SCIENCE

Vol. 101 FRIDAY, JUNE 29, 1945 No. 2635

SCIENCE: A Weekly Journal, since 1900 the official organ of the American Association for the Advancement of Science. Published by the American Association for the Advancement of Science every Friday at Lancaster, Pennsylvania.

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Annual subscription, $6.00 Single copies, 15 cents

HUMAN VISION AND THE SPECTRUM

By Professor GEORGE WALD[1]

BIOLOGICAL LABORATORIES OF HARVARD UNIVERSITY

THE basic relation which describes the response of the eye to radiation is its sensitivity to the various wave-lengths of the spectrum. The limits of this function define what is meant by light. Its form expresses fundamental properties of the retinal receptors, and of the ocular structures which light must penetrate to reach them.

The human retina contains two groups of receptors: rods, which function in dim light; and cones, the organs of vision in bright light, and color vision. The rods are mainly sensitive at lower wave-lengths than the cones. Hence, in the passage from dim to bright light, the spectral sensitivity of the eye shifts toward the red. This is the Purkinje phenomenon.

A small central area of the human retina—the fovea—which subtends a visual angle of about 1.5°, contains only cones. Within this region, therefore, no Purkinje phenomenon is observed.[2] Even in the dark-adapted eye, in which all peripheral responses are dominated by rods, the fovea retains the characteristics of pure cone vision.

The intrinsic sensitivities of rods and cones are

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[1] This research was supported in part by a grant from the Josiah Macy Jr. Foundation. Part of the work was reported to the Optical Society of America at its meeting in October, 1944 (*Jour. Opt. Soc. Amer.*, 34: 769, 1944). The remainder was to have been reported to the society at its meeting in April, 1945, since cancelled. Most of the experiments on aphakic eyes were performed in the summer of 1943 at the Dartmouth Eye Institute, Hanover, N. H., to whose director, Professor Adelbert Ames, Jr., and ophthalmologist-in-chief, Dr. Hermann Burian, I am most grateful. I wish to acknowledge also the technical assistance of Ruth Hubbard with some of the experiments.

[2] A. Kohlrausch and J. Teufer, *Tab. Biol.*, 1: 309, 1925; K. Gross, *Z. Sinnesphysiol.*, 59: 215, 1928; S. L. Polyak, "The Retina," Chicago, 1941, p. 202.

modified by the presence of colored intraocular structures. One of these is the lens, which in man is yellow in color. The cornea and the ocular humors also absorb some light in the violet and ultra-violet. The optical properties of these structures affect the spectral sensitivity of the whole eye.

In man and certain other primates, the retina itself contains a yellow pigment, concentrated in a diffuse central zone about the fovea, the *macula lutea*. This pigmentation imposes special differences in spectral sensitivity upon the central as compared with the peripheral retina.

Repeated measurements have been made of the spectral sensitivity of human vision, either in bright light, involving principally macular cones; or in dim light, involving macular or paramacular rods. The present investigation includes somewhat comparable measurements, performed under conditions of precise fixation, of the spectral sensitivities of foveal cones and of rods well outside the macula.

To these are added three functions not previously described: the spectral sensitivities of peripheral cones, and of rods and cones in the lensless (aphakic) eye. The differences in sensitivity of central and peripheral cones, and of normal and aphakic eyes, yield estimates of the absorption of light by the macular pigment and by the lens. The pigment of the human macula has also been extracted, and certain of its optical and chemical properties have been examined directly.

In these experiments the spectral sensitivity has been determined by measuring at various wave-lengths the absolute threshold of vision—the smallest radiant flux that can be seen. The simple reciprocal of this quantity is the sensitivity.

To measure thresholds a spectral adaptometer was constructed which employs as source a high-pressure mercury arc.[3] From its radiation, ten spectral lines or narrow bands are isolated with color-filters. The intensity at each wave-length is regulated with an annular neutral wedge. A variable fixation point permits the image of the test field to be located foveally or at any point within 12° of the foveal center. A shutter exposes the field for flashes of 1/25 second. In all the experiments to be described, the field was circular, and subtended a visual angle of 1°. All measurements were monocular and ordinarily were performed on alternate eyes.

