DARK ADAPTATION IN DINEUTES*

By LEONARD B. CLARK

(*From the Laboratory of Biophysics, Columbia University, New York*)

(Accepted for publication, September 24, 1937)

Studies of dark adaptation have been made on amoeba (Folger, 1925), *Volvox* (Mast, 1927), some molluscs (Hess, 1910; Hecht, 1918, 1919, 1923, 1927; Crozier and Wolf, 1928), an ascidian (Hecht, 1918, 1927), *Amphioxus* (Hess, 1910), the frog tadpole (Obreshkove, 1921; Hecht, 1927), the chick (Honigmann, 1921), and man (for references see Hecht, 1921, 1927; and Hecht, Haig, and Wald, 1935), but until recently (Hartline, 1929; Wolf and Zerrahn-Wolf, 1935) little information was available describing the course of dark adaptation in arthropods in any but the most general terms (Hess, 1910; Dolley, 1929; von Buddenbrock and Schulz, 1933).

This paper reports a study of dark adaptation in the aquatic beetle, *Dineutes assimilis* commonly called apple bug, coffee bug, or whirligig beetle. It was found (Clark, 1931, 1933) to be an excellent form for study. It reacts well to light, is hardy and easily kept in the laboratory, and can, if necessary, be used in repeated experiments.

Apparatus and Procedure

Starting with the observation that a specimen of *Dineutes* in the dark tends to move around the walls of a container, an apparatus was devised by which all the ommatidia could be about equally light adapted and in which the insect could be oriented in the same relation to the stimulating light for each experimental reading.

The apparatus (Fig. 1) consisted of a turn-table composed of a ring moving on ball bearings and supporting a sheet of bakelite with a square opening in the center. A piece of ground glass set flush with the bakelite covered the opening. An animal compartment was formed by cementing clear glass walls to the ground glass. The turn-table was mounted to allow light to be reflected up through the ground glass after being transmitted through a neutral tint filter or through a red filter. The former was the adapting light, and the latter was used to view

* Investigation pursued during tenure of National Research Fellowship.

the animals while taking readings, as they are insensitive to the deep red of the spectrum.

Another lamp was mounted to give a horizontal beam, the intensity of which could be controlled by a neutral tint wedge and filters. This was the test light.

