14	19.7	2.89
	16.5	4.86	17.7	3.63	15.5	3.43	18.2	3.08	21.9	2.78
	17.8	4.50	19.2	3.50	17.5	3.36	19.4	3.03	24.8	2.86
	19.4	4.28	22.9	3.30	18.7	3.28	23.7	3.00	28.9	2.82
	21.0	4.02	24.2	3.27	21.8	3.15	26.7	2.92		
	22.5	3.76	28.3	3.15	24.4	3.05	29.8	2.94		
	24.0	3.55	30.6	3.12	27.5	3.01	33.1	2.90		
	25.7	3.47	32.8	3.08	30.4	3.01				
	27.8	3.42	34.5	3.06	34.3	3.02				
	30.1	3.34	39.9	3.07	36.2	2.96				
	38.2	3.28	43.5	3.04						
A. M. C.	**0.14**	**8.26**	**0.18**	**7.21**	**0.11**	**6.96**	**0.11**	**6.32**	0.13	4.78
	0.39	**7.50**	**0.51**	**6.75**	**0.33**	**6.56**	**0.40**	**5.65**	0.30	4.03
	0.69	**7.12**	**1.2**	**6.23**	**0.55**	**6.26**	**0.80**	**5.16**	0.83	3.57
	1.2	**6.56**	**1.8**	**5.99**	**1.1**	**6.00**	**1.3**	**5.05**	1.6	3.38
	1.8	**6.26**	**2.4**	**5.84**	**1.6**	**5.83**	**1.8**	**4.91**	2.6	3.25
	2.4	**6.03**	**3.4**	**5.70**	**2.4**	**5.72**	**2.5**	**4.84**	3.7	3.05
	3.6	**5.78**	**5.6**	**5.65**	**3.3**	**5.61**	**3.2**	**4.71**	5.0	2.93
	5.1	**5.61**	**7.9**	**5.61**	**4.2**	**5.60**	4.1	4.50	5.8	2.84
	7.0	**5.54**	**9.3**	**5.47**	**5.4**	**5.57**	4.9	4.28	6.8	2.80
	8.1	**5.43**	10.3	5.28	**6.2**	**5.54**	5.8	4.08	8.2	2.68
	9.6	**5.38**	11.2	5.16	7.1	5.43	6.7	3.89	10.6	2.55
	11.3	**5.39**	12.0	4.66	7.7	5.27	7.6	3.72	12.1	2.48
	12.5	**5.43**	13.7	4.41	8.1	5.08	8.5	3.63	14.0	2.42
	13.3	**5.30**	14.9	4.04	9.1	4.81	9.7	3.53	15.8	2.37
	14.5	5.22	16.2	3.70	10.4	4.46	10.5	3.28	19.1	2.29
	15.2	5.11	17.9	3.48	11.7	4.13	11.4	3.14	20.8	2.21
	16.1	4.83	19.0	3.37	12.7	3.95	12.9	3.07	25.7	2.19
	16.9	4.56	20.6	3.13	14.0	3.65	14.6	2.87	27.6	2.19
	17.9	4.36	23.5	3.03	15.2	3.45	15.7	2.79	30.5	2.20
	18.6	4.09	26.1	2.89	16.4	3.28	17.0	2.74		
	19.8	3.84	28.1	2.83	17.9	3.10	18.1	2.74		
	22.0	3.48	29.9	2.79	19.8	2.95	20.2	2.59		
	23.5	3.30	32.0	2.73	21.0	2.86	22.9	2.45		
	25.2	3.11	34.7	2.72	23.2	2.81	24.3	2.45		
	27.4	2.99	37.4	2.69	26.0	2.69	26.0	2.36		
	30.4	2.89	39.1	2.68	29.1	2.61	28.1	2.42		
	34.1	2.85			30.4	2.60	31.0	2.33		
	37.9	2.77			31.7	2.60	32.4	2.36		
					34.3	2.52	35.5	2.32		

Following light adaptation to 400,000 photons, dark adaptation as measured with extreme violet light shows a striking separation into two sections, obvious in Fig. 2. Judging by all that is already known about dark adaptation (Kohlrausch, 1931; Hecht, Haig, and Wald, 1935), intensity discrimination (Hecht, 1935), and flicker (Hecht and Shlaer, 1936), the first section must be identified as predominantly cone adaptation and the second section as predominantly rod adaptation. This identification is immensely strengthened by the