FOVEAL CONES

The image of a 1° test field, fixated centrally, should fall entirely within the fovea, and should stimulate only cones. Measurements made with such a stimulus in the dark-adapted eye are shown in Figs. 1 and 2, and in Table 1. They represent averages for 22 observers of average age 20. Thresholds and sensitivities are expressed logarithmically to do justice to the huge range of the measurements.

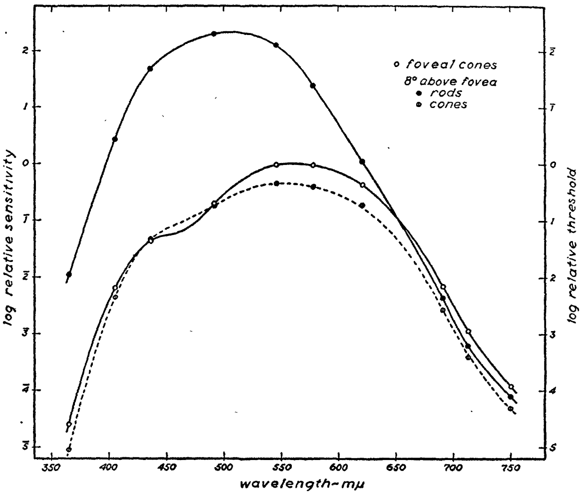

Fig. 1. Spectral sensitivities (1/threshold) of dark-adapted foveal cones, peripheral rods, and peripheral cones (broken line). All sensitivities are expressed relative to the maximum sensitivity of the fovea. The relative positions of these functions on the ordinates are therefore those observed in the eye.

The maximum sensitivity of the fovea, here arbitrarily set at 1 (log sensitivity = 0), occurs at about 562 mμ. To both sides of this wave-length it declines, reaching on an average about 1/10,000 of its maximal value at 750 mμ, and about 1/40,000 at 365 mμ.

That these data are in fact due to cones is attested

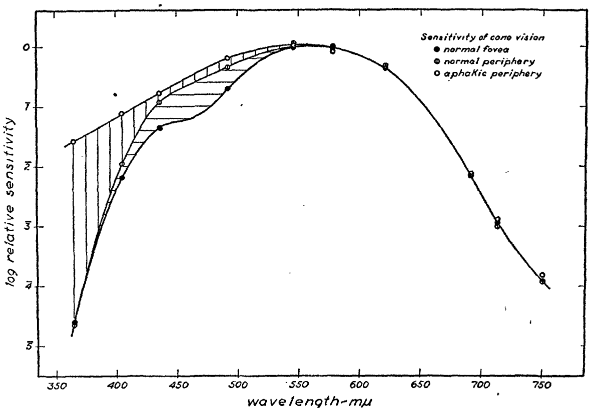

Fig. 2. Spectral sensitivities of cone vision in the normal fovea, and in an area 8° above the fovea in the normal and aphakic eye. All these functions have been brought together above 578 mμ, where all of them are parallel. The horizontally hatched area represents the optical density (log 1/transmission) of the macular pigmentation in the fovea, the vertically hatched area the density of the lens.

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[3] G. Wald, *Jour. Opt. Soc. Amer.*, 35: 187, 1945.

by the following considerations: (1) Dark-adaptation measurements performed at various wave-lengths show that the threshold falls within 4–6 minutes to a constant level, maintained indefinitely thereafter. The threshold stimulus continues to look colored at all wave-lengths. This behavior is characteristic of cone vision. (2) A 1° field fixated centrally has previously been shown repeatedly to reveal no trace of a Purkinje phenomenon.[4] (3) The present data agree well with previous measurements of the spectral sensitivity of central areas at high brightnesses—so-called photopic luminosities.[5] The way in which the foveal curve is drawn in Figs. 1 and 2 has been guided in detail by these earlier observations.