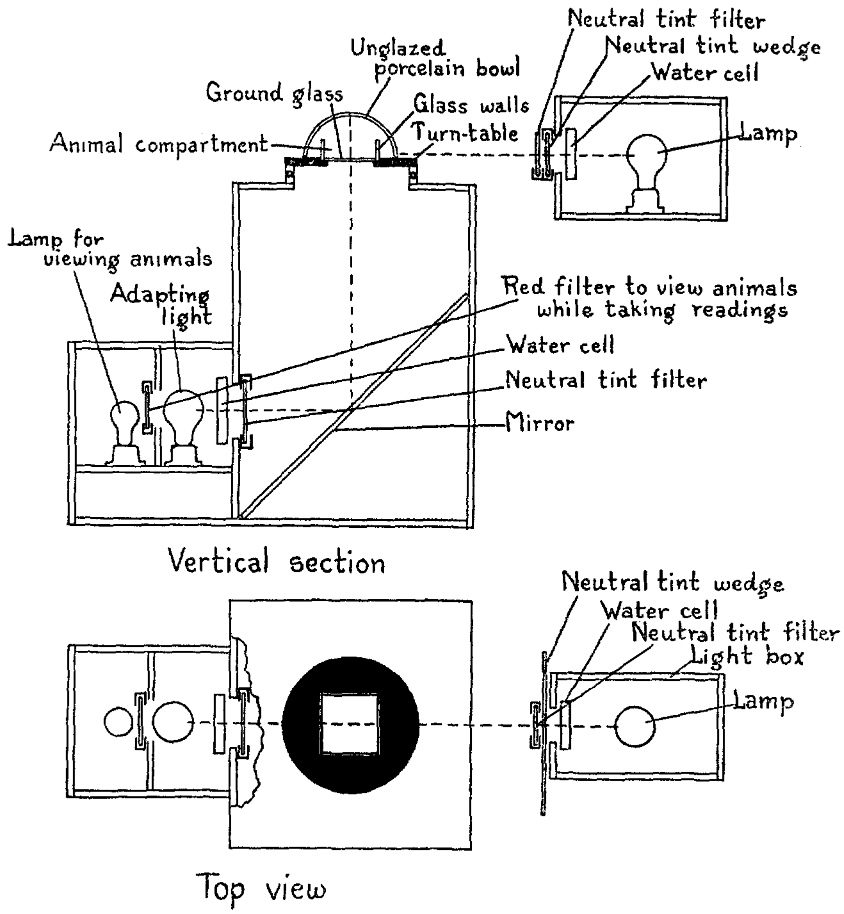
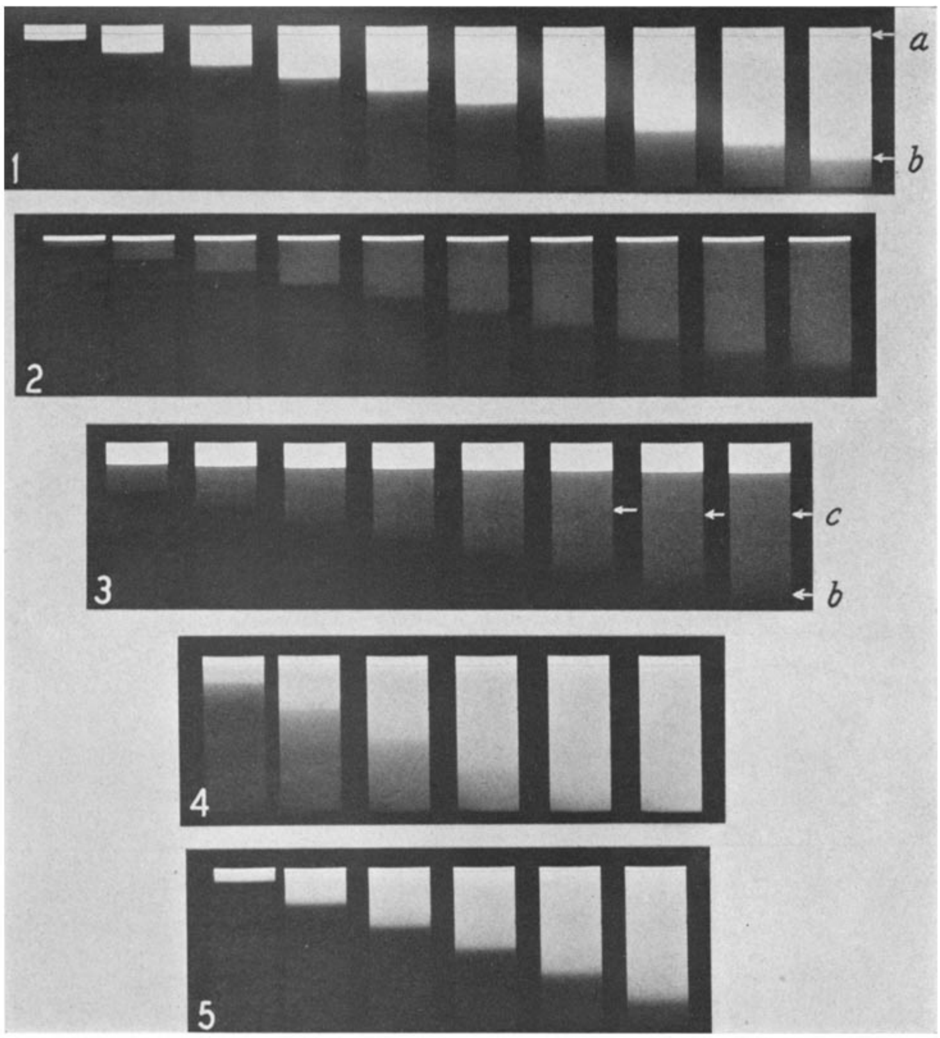
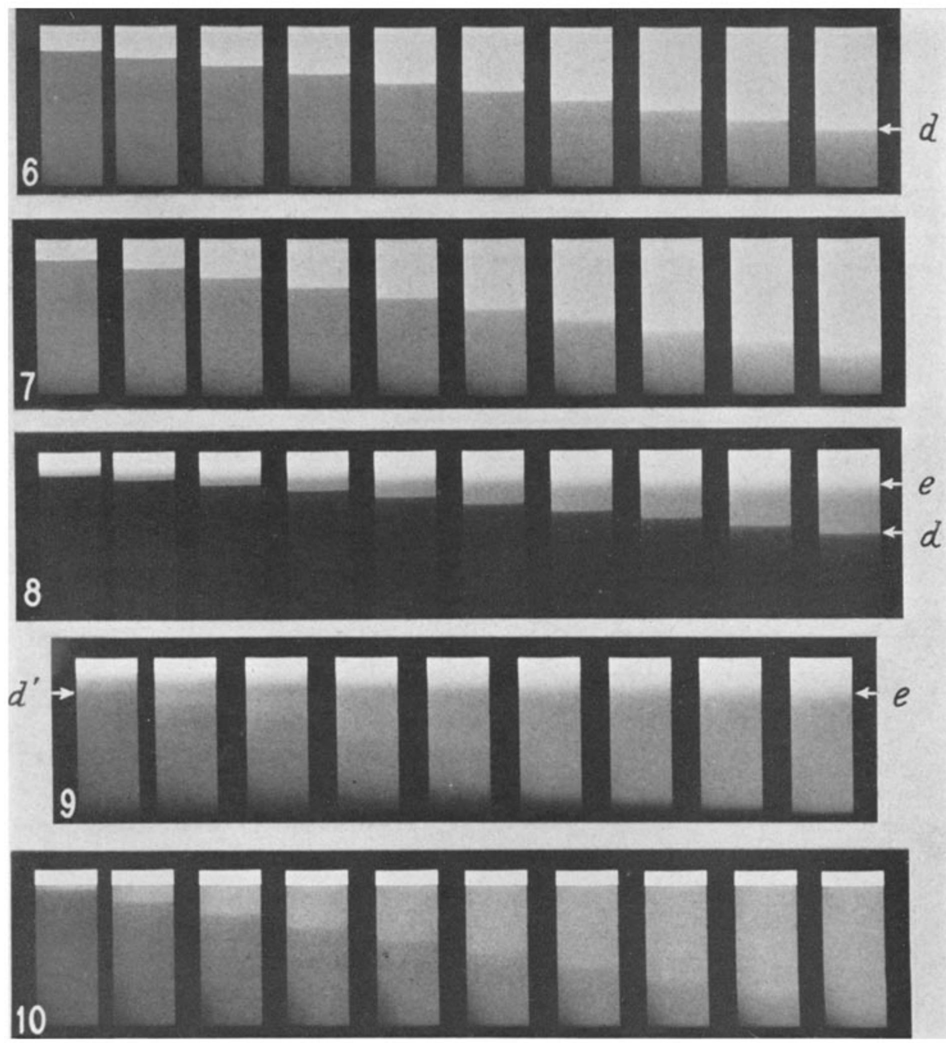