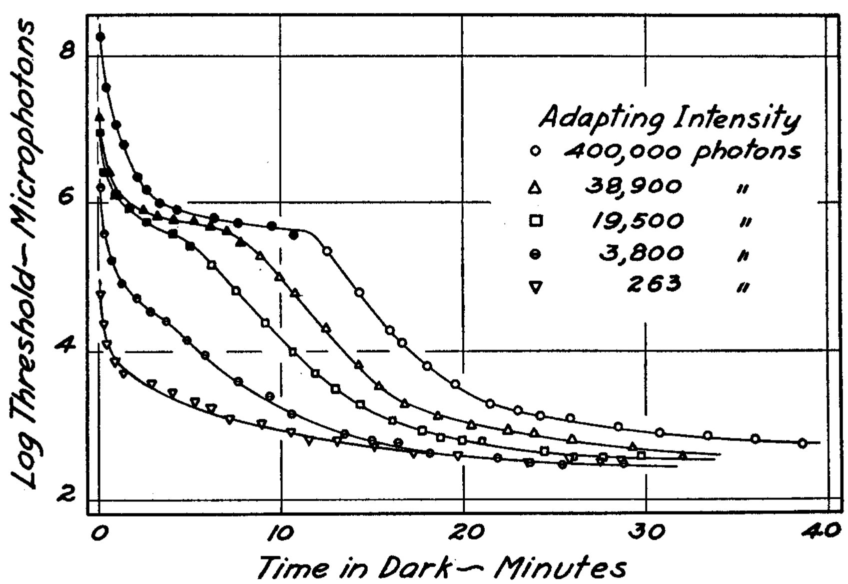

FIG. 2. The course of dark adaptation as measured with violet light following different degrees of light adaptation. The filled-in symbols indicate that a violet color was apparent at the threshold, while the empty symbols indicate that the threshold was colorless.

fact that all the measurements comprising the first section are reported by the observer as distinctly showing a violet color at the threshold of observation, whereas all the measurements comprising the second section are reported as colorless at the threshold. The points reported as colored are shown as black circles in Fig. 2 and are printed in heavier type in Table I, while those reported as colorless are the clear circles in Fig. 2. The transition between colored primary section and the colorless secondary section is quite sharp; occasionally the last colored point is less saturated than the others.

This description of the events in dark adaptation holds also for the measurements which follow light adaptation to 38,900 and to 19,500 photons. In all three, cone and rod adaptation are separate and are distinctly associated with colored and colorless sensations at the threshold. There are, however, certain obvious quantitative differences. As the light adaptation intensity increases, so also does the range of cone dark adaptation. Following the highest light adaptation, the cone dark adaptation range is about 3 log units, which compares favorably with the rod adaptation range. The range of rod dark adaptation, however, remains unchanged, but its appearance is more delayed the higher the light adaptation. This is an important point, and is also apparent in Müller's measurements in which he varied the duration of the preceding light adaptation.

After 263 photons light adaptation, the dark adaptation threshold never shows any color. A. M. C. occasionally records the first point as possibly colored. On the other hand, dark adaptation following exposure to 3,800 photons shows a course which is midway between high and low light adaptation. The first few measurements are definitely reported as violet, and are indicated as such by the use of filled-in symbols in Fig. 2. After a few minutes, the threshold becomes colorless and the transition between the two is fairly gradual.

The color response in this case is not too certain near the transition, but above it it is quite clear. What is startling, however, is that color is definitely associated with threshold intensities well below those which show no color following adaptation to the high intensities. We do not know what this means, and whether it is a special property of violet light; we are therefore investigating other colors as well.

IV

Displacements in Time

Looking at Fig. 2 as a whole, it is apparent that the higher the initial light adaptation, the longer does the eye require to reach a given threshold during dark adaptation. This is true for the colored primary portion as well as for the colorless secondary portion, but shows more strikingly for the latter. For the three high light adaptations, where the range of the colorless portion is the same, it is as if the rod curve as a whole were moved so as to appear later the higher the light adaptation.

In order to compare the time of appearance of the two sections at the different adapting intensities, we have determined the time in the dark which has to elapse for the eye to reach a specific threshold intensity level following each of the light adapting intensities. For the colored primary portion, the level selected is log $I = 6.25$, while for the colorless secondary portion the level selected is log $I = 3.75$. The determinations were made graphically from the data in Table I. They are given in Table II and are shown graphically in Fig. 3, where

TABLE II

Relation between intensity of adapting light and time of appearance of a specific threshold during dark adaptation. Threshold for colored portion is log $I = 6.25$; threshold for colorless portion is log $I = 3.75$. Time is in minutes.