The present measurements depart widely at low wave-lengths, however, from the photopic luminosity function standardized by the International Commission on Illumination at Geneva in 1924 (the I.C.I. function). At 436 mμ they reveal an average sensitivity about 2.4 times, and at 405 mμ about 9 times as high as the I.C.I. factors indicate. This disagreement with the standardized function does not extend to some of the most careful measurements on which it was based, those of Coblentz and Emerson,[6] and of Gibson and Tyndall,[7] which between 450 mμ and 427 mμ—below which they do not penetrate—depart from the I.C.I. curve much as do my own.[8] The I.C.I. function in the blue and violet represents a compromise between the measurements of Nutting[9] and of Hartman,[10] which disagree widely with each other. Nutting's data diverge from the standardized function below 430 mμ, to come close at 400 mμ to my own; while Hartman's data go off in the opposite direction.

PERIPHERAL RODS

When the image of the test field falls 8° above the fovea in the dark-adapted eye, the response at the threshold is due entirely to rods. As one indication of this, the field is seen as colorless at all wave-lengths.

Such measurements of the spectral sensitivity of peripheral rods are shown in Fig. 1 and Table 1. They are averages from the same 22 observers who yielded the foveal function. The sensitivities are here expressed relative to the foveal maximum. Fig. 3 shows similar data from 52 subjects of average age 21; these are plotted relative to their own maximum. These observations differ only in detail from earlier measurements made in more restricted ranges of wave-length, either by a comparable procedure,[11] or by brightness-matching in large central retinal areas at low illuminations.[12]

The rod sensitivity is maximal at about 505 mμ. At 365 mμ it has fallen on the average to about 1/20,000, and at 750 mμ to about 1/2,500,000 of the maximum value. Below 550 mμ the dark-adapted periphery is 100 to more than 1,000 times as sensitive as the fovea (Fig. 1). Above this wave-length the peripheral and foveal functions draw together, and at about 650 mμ they cross. In the farther red the fovea is more sensitive than the periphery. These relations change somewhat in test fields of other sizes and other durations of exposure than were used in the present experiments.

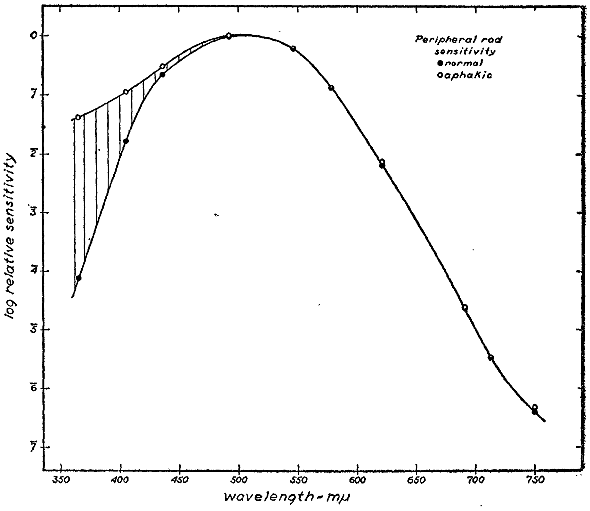

FIG. 3. Spectral sensitivities of rod vision in an area 8° above the fovea in the normal and aphakic eye. Both functions have been brought together above 546 mμ, where they are parallel. The vertically hatched area represents the optical density of the lens.

PERIPHERAL CONES

The following procedure was devised for measuring the spectral sensitivity of cones in peripheral areas of the retina. If the eye is highly light-adapted and then placed in darkness, the threshold for a time is due to cones. During this interval the stimulus looks colored at all wave-lengths. The threshold falls rapidly to a plateau, held constant from about the fourth to the eighth minute or longer. This is the threshold level of the completely dark-adapted cones;

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[4] Reviewed by K. Gross, *Z. Sinnesphysiol.*, 59: 215, 1928.

[5] Reviewed by K. S. Gibson, *Jour. Opt. Soc. Amer.*, 30: 51, 1940.

[6] W. W. Coblentz and W. B. Emerson, *Bull. Nat. Bur. Stand.*, 14: 167, 1918–19.