FIG. 1. Diagram of apparatus used to test dark adaptation of *Dineutes*.

The experimental procedure was as follows: An insect was placed in the animal compartment and a white unglazed porcelain bowl inverted over the chamber. The adapting light was turned on and the insect was adapted to light passing through the ground glass floor and reflected from the white walls of the bowl. This scattered the light so the intensity was about equal from all directions.



(Wyckoff: Ultracentrifugation of bacteriophage)



(Wyckoff: Ultracentrifugation of bacteriophage)

After light adaptation, the adapting light was turned off, the bowl removed, and the animal left in the dark for a known time. Then the minimum intensity to which the insect would react was determined. The red light was turned on to view the animal. The insect usually moved around the walls. If it was moving along the wall away from the test lamp and at right angles to the beam, the test lamp was turned on and the intensity was slowly increased until the insect turned toward the light. If the insect reached the side wall of the compartment and started along it parallel to the beam before it reacted, the turn-table was moved one quarter turn to cause the insect to move across the beam again. At some intensity the insect will turn and move toward the light. The minimum intensity calling forth this reaction is called the threshold or threshold intensity and is given as $\log I + 10$.

When the threshold was determined the time was noted and the test lamp turned off. The insect was left in the dark for a further timed period and then tested again. Thus the threshold was determined at the end of a number of timed periods in the dark during the course of dark adaptation. This was repeated with each of several insects.

RESULTS

Experiments were performed using light adaptation of 6.5, 91.6, and 6100 foot-candles, and curves of dark adaptation secured for each. The results are presented in Table I. Each determination is a single reading from one individual.

The data for each insect behave in the same regular manner. As the intensity of the adapting light increases, the early threshold values also increase. Though the course of dark adaptation is about the same for each adaptation level, the final thresholds may vary. To avoid averaging, the data of each set of readings from each insect are moved as a whole up or down the log I axis to bring them all to approximately the same threshold. This introduces no change in the curves of dark adaptation but does cause a change in the units in which intensity is measured. The shift is made by multiplying the threshold intensity by a constant a. This constant is probably related to the condition of the nervous system as well as to the transmission of the eye pigments, since it may vary from day to day in the same individual (see insect V, experiments 1 and 2 at light adaptation of 91.6 foot-candles). The value of log a for each set of data is given in Table II.