Adaptation Intensity	Colored portion			Colorless portion		
	S. H.	C. H.	A. M. C.	S. H.	C. H.	A. M. C.
photons						
263				1.4	1.7	0.5
3,800	0.20	0.18	0.20	6.9	8.5	7.6
19,500	0.65	0.35	0.55	11.7	12.1	13.5
38,900	0.75	0.90	1.10	14.5	16.0	16.3
400,000	2.45	1.45	1.80	18.3	22.5	20.3

the colored portion is in the upper, smaller figure, while the colorless portion is in the lower, larger figure.

It is clear that the colorless secondary portion appears later as the adapting light intensity is increased; the relation between the time of appearance and the logarithm of the adapting intensity is sigmoid.

The measurements for the colored primary portion show that for it too the time in the dark required to arrive at a specific threshold increases with the logarithm of the adapting intensity. However, whereas the relationship for the colorless rod section is nearly completely covered by the range of intensities used, the relationship for the colored cone section begins to be effective only at the higher light adaptations. It is likely that the relation here would also be sigmoid if we explored adapting intensities still higher than those used.

The meaning of these shifts in the time of appearance of a given threshold with the intensity of the adapting light is fairly clear. Blanchard (1918) has shown that as the light adapting intensity increases, the threshold at zero time in the dark also increases. Dark adaptation therefore has a larger range to cover, and a given threshold will be reached later and later. To a certain extent, it is as if the curve of dark adaptation for each portion were shifted to the right on the time axis. Since the rods and cones are different sensory systems

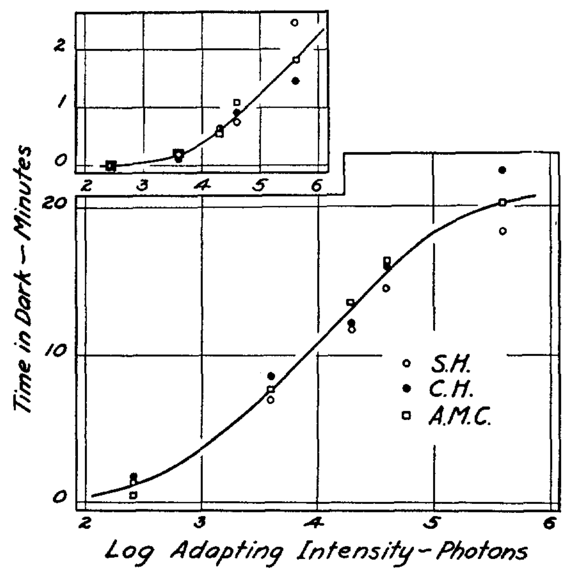

FIG. 3. The relation between the intensity of light adaptation and the time required for the eye to reach a given threshold in the dark. The lower data are for a colorless threshold, indicating rod function, while the upper data are for a color threshold indicating cone function.

with different sensibilities and different rates of dark adaptation, it is not surprising that the amount of shift is different for each system.

Fig. 3 shows that the time displacements for the cones are short, of the order of 1 or 2 minutes, while for the rods they are about 10 times as long. The time for complete dark adaptation of the two systems also differs in about the same ratio: cone adaptation is nearly complete in 4 or 5 minutes, while rod adaptation takes about 10 times as long. Thus the time shifts shown by the cones and by the rods are about the same fractions of the total adaptation time for each.

V

Similarities among Individuals

Dark adaptation has usually been considered a fairly variable property of vision, and Matthey (1932) has felt it necessary to measure over 50 people in order to arrive at an average or standard curve of dark adaptation useful for clinical purposes. In our experience of over 10 years, we have found that most of the variations in the data arise from the failure to specify conditions of measurement. The major differences may be eliminated by fixing the intensity and duration of light adaptation, and the position, area, and color of the light used for measuring dark adaptation.

With all these specified, there is nevertheless a slight day to day variation even in a single experienced investigator. The final threshold varies and the time of appearance of the two parts of adaptation varies. What is specially significant is that the variations may be different in sign and in extent for the two parts of dark adaptation.