[7] K. S. Gibson and E. P. T. Tyndall, *Sci. Pap. Nat. Bur. Stand.*, 19: 131, 1923–24.

[8] See also W. S. Stiles, *Nature*, 154: 290, 1944.

[9] P. G. Nutting, *Phil. Mag.*, London, 29: 301, 1915; revised data in *Jour. Opt. Soc. Amer.*, 4: 55, 1920.

[10] L. W. Hartman, *Astrophys. Jour.*, 47: 83, 1918.

[11] W. deW. Abney and W. Watson, *Phil. Trans. Roy. Soc. London*, A216: 91, 1915.

[12] S. Hecht and R. E. Williams, *Jour. Gen. Physiol.*, 5: 1, 1922–23; K. S. Weaver, *Jour. Opt. Soc. Amer.*, 27: 36, 1937.

it is maintained long enough to permit its measurement with some precision. Later, the dark-adaptation of the rods supervenes; the threshold falls again to a new and final level. By repeatedly light-adapting the eye and measuring the cone plateaux at various wave-lengths, one can determine the spectral sensitivity of dark-adapted cones in any desired area of retina.

Such measurements have been performed with 10 of the 22 subjects who yielded the data previously described. The same retinal area was employed as in the rod measurements. The averaged sensitivities of the peripheral cones, relative to the foveal maximum, are shown in Fig. 1 and Table 1. These data are re-plotted, relative to their own maximum, in Fig. 2.

The maximum sensitivity of the peripheral cones is found at about 550 mμ, about 12 mμ below that of the fovea. Except for a narrow region between 440 mμ and 490 mμ, the sensitivity of the peripheral cones is lower than that of the fovea. Above 550 mμ both functions, plotted logarithmically, are parallel; throughout this region the fovea is about 0.4 log unit (about 2.5 times) more sensitive than the cones of a corresponding area of peripheral retina.

The difference between the achromatic threshold due to stimulation of rods and the color threshold due to the excitation of cones is called the photochromatic interval. Fig. 1 shows two aspects of this: (1) In a large retinal area which includes the fovea the achromatic threshold is mediated by peripheral rods, the color threshold by the fovea itself. In this instance the photochromatic interval decreases sharply in the yellow and orange, and ceases to exist above 650 mμ. (2) In a fixed peripheral area, the interval between rod and cone thresholds is larger, and continues throughout the spectrum. Even in the far red, a peripheral stimulus is seen at the threshold as colorless, and its intensity must be raised about 0.2 log unit for color to appear.

When the sensitivity functions of foveal and peripheral cones are plotted to the same maximal value, as in Fig. 2, they are seen to be very different in shape. The foveal cones are relatively less sensitive than those of the periphery between about 380 mμ and 550 mμ. The difference, shown in the figure as a horizontally hatched area, is due to the absorption of light in the fovea by the macular pigmentation.

THE MACULAR PIGMENT

The macular pigmentation lowers the relative sensitivity of the central retina at various wave-lengths by a factor equivalent to the fraction of incident light which it transmits. The macular transmission is obtained directly by dividing the foveal by the peripheral cone sensitivity. Consequently the difference between the logarithms of the peripheral and foveal sensitivities—the horizontally hatched area of Fig. 2—represents directly log 1/transmission, or the optical density, of the macular pigment. This is plotted in Fig. 4 (open circles). It rises steeply from about 550 mμ to a broad maximum in the region 430–490 mμ, then falls to negligible values in the near ultra-violet. Earlier estimates of macular absorption have involved only the long-wave-length limb of this function;[13] in this restricted region they agree approximately with the present data.

