

## VISUAL ADAPTATION AND CHEMISTRY OF THE RODS\*

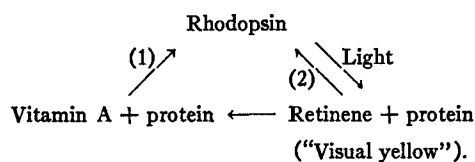
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Sixty years ago Kühne<sup>1</sup> concluded from direct observation of frog and rabbit retinas that visual purple may be synthesized by two processes: a slow "neogenesis" from colorless initial stages, following intense and protracted irradiation; and a three to four times faster "anagenesis" from yellow initial stages, following "incomplete bleaching."

Neogenesis and anagenesis may now be identified with the formation of rhodopsin from vitamin A and from retinene respectively, as described in part in the equations (Wald, 1935-36 *a, b*):



The synthesis and removal of rhodopsin in the retina are reflected in the sensory phenomena of dark and light adaptation (Hecht, 1919-20). It should be possible, therefore, to test the reality of the chemical formulation *in vivo* with properly designed adaptation experiments.

The chemical equations permit the following specific predictions concerning dark adaptation:

1. Exposure of the dark adapted eye to a short, intense flash of light should convert a large quantity of rhodopsin to retinene, but little retinene should have had time to form vitamin A. Directly following

\* A report of these experiments was presented at the Spring meeting of the American Physiological Society, 1936. A partial abstract has been published (Wald and Clark, 1936).

<sup>1</sup> Ewald and Kühne, 1878, p. 276; Ayres and Kühne, 1878, p. 234; summarized by Kühne, 1879, p. 317.

such exposure, dark adaptation should depend principally upon reaction (2), and so should be relatively rapid.

2. Long illumination of the eye should bring the visual cycle to a steady state. Dark adaptation following such exposure should contain a maximal contribution from reaction (1), and so should be relatively slow.

3. Since retinene is removed to form vitamin A in addition to rhodopsin, dark adaptation as it proceeds should depend increasingly, and finally entirely, upon reaction (1). The latter portions of dark adaptation, therefore, should display the comparatively simple character of the slow process alone.

Our experiments verify these predictions. Between given initial and final thresholds the rods may dark adapt along many paths, depending upon the period and intensity of the preceding light adaptation. The early portions of dark adaptation are rapid following short, slow following long irradiation. As dark adaptation proceeds, the slow process grows increasingly prominent, and occupies completely the later stages of adaptation.

The complete description of light adaptation includes these phenomena. Following increasing lengths of exposure to light of constant intensity, the visual threshold rises, as the concentration of rhodopsin decreases. Independently, the speed of dark adaptation falls, as the proportion of vitamin A to retinene rises. Both variations cease as the visual cycle attains a steady state, the end of the light adaptation process.

## I

### *Methods*

*Light Adaptation.*—The subject faced an opal glass screen  $18.3 \times 23.5$  cm. placed about a foot from the eyes. This transmitted the illumination from a 1000 watt lamp mounted upon a track. Brightness was varied by moving the lamp toward and away from the screen. No artificial pupil was used.

In most experiments the two eyes were adapted to different brightnesses and for different times. For this the subject wore goggles, over either window of which a blind or a neutral filter could be fitted. To adapt the eyes for different periods, the blind was placed over one eye during the initial portion of a light adaptation, and removed for its final portion. To adapt the eyes to different brightnesses, a neutral filter was fitted over one eye, the other receiving the full

illumination from the screen. Both procedures were frequently combined. One eye, fitted with a filter, was adapted for a long period to a low intensity; the other eye, darkened for the first portion of the irradiation, was exposed for a shorter interval to the full adapting intensity.

*Dark Adaptation.*—Periodically during dark adaptation, the threshold of either eye was measured, using a circular test field,  $0.44^\circ$  in diameter, located  $9.8^\circ$  to the right of a small, bright fixation point. The latter was illuminated continuously, the field itself exposed for short flashes by means of a camera shutter operated by the subject and set at  $1/50$  second. The intensity of the test field was regulated with the adaptometer of Derby, Chandler, and Sloan (1929), loaned to us through the courtesy of Dr. J. Herbert Waite of Boston. In this instrument the illumination is varied by means of a pair of neutral circular wedges, rotating in opposite directions so as to compensate each other. The adaptometer was mounted in a special assembly and was recalibrated by Dr. C. P. Winsor of this Laboratory.