In spite of these slight differences, the shapes of the data are identical at different times for the same observer, and even for the three observers. For example, although the time of appearance of the rod curve following the highest light adaptation differs by about 2 minutes for A. M. C. and S. H., nevertheless the rod curves for the two investigators are identical if the data of one are shifted 2 minutes along the time axis. To show this, we have superimposed in Fig. 4 the data for the three observers, but have kept the colored and colorless portions of the data separate. We have included in Fig. 4 only the highest three light adaptations, because in them the two sections of the subsequent dark adaptation are easily separable. For each person there has been made the necessary time shift, and whenever required, a small vertical intensity shift. It is apparent that the three observers show identical curves under these circumstances.

Because of the individual differences in time of appearance of the transition from cone section to rod section, a simple averaging of data of different individuals is bound to yield an erroneous appearance of the dark adaptation curve. The region of transition, from being a reasonably abrupt change for each individual, will become smooth and gradual in the average, and may indeed almost disappear. This is actually the case with Matthey's average curve for 54 individuals, which shows almost no sign of transition, though the measurements were made with the apparatus and specified conditions worked out by Müller (1931) whose measurements on his own eye clearly show the usual fairly abrupt transition (*cf.* Hecht, 1937 *a*). If it is necessary to have an average dark adaptation curve for clinical purposes, the cone sections and the rod sections should be averaged separately, and

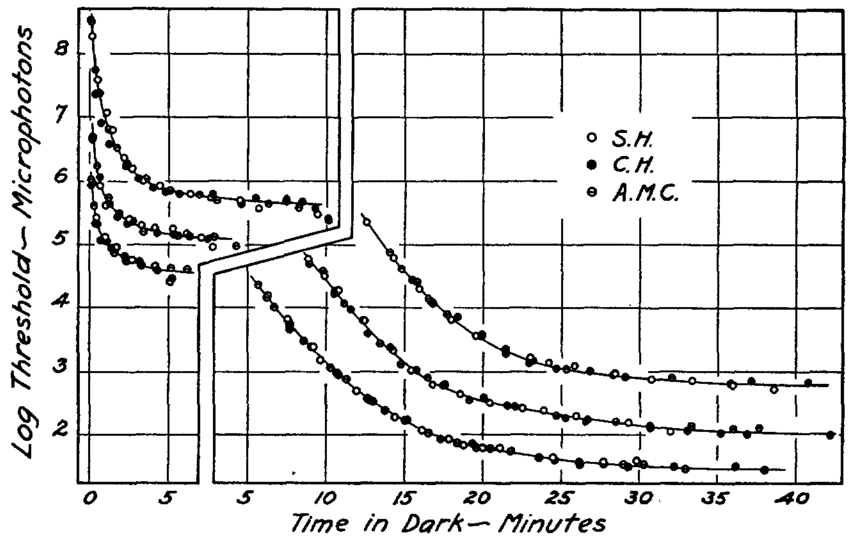

FIG. 4. Dark adaptation following the highest three intensities of light adaptation. The colored cone thresholds are plotted separately from the colorless rod thresholds. The abscissas are the same for all the data; the ordinate scale, however, applies only to the upper data because the two other sets have been displaced 0.5 and 1.0 log units respectively downward.

the two combined at a point which is the average transition time for the same observers.

The curves drawn through the cone portions in Fig. 4 are the same for the three adapting intensities. By making the time shifts indicated in Fig. 3 the data themselves may be superimposed, showing that they fall on the same curve of which more and more becomes available as the light adaptation intensity increases. The three curves for the colorless portions in Fig. 4 are very nearly but not quite the same. The slope of the rising branch becomes just perceptibly faster the higher the light adaptation. However, the difference is so slight that it is possible to superimpose the three sets of points, and to draw one curve through them. Apparently then, above a light adaptation intensity of 20,000 photons, the subsequent dark adaptation has a fixed shape but a variable position on the time axis.

VI

Measurements with Red Light

In terms of the visibility curves of cone vision and rod vision (*cf.* Hecht, 1937 *a*), we may expect the difference in threshold between rods and cones to be greatest with violet light, and least with red light. In fact, with extreme red light (Hecht, 1921; Kohlrausch, 1922; 1931) the difference in threshold may disappear entirely, so that the resulting dark adaptation curve records only the more rapidly acting cone function.