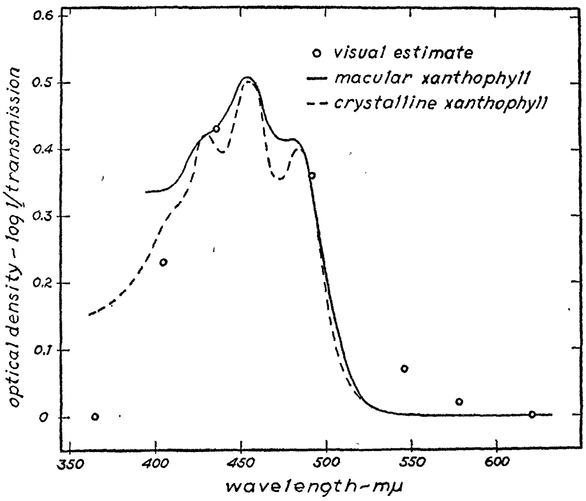

FIG. 4. The absorption spectrum of the macular pigment. The open circles are visual estimates of this, differences in log sensitivity of peripheral and foveal cones, taken from Fig. 2. The solid line is the absorption spectrum of a partially purified preparation of xanthophyll extracted from human maculas. The broken line is the spectrum of a preparation of crystalline leaf xanthophyll.

In our 10 subjects the macular pigment absorbs on the average about 60 per cent. of light of wave-length 430–490 mμ incident on the fovea. This pigment is responsible for the deep inflection in the foveal sensitivity function in the neighborhood of 450–470 mμ. The depth of pigmentation, however, varies greatly in our observers. In one of them no pigmentation was perceptible; in another the pigment absorbed more than 90 per cent. of light incident at 436 mμ. These wide variations probably account for marked disagreements in the anatomical literature regarding the occurrence and depth of pigmentation in the fovea.[14] It is clear from our data that some foveas are virtually unpigmented, while others are intensely colored. In the latter instance, the pigment must affect profoundly the contributions of blue and violet light to the color sensations of the

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[13] M. Sachs, *Arch. ges. Physiol.*, 50: 574, 1891; A. Kohlrausch, *Ber. ges. Physiol.*, 22: 495, 1923; S. W. Kravkov, *Arch. ges. Physiol.*, 210: 781, 1925.

[14] S. L. Polyak, "The Retina," Chicago, 1941, p. 222.

fovea; this matter will be discussed at some later opportunity.

The shape of the macular absorption spectrum as estimated visually suggests that the pigment is a carotenoid. This class of yellow, fat-soluble substances typically possesses absorption spectra which rise from about 550 mμ to a broad, complicated maximum in the blue and violet, then fall again at lower wave-lengths.

To explore this possibility I have extracted a small number of human maculas. They yield to benzine or chloroform a yellow pigment which has proved to be a hydroxy-carotenoid or xanthophyll, in all probability lutein or leaf xanthophyll itself ($C_{40}H_{54}(OH)_2$). This marks the first appearance of a carotenoid of this type in a mammalian retina.

The absorption spectrum of a crude preparation of macular xanthophyll is shown in Fig. 4. It has been brought to the height indicated by the visually estimated absorption. The spectrum of crystalline leaf xanthophyll is also shown in the figure. It differs no more from the spectrum of the macular pigment than is to be expected in a comparison of a crude tissue extract with the pure substance.

Extra-macular portions of the human retina also contain some xanthophyll, but only about 1/15–1/20 as much per unit area of retina as the maculas. This general pigmentation probably accounts for the small inflection in the region of 470 mμ in the spectral sensitivity function of peripheral cones.

APHAKIC VISION, ROD AND CONE

Measurements of spectral sensitivity, rod and cone, centrally and peripherally, have been performed in subjects whose lenses had been removed in the operation for cataract. With the loss of the yellow lens the eye gains enormously in sensitivity in the violet and ultra-violet.

Measurements on aphakic subjects are shown in Figs. 2 and 3, and in the last two columns of Table 1. In the figures the aphakic data have arbitrarily been brought together with normal results above 550 mμ, where all the functions are parallel. The data on aphakic rod sensitivities include measurements on 39 eyes of 24 subjects; those on aphakic cones are from 6 subjects.

The spectral sensitivity curves of the aphakic eye decline much less steeply at low wave-lengths than the normal functions. At 365 mμ, aphakic rod or cone vision is still about 1/30 as sensitive as at the maximum. At this wave-length the aphakic rods are as sensitive as in yellow light, the cones as sensitive as in the near red. The average sensitivity of the aphakic eye at 365 mμ is about 1,000 times that of normal observers.