*Procedure.*—The subject was left in complete darkness for 15 to 30 minutes, depending upon previous exposure to light. She was then light adapted for the prescribed interval. At its close the adapting light was turned off. The observer, having fixated her eye, proceeded to flash the test illumination initially set at a sub-threshold intensity. Between clicks of the shutter the operator raised the intensity by regular steps of about 0.02 log unit, until the subject reported that the field had been seen. The operator noted time and wedge reading. Periodically this procedure was repeated. All observations were monocular, usually with alternate eyes. It was found that readings could be made as often as desired—occasionally up to twice within a minute upon a single eye—without materially disturbing the course of adaptation.

#### *Measurements*

*Light Adaptation to Various Intensities, Long Exposures.*—The dark adaptation of the subject's left eye was measured following 7 minute exposures to 30.3, 105, and 643 millilamberts. Individual threshold determinations are presented in Table I and Fig. 1.

Dark adaptation following exposure to 643 millilamberts shows a distinct break at about 4 minutes. This occurs earlier and less abruptly in the 105 millilambert curve, and is absent from the 30.3 millilambert function. Similar breaks appear in the uppermost curves of Figs. 2 and 3. They are due to transitions from cone to rod thresholds (Hecht, Haig, and Wald, 1935-36). The cone functions precede the breaks, and when present seriously hinder the experiments by preventing the measurement of initial rod thresholds. The extended smooth functions which follow the breaks are due to rods, and are the concern of the present investigation.

If rod dark adaptation curves depended upon a single process, they should all form segments of a single function. However, the curves shown in Fig. 1 vary in form, and cannot be superimposed by any displacement on the time axis. The general implications of this variation have been discussed by Winsor and Clark (1936). The first few minutes of rod dark adaptation become markedly slower as the intensity

TABLE I

Dark adaptation following 7 minutes exposure to 30.3, 105, and 643 millilamberts; and following 10 seconds exposure to 1890 millilamberts. Subject A.-B.C. Time in minutes, thresholds in millilamberts.

Left eye 7 min. exposure						Right and left eyes 10 sec. exposure	
30.3 millilamberts		105 millilamberts		643 millilamberts		1890 millilamberts	
Time in dark	Log threshold	Time in dark	Log threshold	Time in dark	Log threshold	Time in dark	Log threshold
0.5	2.26	0.7	2.68	0.5	2.99	0.6	1.07
1.7	3.86	1.4	2.49	1.5	2.85	1.0	2.80
2.7	3.77	2.3	2.42	3.3	2.82	1.4	2.68
3.5	3.68	3.1	2.32	4.2	2.66	2.0	2.44
4.6	3.58	3.9	2.21	5.6	2.49	3.0	2.26
5.7	3.46	5.2	3.97	6.9	2.32	3.8	2.06
7.4	3.41	6.8	3.85	8.6	2.04	4.9	3.83
8.5	3.36	8.5	3.74	10.7	3.78	6.3	3.67
10.1	3.31	10.5	3.62	13.7	3.51	7.9	3.44
11.6	3.26	12.8	3.39	17.1	3.34	9.6	3.29
13.6	3.19	17.1	3.24	21.7	3.34	11.2	3.16
19.2	3.09	20.6	3.24	23.0	3.34	13.0	3.08
23.8	3.06	25.5	3.22	26.8	3.31	16.5	3.06
28.0	4.99	29.1	3.19	30.6	3.24	20.5	3.04
33.7	3.04	35.0	3.17	34.8	3.21	25.7	3.04
		36.3	3.14			30.5	3.03
						35.4	3.04

of the adapting light rises, indicating more complete dependence upon the slow synthesis of rhodopsin from vitamin A. This result is due to some precise arrangement of reaction orders in the visual cycle, and could not have been predicted from chemical information now available. Following long exposures to light more intense than about 200 millilamberts the early portions of rod dark adaptation are hidden

behind the cone function, and these changes in velocity can no longer be detected.<sup>2</sup>