By plotting the log threshold + log a values against time in the dark and by using the appropriate time intervals on the abscissa, all data

TABLE I

Dark Adaptation of Dineutes after Different Levels of Light Adaptation

Each datum is a single reading with a single animal. Time in dark is in minutes; intensities in log foot-candles + 10.

Light adaptation to 6.5 foot-candles

Insect III—1		IV—1		IV—2		IV—6	
Time in dark	Log I	Time in dark	Log I	Time in dark	Log I	Time in dark	Log I
3.0	8.54	3.0	7.98	3.5	7.98	2.2	8.25
5.1	8.09	5.9	7.67	9.9	7.51	4.4	8.09
7.3	8.00	8.0	7.47	11.6	7.26	6.3	7.89
10.9	7.85	10.6	7.35	15.0	7.16	8.4	7.75
18.2	7.49	15.3	7.19			12.9	7.37
24.3	7.34	22.1	7.02			18.4	7.14
35.7	7.20	32.4	6.96			24.8	6.93
						35.1	6.73

Light adaptation to 91.6 foot-candles

Insect IV—4		IV—5		V—1		V—2		VI—1	
Time in dark	Log I	Time in dark	Log I	Time in dark	Log I	Time in dark	Log I	Time in dark	Log I
2.25	9.71	2.6	9.16	2.8	9.59	2.9	9.33	2.3	9.56
4.4	8.76	5.5	8.76	4.8	9.02	4.6	8.86	5.1	8.35
6.6	8.42	10.1	8.36	6.3	8.82	6.2	8.58	10.8	8.08
8.8	7.95	16.5	7.59	14.2	8.28	7.7	8.27	15.9	7.75
10.5	7.63	23.2	7.35	22.3	8.09	9.7	8.25	20.5	7.53
15.1	7.34	28.4	7.12	32.2	7.75	15.4	7.83	27.7	7.39
21.4	7.29	35.6	6.86			25.2	7.59	34.2	7.22
32.6	7.06					32.6	7.28		
						37.3	7.14		

Light adaptation to 6100 foot-candles

Insect XIII—1		XIII—2		XIV—1		XV—1		XVI—1		XVII—1	
Time in dark	Log I	Time in dark	Log I	Time in dark	Log I	Time in dark	Log I	Time in dark	Log I	Time in dark	Log I
2.8	9.67	4.7	9.89	2.6	10.76	3.3	10.38	4.1	9.36	3.1	11.04
8.4	8.78	7.5	8.86	6.4	8.82	7.6	9.18	8.4	8.68	5.6	9.79
16.1	7.57	10.0	8.44	14.0	7.97	14.7	8.68	15.8	7.77	10.1	8.62
19.4	7.69	41.2	7.06	24.1	7.48	26.1	7.65	18.0	7.34	19.2	7.83
19.9	7.81			35.8	7.16	36.3	7.24	31.3	7.04	26.1	7.49
32.7	7.06									38.4	7.12

TABLE II

Values of Log a, to Bring Data of All Animals to Approximately Same Final Threshold

Insect	Log *a*	Insect	Log *a*	Insect	Log *a*
III—1	−0.20	IV—6	0.15	XIII—2	0.00
IV—1	0.12	V—1	−0.73	XIV—1	0.00
IV—2	0.15	V—2	−0.24	XV—1	−0.35
IV—4	0.00	VI—1	−0.23	XVI—1	0.22
IV—5	0.00	XIII—1	0.20	XVII—1	−0.05