Using such extreme red light we repeated our measurements of dark adaptation following different intensities of light adaptation. The data are in Table III, and are the averages of two runs for each of the three observers. We used only four intensities of light adaptation; the fifth was too low to cause any dark adaptation measurable with red light.

Fig. 5 shows the measurements of A. M. C. and brings to light several interesting things. The data behave much like the primary cone sections with violet light shown in Fig. 2, except that the red threshold remains at the level it reaches after the first 5 minutes. Clearly this is pure cone adaptation. Nevertheless, even with red light, rod adaptation makes its appearance. Following light adaptation to 400,000 photons, the threshold during dark adaptation is red in appearance for over 35 minutes. This is shown by the solid circles in Fig. 5. After 35 minutes there appears a slight drop in threshold, and this new threshold is characterized by being either very dilute pink or quite colorless (open circles). Moreover, just as with violet light, the drop in threshold and the loss of color come sooner the lower the intensity of preceding light adaptation. Fig. 5 shows this quite clearly and leaves no doubt that the change records the belated appearance of the bottom of the rod adaptation curve.

TABLE III

Dark adaptation measured with red light following adaptation to different intensities of white light. Time is in minutes; intensities in microphotons.

Observer	400,000 photons		38,900 photons		19,500 photons		3,800 photons	
	Time	Log *I*	Time	Log *I*	Time	Log *I*	Time	Log *I*
S. H.	0.55	7.87	0.28	7.85	0.15	7.63	0.08	6.93
	1.0	7.15	0.53	7.44	0.40	7.14	0.25	6.50
	1.7	6.71	1.1	6.91	0.68	6.97	0.48	6.25
	2.3	6.34	1.7	6.63	1.3	6.56	0.99	6.07
	2.9	6.22	2.3	6.38	1.8	6.34	3.0	6.03
	3.8	5.98	3.0	6.12	2.9	6.00	4.3	5.94
	4.5	5.89	3.9	5.98	4.7	5.99	7.4	5.90
	5.7	5.86	5.2	6.01	9.3	6.04	9.5	5.92
	7.1	5.84	6.5	5.99	11.5	5.98	11.4	5.89
	9.0	5.81	10.3	6.00	13.7	5.98	13.0	5.87
	10.8	5.83	14.0	6.01	16.6	5.92	15.4	5.86
	14.4	5.86	16.1	5.97	19.4	5.93	19.9	5.79
	16.9	5.76	18.0	5.94	21.6	5.87	24.0	5.77
	18.5	5.80	20.7	5.92	24.5	5.80	27.0	5.78
	20.0	5.79	22.2	5.93	27.5	5.76	30.6	5.75
	21.6	5.76	24.9	5.91	30.6	5.77	34.7	5.75
	23.9	5.83	29.6	5.89	33.1	5.68		
	27.7	5.76	32.5	5.84	36.4	5.67		
	29.6	5.77	37.5	5.78				
	33.3	5.78						
	36.0	5.75						
	39.5	5.79						
C. H.	0.36	7.85	0.14	7.63	0.07	7.37	0.10	7.28
	0.90	7.48	0.41	7.14	0.35	6.64	0.48	6.50
	1.3	7.27	0.81	6.73	0.93	6.28	0.83	6.38
	2.0	6.85	1.5	6.21	1.7	6.11	1.9	6.25
	3.0	6.54	2.9	6.05	3.0	6.05	3.5	6.18
	4.2	6.22	4.2	5.98	4.0	6.00	4.9	6.19
	5.4	6.09	7.6	6.03	5.8	5.97	6.6	6.13
	6.8	6.06	9.0	6.02	8.5	6.09	9.2	6.10
	9.0	6.05	10.6	6.03	10.9	6.02	14.5	6.06
	10.9	6.04	14.2	6.01	14.2	6.00	20.2	5.83
	14.8	6.08	18.1	6.06	21.2	5.86	22.0	5.77
	16.2	6.04	21.0	6.02	23.0	5.83	27.5	5.77
	20.6	6.07	26.1	6.04	26.4	5.82	30.8	5.73
	26.8	6.17	31.1	5.98	30.5	5.79		
	33.0	6.22	36.8	5.98	33.8	5.77		