*Duality of Rod Dark Adaptation.*—Simultaneous with the three 7 minute exposures of the subject's left eye described above, the right eye was exposed to 1890 millilamberts for 10 seconds. In an added experiment, to permit comparison of all functions in the left eye, both eyes were simultaneously adapted to 1890 millilamberts for 10 seconds. The dark adaptation curves obtained in these five experiments were

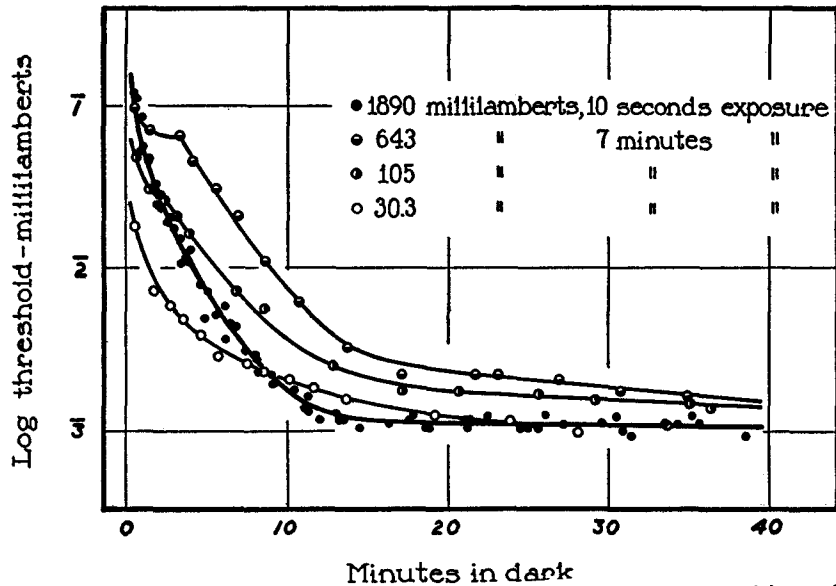


FIG. 1. Dark adaptation following long exposures to moderate intensities and short exposure to a high intensity. Following 7 minute exposures, rod dark adaptation is slower the higher the light adapting intensity. Following the 10 second exposure, dark adaptation is extremely rapid.

identical. The individual measurements are plotted as solid circles in Fig. 1; their averages are presented in the last two columns of Table I.

Dark adaptation following 10 seconds' irradiation is very much more rapid than following long exposures. Comparison of the 10 second function with each of the 7 minute curves in Fig. 1 illustrates three aspects of this relation.

<sup>2</sup>Hecht, Haig, and Chase (1936-37) have measured dark adaptation following 2 minute exposures to a wide range of intensities. The portions of their results pertinent to the present discussion agree essentially with those of Winsor and Clark and with our own experiments.

The 10 second and the 7 minute 643 millilambert curves possess the same initial thresholds, but the former reaches a constant minimum within about 15 minutes, while the latter is still incomplete after 35 minutes. This comparison is complicated by the fact that the initial thresholds of the 10 second curve appear due to rods, those of the 7 minute curve to cones; the degree of rod light adaptation was apparently very much higher in the 7 minute exposure.

The 7 minute 105 millilambert curve appears to correct this discrepancy. Its initial rod thresholds seem to coincide approximately with those of the 10 second function. Still the 7 minute curve is clearly very much slower, and adaptation remains incomplete after 35 minutes.

Finally, comparison of the 10 second with the 7 minute 30.3 millilambert function shows this distinction unequivocally. The former adaptation starts with thresholds more than five times higher than the latter, yet is so much faster that it overtakes and crosses the 7 minute curve after about 8 minutes of dark adaptation, and is complete about 8 minutes sooner. This experiment has been repeated a number of times, interchanging the light adaptations of the two eyes, with identical results.

It is clear that the length of exposure to light introduces changes in the character of rod dark adaptation for which adjustment of the intensity fails to compensate. Dark adaptation following short exposures is much more rapid than that following long irradiation. This is the result predicted from the chemical formulation.<sup>3</sup>

*Light Adaptation to Various Intensities, Short Exposures.*—Dark adaptation was measured following 5 second exposures to 3.6, 12, 120, 245, 750, and 890 millilamberts and after the 0.02–0.04 second exposure to a photoflash lamp (Mazda, No. 20; 45,000 lumen-seconds). Typical results are presented in Table II and Fig. 2.