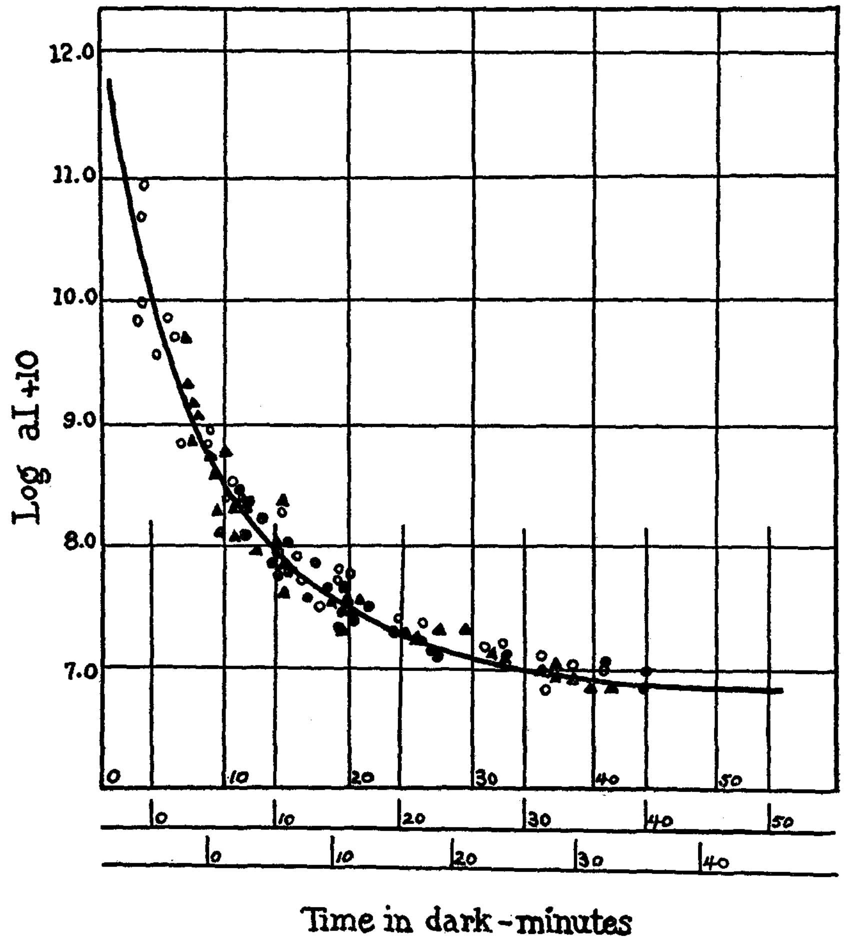


FIG. 2. Curve of dark adaptation of *Dineutes*. Open circles, triangles, and closed circles, individual observations after light adaptation to 6100 foot-candles, 91.6 foot-candles, and 6.5 foot-candles respectively.

can be described by a single curve (Fig. 2). This indicates that the course of dark adaptation follows parts of the same curve irrespective of the level of light adaptation. The intensity of the adapting light determines the level at which dark adaptation will begin.

It is obvious that it is extremely difficult to secure experimental values for the so called instantaneous threshold, the threshold at zero time in the dark. But they may be readily secured from the curve of Fig. 2. When the instantaneous log *aI* is plotted against

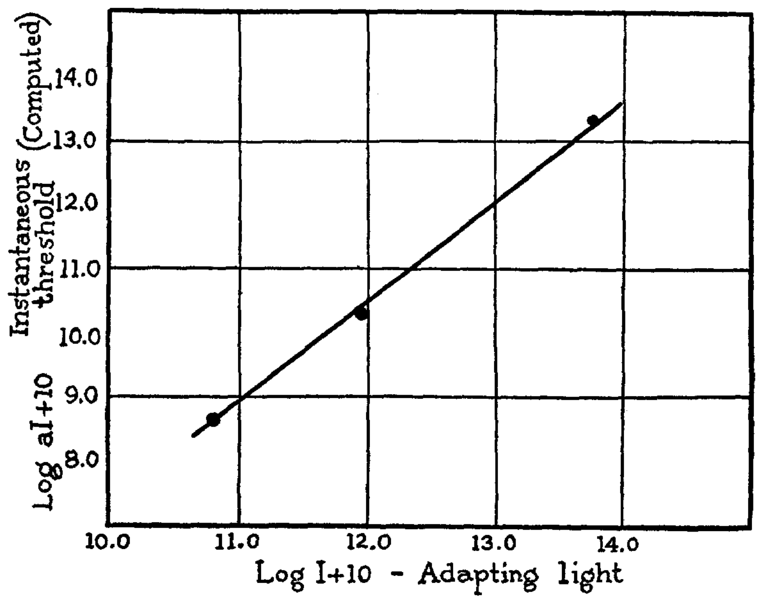


FIG. 3. Relation between log of instantaneous threshold and log of adapting intensity.

the log of the adapting light, the result is as shown in Fig. 3. Although the relation seems linear, it is more likely that the range of intensities covered falls in the central part of a sigmoid curve similar to that found for certain other organisms.