TABLE III—*Concluded*

Observer	400,000 photons		38,900 photons		19,500 photons		3,800 photons	
	Time	Log *I*	Time	Log *I*	Time	Log *I*	Time	Log *I*
A. M. C.	0.30	7.85	0.15	7.71	0.19	7.28	0.09	6.58
	0.60	7.33	0.35	7.27	0.35	6.96	0.36	6.10
	0.93	7.02	0.76	6.71	0.80	6.57	0.81	5.78
	1.4	6.69	1.2	6.48	1.1	6.36	2.2	5.68
	1.8	6.41	1.7	6.26	1.5	6.22	3.2	5.63
	2.6	6.12	2.5	5.91	1.9	6.04	4.4	5.63
	3.4	5.88	3.5	5.78	2.6	5.86	6.1	5.62
	4.4	5.81	5.2	5.73	4.0	5.73	7.0	5.54
	5.9	5.72	6.8	5.66	5.8	5.67	8.0	5.46
	7.6	5.70	8.2	5.62	6.7	5.67	8.8	5.49
	8.6	5.60	12.8	5.69	8.1	5.67	11.9	5.48
	10.2	5.61	14.3	5.69	9.3	5.63	14.2	5.43
	12.5	5.66	16.6	5.65	11.2	5.66	15.8	5.29
	14.1	5.66	19.4	5.60	12.6	5.60	18.4	5.21
	17.3	5.66	22.1	5.61	14.2	5.56	21.4	5.22
	19.4	5.66	26.1	5.56	16.4	5.59	23.8	5.23
	24.9	5.67	28.3	5.55	17.9	5.61	27.2	5.19
	27.4	5.64	30.6	5.55	19.9	5.54	28.8	5.16
	31.7	5.64	33.0	5.55	21.0	5.54	31.4	5.16
	37.0	5.56			22.0	5.51		
	40.0	5.57			24.6	5.50		
					27.1	5.52		
					30.5	5.43		
					33.1	5.48		

To the first three curves in Fig. 5, we have added as crosses the cone portions of the measurements with violet light made by A. M. C. It is apparent that they correspond reasonably well with the red light measurements, and thus furnish additional evidence of their character as cone function. After the highest light adaptation the violet light measurements tend to drop below the red light measurements as the former approach the transition point for rod appearance.

As with the cone portions of the violet light data, the same curve may be drawn through the three series. It is merely its vertical extent and its position on the time axis which change. The displacement along the time axis is also much as with the violet light data. In fact the average shift plotted against the logarithm of the adapting intensity has precisely the same slope and appearance as the violet light data in Fig. 3. All this confirms the conclusion that the two series of measurements record the same phenomenon, namely cone adaptation.

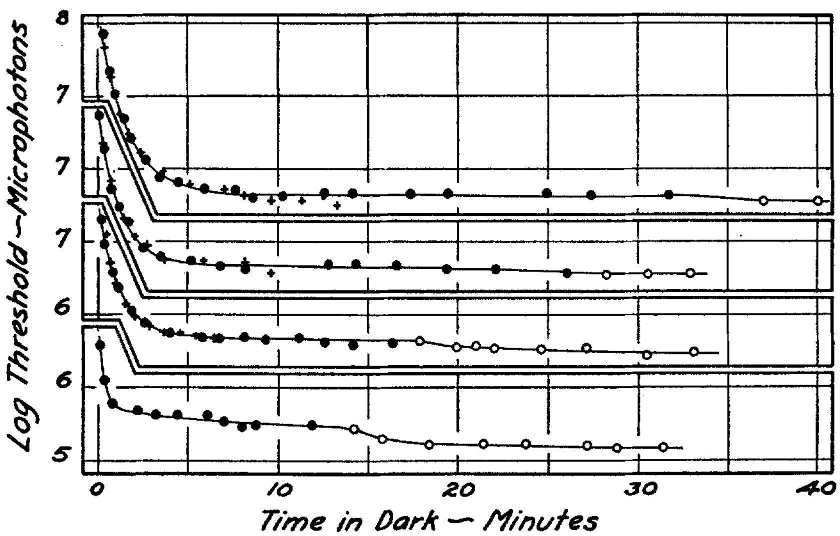

FIG. 5. The course of dark adaptation as measured with red light following different degrees of light adaptation. Here too the filled-in symbols indicate that the threshold was colored red, and the empty symbols indicate that the threshold was colorless.