It has long been known that certain insects are highly sensitive to ultra-violet light, and it has been alleged that they respond to it with a special quality of color sensation.[15] There has also been some discussion in the past of the unique visual experiences which may accompany such properties.

This need no longer be a matter of pure speculation, for aphakic persons see very well in the ultra-violet. That this ordinarily produces no striking distortion of their visual experiences may be judged from the fact that they usually are wholly unaware of their extraordinary capacities. The relatively low ultra-violet content of sunlight and most artificial illuminations is of course partly responsible for this. Nor does the hypersensitivity of aphakics in the ultra-violet bring them new sensations; they seem to see this region as they do 405 mμ, as blue or violet.

TABLE 1

LOG SENSITIVITY (LOG 1/THRESHOLD) AT VARIOUS WAVE-LENGTHS IN A 1° CIRCULAR FIELD, EXPOSED FOR FLASHES OF 1/25 SECOND. DATA FOR FOVEAL CONES, AND PERIPHERAL RODS AND CONES OF THE NORMAL EYE ARE EXPRESSED RELATIVE TO THE FOVEAL MAXIMUM SENSITIVITY. DATA FOR APHAKIC RODS AND CONES ARE PRESENTED RELATIVE TO THEIR OWN MAXIMAL SENSITIVITY VALUES

Wave-length (mμ)	Log sensitivity				
	Normal eyes			Aphakic eyes	
	Foveal cones	8° above fovea		8° above fovea	
		Rods	Cones	Rods	Cones
365	$\bar{5}.401$	$\bar{2}.042$	$\bar{6}.95$	$\bar{2}.62$	$\bar{2}.42$
405	$\bar{3}.806$	0.427	$\bar{3}.64$	$\bar{1}.05$	$\bar{2}.88$
436	$\bar{2}.643$	1.675	$\bar{2}.67$	$\bar{1}.48$	$\bar{1}.22$
492	$\bar{1}.288$	2.295	$\bar{1}.25$	0.00	$\bar{1}.80$
546	$\bar{1}.980$	2.095	$\bar{1}.65$	$\bar{1}.78$	0.01
578	$\bar{1}.966$	1.375	$\bar{1}.59$	$\bar{1}.12$	$\bar{1}.90$
621	$\bar{1}.626$	0.038	$\bar{1}.27$	$\bar{3}.87$	$\bar{1}.63$
691	$\bar{3}.840$	$\bar{3}.635$	$\bar{3}.43$	$\bar{5}.39$	$\bar{3}.87$
713	3.048	4.787	4.59	6.52	3.11
750	$\bar{4}.072$	5.890	$\bar{5}.68$	$\bar{7}.68$	$\bar{4}.18$
Number of subjects	22	22	10	24 (39 eyes)	6

When the illumination is confined to the region of 365 mμ, nevertheless, the vision of aphakics is sufficiently remarkable. In this radiation I have frequently had 60- to 70-year-old aphakics read a Snellen chart from top to bottom, under circumstances in which I was unable to see the chart.

The high sensitivity of the aphakic eye to the ultra-violet has only recently been described, as the result of a chance observation by Gaydon, who suffered the loss of one eye and the lens of the other in a laboratory accident.[16] The sensitivity of Gaydon's periph-

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[15] L. M. Bertholf, *Jour. Agr. Res.*, 43: 703, 1931; *Z. vergl. Physiol.*, 18: 32, 1932–33; A. Kühn, *Z. vergl. Physiol.*, 5: 762, 1927.

[16] A. G. Gaydon, *Proc. Phys. Soc.*, 50: 714, 1938.

eral rods was later measured at 365 and 546 mμ, and found to be nearly equal at these wave-lengths. On comparison of this result with other types of data, it was concluded that the aphakic rod sensitivity passes through a minimum at about 400 mμ, to rise again at lower wave-lengths.[17] The present measurements show no indication of such changes.