As the intensity of the adapting light falls, the speed of dark adaptation increases, progressing toward more complete dependence upon the rapid synthesis of visual purple from retinene. We were unable by lowering the intensity to drive the system into a limiting state, in which further dimming of the adapting light produced no further changes in the speed of dark adaptation. It appears impossible,

<sup>3</sup> Riggs (1937), using an electrometric procedure, has found a similar phenomenon in the "cone" dark adaptation of the frog eye.

therefore, to isolate the rapid reaction by these means. This confirms a prediction from the chemical formulation. Since retinene

TABLE II

Dark adaptation following 5 sec. exposures to 3.6-1890 millilamberts, and following 1/50-1/25 sec. exposure to a photoflash lamp (Mazda, No. 20). Subject A.-B.C. Time in minutes, thresholds in millilamberts. Thresholds of the left eye are printed in bold-face type.

Intensity of exposure									
3.6 millilamberts		245 millilamberts		750 millilamberts		1890 millilamberts		Photoflash	
Time in dark	Log threshold	Time in dark	Log threshold	Time in dark	Log threshold	Time in dark	Log threshold	Time in dark	Log threshold
0.1	3.68	0.2	<b>2.73</b>	0.3	<b>2.92</b>	0.4	<b>1.07</b>	1.2	1.02
0.4	<b>3.21</b>	0.5	2.23	0.6	2.61	0.7	1.02	2.1	2.96
0.7	3.11	1.0	<b>3.94</b>	0.9	<b>2.40</b>	1.0	<b>2.95</b>	3.2	2.92
1.1	<b>4.99</b>	1.4	3.71	1.3	2.23	1.4	2.89	4.2	2.86
1.4	4.99	2.0	<b>3.62</b>	1.8	<b>3.99</b>	2.1	<b>2.75</b>	5.6	2.85
2.2	<b>4.94</b>	2.5	3.39	2.7	3.62	2.7	2.53	6.8	2.59
4.0	<b>4.92</b>	3.2	<b>3.42</b>	3.3	<b>3.59</b>	3.5	<b>2.40</b>	7.4	2.46
4.9	4.97	3.9	3.12	4.0	3.54	4.3	2.03	8.7	2.19
6.0	<b>4.92</b>	4.4	<b>3.07</b>	4.7	<b>3.37</b>	5.0	<b>2.15</b>	9.6	3.99
6.9	4.94	5.1	3.05	5.2	3.34	6.5	<b>3.74</b>	11.0	3.78
8.4	<b>4.94</b>	5.7	<b>3.02</b>	6.0	<b>3.22</b>	7.8	3.47	12.9	3.49
9.6	4.94	6.5	3.00	6.7	3.12	8.5	<b>3.42</b>	15.6	3.34
10.3	<b>4.92</b>	8.0	<b>4.97</b>	7.3	<b>3.02</b>	9.6	3.24	17.3	3.24
		9.3	3.00	8.3	3.07	10.4	<b>3.14</b>	20.5	3.19
		10.4	<b>4.95</b>	8.9	<b>3.00</b>	11.6	3.07	24.0	3.12
		12.6	4.87	10.1	3.00	12.3	<b>3.05</b>	29.0	3.02
		14.3	<b>4.95</b>	10.5	<b>4.92</b>	13.8	4.97	34.2	4.97
		19.7	4.92	11.8	4.90	14.9	<b>4.95</b>	35.7	3.00
		20.9	<b>4.87</b>	12.8	<b>4.85</b>	17.0	4.97		
		27.6	4.95	15.3	4.92	19.1	<b>4.95</b>		
		30.2	<b>4.95</b>	19.5	4.92	27.1	4.92		
		32.2	4.92	20.1	<b>4.87</b>	27.5	<b>4.90</b>		
		32.5	<b>4.87</b>	22.7	4.92	33.1	4.95		
		40.6	4.90	27.3	<b>4.95</b>	35.7	<b>4.90</b>		
				28.6	4.97	36.3	<b>4.92</b>		
				31.1	<b>4.85</b>	36.7	4.92		
				31.5	4.87				
				37.0	4.85				

forms vitamin A in addition to rhodopsin, every dark adaptation as it progresses depends increasingly, and finally entirely, upon the slow synthesis of rhodopsin from vitamin A.