Theory

On analysis the data were found to be described by the equation for human dark adaptation derived by Hecht (1929) on the assumption that the sensitive material is formed from two of its photoproducts, and that the concentration of sensitive material is inversely proportional to the logarithm of the threshold intensity at the moment. The equation is

$$k_2 t = \frac{\log aI_t \times \log aI_\infty}{\log aI_t - \log aI_\infty} + C$$

where k_2 may be considered similar to a velocity constant; t is the time in the dark; log I_t is the log of the threshold intensity at time t; log I_∞ is log of threshold intensity at complete dark adaptation; and a is the constant described above.

Computations of the individual points yielded average values of $k_2 = 1.32$, 1.48, and 1.28 for the three series. These values are most probably not significantly different, a conclusion shown by the drawing of a common curve through all data. The average k_2 for all points was 1.37 and was used in securing the curve of Fig. 1.

CONCLUSION

Theory apart, it is obvious that (*a*) all the data fall on one curve and merely represent different starting levels on the same curve of dark adaptation; and (*b*) the relation between the log instantaneous threshold and log adapting light is linear over the range covered.

SUMMARY

The level of dark adaptation of the whirligig beetle can be measured in terms of the threshold intensity calling forth a response.

The course of dark adaptation was determined at levels of light adaptation of 6.5, 91.6, and 6100 foot-candles. All data can be fitted by the same curve. This indicates that dark adaptation follows parts of the same course irrespective of the level of light adaptation. The intensity of the adapting light determines the level at which dark adaptation will begin.

The relation between log aI_0 (instantaneous threshold) and log of adapting light intensity is linear over the range studied.

BIBLIOGRAPHY

Buddenbrock, W. v., and Schulz, E., Beiträge zur Kenntnis der Lichtkompassbewegung und der Adaptation des Insektenauges, *Zool. Jahrb. Abt. allg. Zool. und Physiol.*, 1933, **52**, 513.

Clark, L. B., Some factors involved in the reactions of insects to changes in luminous intensity. Shock reactions in *Dineutes assimilis*, *J. Exp. Zool.*, 1931, **58**, 31.

Clark, L. B., Modification of circus movements in insects, *J. Exp. Zool.*, 1933, **66**, 311.

Crozier, W. J., and Wolf, E., Dark adaptation in *Agriolimax*, *J. Gen. Physiol.*, 1928, **12**, 83.

Dolley, W. L., Dark adaptation in the eye of *Eristalis tenax*, *Physiol. Zool.*, 1929, **2**, 483.

Folger, H. T., A quantitative study of reactions to light in amoeba, *J. Exp. Zool.*, 1925, **41**, 261.

Hartline, H. K., The dark adaptation of the eye of *Limulus*, as manifested by its electrical response to illumination, *J. Gen. Physiol.*, 1929, **13**, 379.

Hecht, S., The photic sensitivity of *Ciona intestinalis*, *J. Gen. Physiol.*, 1918, **1**, 147.

Hecht, S., Sensory equilibrium and dark adaptation in *Mya arenaria*, *J. Gen. Physiol.*, 1919, **1**, 545.

Hecht, S., The dark adaptation of the human eye, *J. Gen. Physiol.*, 1920, **2**, 499.

Hecht, S., The nature of foveal dark adaptation, *J. Gen. Physiol.*, 1921, **4**, 113.

Hecht, S., Sensory adaptation and the stationary state, *J. Gen. Physiol.*, 1923, **5**, 555.

Hecht, S., The kinetics of dark adaptation, *J. Gen. Physiol.*, 1927, **10**, 781.

Hecht, S., The nature of the photoreceptor process, in Murchison, C., The foundations of experimental psychology, Clark University Press, Worcester, 1929, p. 216.

Hecht, S., Haig, C., and Wald, G., The dark adaptation of retinal fields of different size and location, *J. Gen. Physiol.*, 1935, **19**, 321.

Hess, C., Neue Untersuchungen über den Lichtsinn bei wirbellosen Tieren, *Arch. ges. Physiol.*, 1910, **136**, 282.

Honigmann, H., Untersuchungen über Lichtempfindlichkeit und Adaptierung des Vogelauges, *Arch. ges. Physiol.*, 1921, **189**, 1.

Mast, S. O., Reversal in photic orientation in *Volvox* and the nature of photic stimulation, *Z. vergleich. Physiol.*, 1927, **5**, 730.

Obreshkove, V., The photic reactions of tadpoles in relation to the Bunsen-Roscoe law, *J. Exp. Zool.*, 1921, **34**, 235.

Wolf, E., and Zerrahn-Wolf, G., The dark adaptation of the eye of the honey bee, *J. Gen. Physiol.*, 1935, **19**, 229.