The Lens

The differences in log sensitivity of normal and aphakic eyes, shown as vertically hatched areas in Figs. 2 and 3, represent directly the optical density of the human lens. These values are for subjects averaging 20 years of age. It is well known that in older persons the lens is more deeply pigmented.

The rod and cone estimates of lens absorption agree reasonably well with each other. The rod data involve many more subjects and are the more reliable. They show that the density of lens absorption rises rapidly and regularly from about 500 mμ into the ultra-violet. At 405 mμ the average lens transmits about 15 per cent., at 365 mμ about 0.1 per cent. of the radiation incident upon it.

The pigmentation of the lens varies greatly in different individuals even within a narrow age-group. In our normal subjects this factor alone adds more than a logarithmic unit to the variation in sensitivity at 365 mμ.

We have measured the absorption spectra of a number of isolated lenses from persons 63–68 years of age. As expected, these involve much higher optical densities than we have estimated visually in young subjects. They do, however, exhibit the same general character of absorption, the density rising without inflection into the ultra-violet.

Conclusion

Measurements made in the periphery of the aphakic eye come as close to the intrinsic sensitivities of rods and cones as it is possible to approach *in vivo*. The lens has been removed, the macular pigmentation avoided. Only the minor pigmentations of the cornea, ocular humors and extramacular retina remain to screen the receptors. This is as far as the analysis of spectral sensitivity in the functioning eye can penetrate.

The sensitivities of the rods and cones are related intimately to the absorption spectra of their photosensitive pigments, rhodopsin and iodopsin.[18] The spectrum of rhodopsin is known with some assurance. The over-all transmission of the human eye has also been measured.[19] With these data one can compute a spectral sensitivity function for normal rod vision which agrees well with that observed.[20] We still lack adequate information concerning the absorption spectrum of iodopsin, and of some of the separate ocular structures through which light passes before striking the receptor cells. When these have become available we shall be in position to synthesize from their basic components the spectral sensitivity functions of rod and cone vision, centrally and peripherally, and in the normal and aphakic eye.

OBITUARY

LEWIS RALPH JONES

1864–1945

Lewis Ralph Jones, professor emeritus of plant pathology of the University of Wisconsin, died at Orlando, Florida, on April 1, 1945, in his eighty-first year. In his passing biological science loses one of its foremost leaders.

He was born on a farm near Brandon, Wisconsin, on December 5, 1864, the third of six children of David and Lucy Knapp Jones, leaders in the settlement and early development of that community. His early education was at Brandon, followed by three years at Ripon College. For advanced studies he went to the University of Michigan, from which he received the Ph.B. degree in 1889 and the Ph.D. in 1904. At Michigan he gained much from the influence of such great men as President Angell, Professors Spalding, Vaughan and Novy, and Erwin F. Smith, then an exceptionally brilliant and mature graduate student who was later to become an outstanding leader in plant pathology and experimental biology.

In 1887 and 1888 he taught natural science for a year and a half at the Mt. Morris Academy, Mt. Morris, Illinois. The success of this early teaching is attested by the life-long friendship and devotion of members of his classes.

In 1889 he was called to the University of Vermont, where, after a brief period as instructor in natural history, he served as assistant professor of natural history, 1891–92, associate professor of natural history, 1892–93, professor of botany, 1893–1910, and botanist of the Vermont Agricultural Experiment Station, 1889–1910.

On June 24, 1890, he married May I. Bennett, who

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[17] C. F. Goodeve, R. J. Lythgoe and E. E. Schneider, *Proc. Roy. Soc. London,* B130: 380, 1942.

[18] G. Wald, *Nature,* 140: 545, 1937.

[19] E. Ludvigh and E. F. McCarthy, *Arch. Ophth.,* 20: 37, 1938.

[20] G. Wald, *Jour. Gen. Physiol.,* 21: 795, 1937–38; E. Ludvigh, *Arch. Ophth.,* 20: 713, 1938; S. Hecht, S. Shlaer and M. H. Pirenne, *Jour. Gen. Physiol.,* 25: 819, 1941–42.