This is also the explanation of the fact that at the highest intensities investigated the dark adaptation curves following short exposures do enter a limiting condition, indistinguishable from that reached at high intensities with long exposures. In the uppermost curve of Fig. 2, approximately the first 6 minutes of rod dark adaptation are concealed behind the cone function. By the time the rod segment has emerged apparently all but a negligible portion of retinene has already been removed. The entire measurable portion of rod adaptation therefore possesses the simple character of the slow process alone.

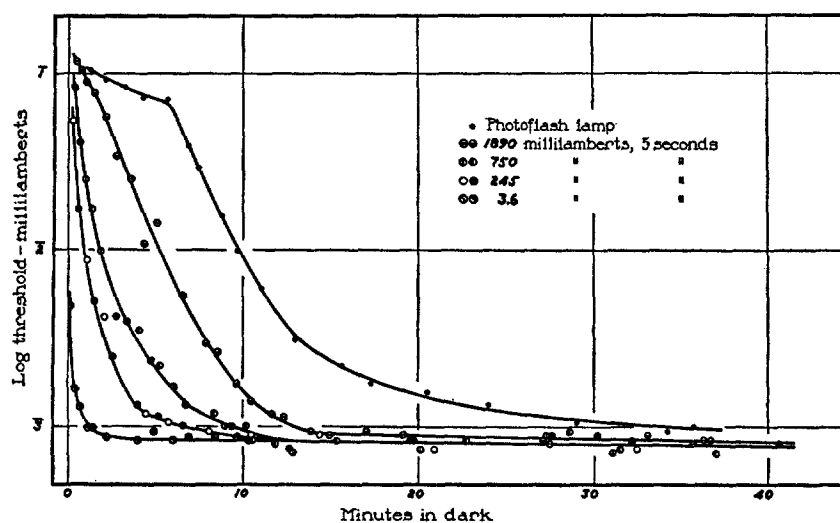


FIG. 2. Dark adaptation following short exposures to various intensities. The initial portions of rod dark adaptation increase in velocity as the light adapting intensity falls.

*Various Durations of Light Adaptation, Constant Intensity.*—Both eyes were exposed to 333 ml., the right eye repeatedly for 5 minutes to serve as control, the left eye for various durations from 10 seconds to 20 minutes. The data for the left eye are presented in Table III and Fig. 3.

Increase in the period of light adaptation results in two changes:

1. The initial dark adaptation thresholds rise. This effect, the classic index of light adaptation, is complete within 10 minutes'



irradiation. Doubling this interval produces no further change beyond the normal scatter of the function.

2. The velocity of rod dark adaptation decreases. In the present measurements this change appears complete after 2 minutes of light adaptation. Beyond this interval, however, the initial segments of rod dark adaptation are hidden behind the cone function, and probably continue to change in form as light adaptation progresses.

TABLE III

Dark adaptation following exposure to 333 millilamberts for various periods. Subject A.-B.C. Left eye. Time in minutes, thresholds in millilamberts.