VII

Two Types of Rod Adaptation

These data are of theoretical interest in a way that has already been emphasized by Winsor and Clark (1936) and by Wald and Clark (1936) from a different point of view. Rod dark adaptation apparently can follow two different courses depending upon the intensity of the light used for preadaptation. Fig. 2 shows that following low intensities of light adaptation, rod dark adaptation begins at once and changes its rate so that the points leave the log I axis gradually and approach the final threshold on the time axis asymptotically. Following high intensities of light adaptation, rod dark adaptation does not show itself at once, and when it does appear, its speed seems to remain roughly constant for some time so that its curve on a t-log I plot begins in an almost linear fashion. It leaves the log I axis sharply and only after several minutes does it begin to slow up and approach the t axis asymptotically. We may refer to these two kinds of rod dark adaptation as the rapid type and the delayed type. Data at intermediate intensities present a combination of the two; in Fig. 2 showing the data for S. H., the two are just apparent even in the lowest curve.

To judge by these two courses of dark adaptation, it is justifiable to conclude, as have Winsor and Clark, and Wald and Clark, that the accumulation of sensitive material, which dark adaptation undoubtedly represents, may occur in two ways. It is important to recognize precisely when these two types of adaptation appear. Examination of Fig. 2 shows that the delayed type is definitely established above 20,000 photons, and that the rapid type is clearly established below 200 photons. Between these two values, the adaptation shows both characteristics.

It is significant that even the lowest preadaptation intensity here used is many times higher than that required to achieve a maximum effectiveness of the rods in all the other functions in which they have been studied. For example, the maximum flicker frequency shown by the rods is achieved between 0.1 and 1 photon (Hecht and Smith, 1936). Similarly, the maximum visual acuity attained by the rods is also apparent below 1 photon (*cf.* Hecht, 1937 *a*) and so is the maximum intensity discrimination of the rods (Hecht, 1935), and the maximum instantaneous threshold (Blanchard, 1918; Hecht, 1937 *b*). In other words, at a stationary state produced by a retinal illumination of 1 photon, the visual functions of the rods are at their maximum. Therefore the delayed type of dark adaptation first appears only after adaptation to intensities 200 times as great as those which are known to produce the maximum visual effectiveness in the rods and becomes established only at intensities 20,000 times as great. Thus, what we call dark adaptation following preadaptations above 20,000 photons is probably a different phenomenon than dark adaptation following preadaptations below 200 photons, though in both cases the same sensitive material, visual purple, accumulates in the rods.

Kühne (1879) first showed that visual purple in the retina may be regenerated by two methods after being bleached: from the products of decomposition, and *de novo*. This has been confirmed and developed by Wald (1935 *a*, *b*) in a series of excellent researches with various retinas; moreover, Wald has been able to identify components of this visual cycle as vitamin A and a carotenoid, retinene, and has shown that retinene is the first product of bleaching in the retina and becomes converted later into vitamin A. We have recently been able to regenerate visual purple in solution from the products of its bleaching by light (Hecht, Chase, Shlaer, and Haig, 1936).

It is quite likely that the two modes of formation of visual purple have different courses and different velocities. Wald and Clark (1936) have suggested that the faster course is the regeneration by way of photoproducts, and the slower by way of fresh substances from the retina or from the blood stream. These would then correspond to the rapid and the delayed types of dark adaptation which we find here. We are now engaged in measurements which will formulate this correspondence more precisely.

SUMMARY

The course of dark adaptation of the human eye varies with the intensity used for the light adaptation which precedes it. Preadaptation to intensities below 200 photons is followed only by rod adaptation, while preadaptation to intensities above 4000 photons is followed first by cone adaptation and then by rod adaptation.

With increasing intensities of preadaptation, cone dark adaptation remains essentially the same in form, but covers an increasing range of threshold intensities. At the highest preadaptation the range of the subsequent cone dark adaptation covers more than 3 log units.

Rod dark adaptation appears in two types—a rapid and a delayed. The rapid rod dark adaptation is evident after preadaptations to low intensities corresponding to those usually associated with rod function. The delayed rod dark adaptation shows up only after preadaptation to intensities which are hundreds of times higher than those which produce the maximal function of the rods in flicker, intensity discrimination, and visual acuity. The delayed form remains essentially

constant in shape following different intensities of preadaptation. However, its time of appearance increases with the preadaptation intensity; after the highest preadaptation, it appears only after 12 or 13 minutes in the dark.

These two modes of rod dark adaptation are probably the expression of two methods of formation of visual purple in the rods after its bleaching by the preadaptation lights.

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