Exposure periods											
10 sec.		1 min.		2 min.		5 min.		10 min.		20 min.	
Time in dark	Log thresh-old	Time in dark	Log thresh-old	Time in dark	Log thresh-old	Time in dark	Log thresh-old	Time in dark	Log thresh-old	Time in dark	Log thresh-old
0.4	2.06	0.35	2.77	0.3	2.77	0.6	2.75	0.35	2.92	0.4	1.05
1.3	3.87	1.1	2.26	1.1	2.46	1.3	2.65	1.0	2.88	0.9	2.97
2.5	3.44	2.0	3.91	2.1	2.21	2.4	2.57	2.0	2.86	1.3	2.97
3.5	3.14	2.5	3.86	3.1	2.06	3.4	2.46	2.9	2.80	2.2	2.92
4.8	3.14	3.4	3.72	4.3	3.87	4.5	2.38	4.2	2.72	2.8	2.86
6.0	3.10	4.5	3.54	5.4	3.76	5.7	2.19	5.6	2.49	3.7	2.83
7.6	3.10	5.7	3.47	7.0	3.52	6.8	3.97	7.8	3.99	5.0	2.62
9.2	3.07	8.0	3.17	9.6	3.32	8.6	3.66	9.4	3.69	5.8	2.41
10.1	3.05	12.6	3.05	11.3	3.12	11.9	3.34	11.8	3.54	7.1	2.14
13.0	3.00	14.3	3.05	13.5	3.12	16.6	3.22	13.4	3.42	8.7	3.91
15.7	3.02	20.1	3.07	17.7	3.05	19.5	3.19	15.2	3.32	11.6	3.57
18.3	3.00	28.2	3.00	22.0	3.07	23.4	3.14	19.6	3.22	15.0	3.37
23.9	3.00	30.4	4.92	24.6	3.12	29.2	3.14	26.2	3.10	18.2	3.22
38.1	3.00	33.5	3.02	29.2	3.00	30.5	3.07	31.4	3.10	22.9	3.15
		37.0	3.05	32.8	3.02	34.5	3.07	37.0	3.10	30.2	3.10
				35.2	3.00			40.1	3.05	35.2	3.07
				37.2	3.00						

The relation between dark adaptation and exposure to a constant intensity has been measured previously by Lohmann (1907), Rabinowitsch (1908), and Müller (1931).

Lohmann's measurements were inaccurate. His dark adaptation curves show some evidence of slowing as light adaptation proceeds, and appear to become constant following 6 to 10 minutes of irradiation.

Rabinowitsch measured roughly no more than the first 15 minutes of dark adaptation following  $\frac{1}{2}$  minute to 2 hour exposures to a constant adapting light. She concluded that the velocity of dark adaptation decreases markedly as light adaptation progresses.

Müller has recently measured accurately the first 27 minutes of dark adaptation following 1 to 40 minute exposures to 3000 lux (about 300 millilamberts). Despite important differences in technique, his conclusions are almost identical with those stated here. The rod portion of dark adaptation was found to become practically constant in position following exposures longer than 10 minutes. Following 1, 2, and 5 minute exposures, the speed of rod adaptation decreases progressively.

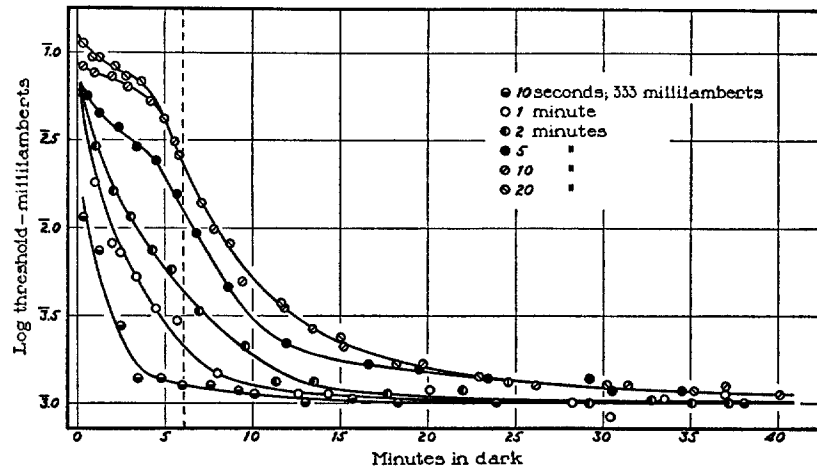


FIG. 3. Dark adaptation following various lengths of exposure to 333 millilamberts. As light adaptation proceeds the visual threshold rises and independently the speed of rod dark adaptation decreases. Intercepts with these curves of the ordinate drawn at 6 minutes furnish most of the points in Fig. 4.

Beyond 5 minutes exposure changes in velocity can no longer be detected; as in the present experiments this situation is associated with the concealment of the first few minutes of rod adaptation by the cone function.

*Light Adaptation.*—Light adaptation is commonly defined as the rise in visual threshold which accompanies irradiation of the eye. Ideally this process should be measured by determining thresholds during instantaneous interruptions of the adapting light. Such an experiment has not yet been successfully performed. Lohmann (1907) substituted for this procedure the measurement of thresholds after

an arbitrary interval in darkness, interpolated from a series of dark adaptation curves such as Fig. 3. Lohmann chose for this purpose a 10 second interval. It is clear from Fig. 3 that thresholds after 10 seconds in darkness are due in the early stages of light adaptation to rods, in later stages to cones, and therefore yield no clear information concerning either type of receptor.

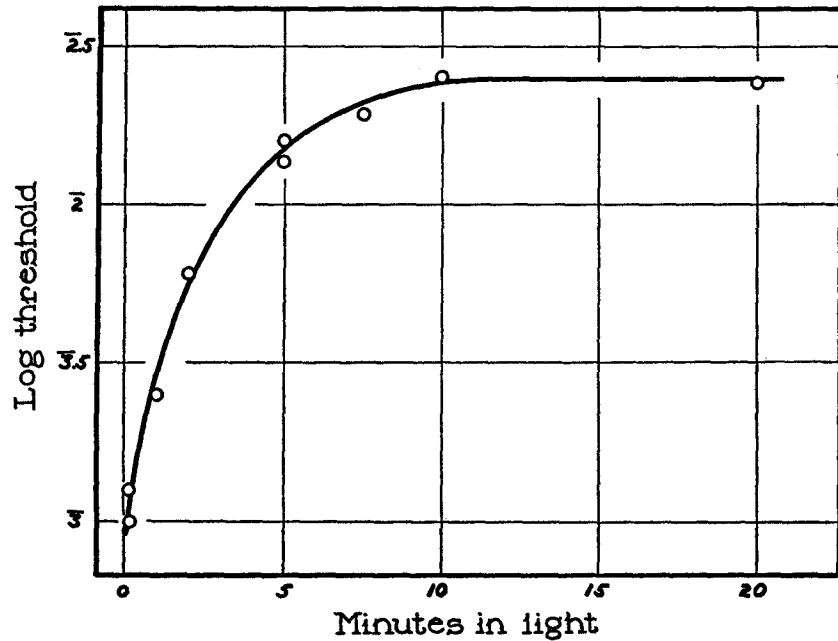


FIG. 4. Light adaptation. Thresholds at 6 minutes in darkness following various lengths of exposure to 333 millilamberts.

An ordinate drawn at 6 minutes through the curves of Fig. 3 intercepts only rod functions. The series of interpolated thresholds so obtained partly expresses the light adaptation of the observer's rods to 333 millilamberts. These thresholds, with a number of others similarly obtained from data not shown in Fig. 3, are plotted against the period of light adaptation in Fig. 4. The precise shape of the curve is of no importance, since it varies with the position of the time intercept in Fig. 3, here quite arbitrarily chosen. The curve merely

expresses conveniently the fact, apparent in Fig. 3, that on exposure to 333 millilamberts the rod threshold rises, at first rapidly, then more slowly, finally becoming constant in about 10 minutes.

In addition to, and independently of, this change, the speed of rod dark adaptation falls as the exposure to light lengthens. This presents an added and hitherto neglected aspect of light adaptation. We may assume with Hecht that the rise in visual threshold which classically defines light adaptation corresponds with a fall in rhodopsin concentration in the rods. Then, following our chemical formulation, the decrease in speed of dark adaptation is due to increase in the proportion of vitamin A to retinene during light adaptation. The complete process of light adaptation includes both types of variation, and is expressed adequately only with a family of dark adaptation curves as in Fig. 3. The steady state in which light adaptation ends is characterized by constancy both of form and position of the dark adaptation function.

It is commonly stated that light adaptation is very much more rapid than dark adaptation. This is only qualifiedly true. We have found light adaptation to 333 millilamberts to occupy about 10 minutes. Dark adaptation requires no longer, following 5 seconds exposure to light as intense as 750 millilamberts.

#### SUMMARY

1. The reality of a chemical cycle proposed to describe the rhodopsin system is tested with dark adaptation measurements.
2. The first few minutes of rod dark adaptation are rapid following short, slower following long irradiation. As dark adaptation proceeds, the slow process grows more prominent, and occupies completely the final stages of adaptation.
3. Light adaptation displays similar duality. As the exposure to light of constant intensity lengthens, the visual threshold rises, and independently the speed of dark adaptation decreases.
4. These results conform with predictions from the chemical equations.

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