

THE VISIBILITY OF MONOCHROMATIC RADIATION
AND THE ABSORPTION SPECTRUM OF
VISUAL PURPLE.

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I.

Reasons for Experiments.

When the visible spectrum is reduced to a very low intensity, and is viewed by a dark adapted eye, it appears colorless. The different portions of the spectrum, however, possess different degrees of brightness, the center being much brighter than the ends. Apparently, a given quantity of light energy will produce a quantitatively different effect depending on its frequency. It seemed to us that an exact knowledge of the relation between frequency and brightness at low intensities of illumination should furnish data bearing on the mechanism of dim vision, a hint of which had already been received in a study of dark adaptation (Hecht, 1919-20). We therefore set ourselves the task of determining accurately this relation between the frequency of light and its ability to produce a colorless sensation in the eye.

Attempts to do precisely this have already been made by several investigators. Perhaps the earliest were Ebert (1888), Langley (1888) and Hillebrand (1890). They were followed soon afterward by Abney and Festing (1893) and von Kries and Nagel (1896), and later by Schaternikoff (1902), Pflüger (1902) and Trendelenburg (1904). It might therefore seem superfluous for us to have undertaken this work, and to add another to the already overwhelming number of papers on vision. Unfortunately, however, the work of the above mentioned investigators is far from adequate, first because of the failure to recog-

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nize certain factors entering into the problem, and second because of the sparse and irregular nature of the data.

It seems quite obvious that in order to make any correct comparisons of the relative effects and stimulating power of the different portions of the spectrum, it is necessary to know their energy content. Yet Langley and Pflüger were the only investigators who took this into consideration, and actually measured the energy distribution of the light which they used. The remaining authors either seemed unaware of this point (Ebert, Hillebrand, Abney and Festing, von Kries and Nagel, and Schaternikoff), or being aware, made no measurements with which to correct their data (Trendelenburg). Schaternikoff, for example, determined the relation between wave-length and brightness for the spectrum of gas light, of sunlight, and of diffuse daylight, and notes without further comment that the maxima are in different positions. Pflüger's results, though corrected for energy distribution, are so irregular that they contribute very little to our knowledge except that light between 495 and 525 $\mu\mu$ possesses the maximum capacity for stimulating the dark adapted eye. Langley's results, though much better, are too few to serve our purpose, his measurements having been made with only three or four individuals.

A second factor that enters into the measurements is again ignored by all the investigators except Langley and Pflüger. In making determinations of the relative stimulating power of different lights it is necessary to make comparisons of the intensities which will produce the *same* effect in the eye. In other words, one must find the amount of light at different frequencies which will produce the same brightness in the eye. Both Langley and Pflüger determined the energy at the threshold of visibility. The other investigators kept neither the brightness nor the energy constant, but varied both during the experiments.

In short, it seemed high time to secure results by a method which should not only be free from the errors previously committed, but which should be applicable for use with a large number of individuals so as to yield data sufficient to establish the relationship for the eye in general.

Such data are urgently necessary at this time. Ever since Koenig's (1894) first determination of the absorption spectrum of visual purple, there has been a growing conviction, stimulated by the work of Trendelenburg (1904) and the publicity of Henri and Larguier des Bancelles (1911), that visual purple is the receptor substance for dim or twilight vision. The main point in the evidence has been that the absorption spectrum and the velocity of bleaching of visual purple coincide with the stimulating power of spectral radiation at low intensities. The degree of coincidence of these three phenomena is, however, far from convincing. Due to the inadequacy of the data, their rather large deviations may be ascribed to individual variation, and to the necessity for making energy distribution corrections in the available data. These matters, however, lie at the very root of the photochemistry of photoreception, and cannot be dismissed in such an off hand manner. They demand an accurate, quantitative investigation.

This we have endeavored to do. As will be apparent, the effort has been amply repaid by the demonstration of new regularities and suggestive correlations, quite different from what would be expected in terms of the inadequate data heretofore available.

II.

Apparatus, Methods, and Calibrations.

1. The method which we first used consisted in determining the minimum intensity of a series of monochromatic illuminations which could just be perceived by the periphery of the eye. The apparatus was essentially a spectrometer, the light from which, after passing through a pair of Nicol prisms, was spread out on a plate of ground glass. Although we used highly intelligent subjects, our results were irregular. They resembled the data published by Pflüger, and for our purposes were flat failures.

The causes of the failure of such a method are instructive. In the first place, the experiments take a certain length of time, and during that time the eye of the subject varies. We do not speak of dark adaptation—a source of error which we recognized and carefully controlled. We refer more to the normal variations in the visual

mechanisms from minute to minute, and to the effects of the strain involved in looking for these extremely dim lights. These variations involve changes of 100 per cent or more, and with this method there is no way of controlling them or of compensating for them. In the second place, it is extremely difficult to tell when one sees a very dim light and when one does not; and to be able to indicate the exact stage of the intensity when a light first appears or ceases to exist is a taxing task, especially if it has to be done a dozen times with different portions of the spectrum. After our experience, Pflüger's irregular results are not surprising. Our results with this method are easily as erratic as those of Pflüger.

The method that we eventually adopted eliminated both these sources of variation. Instead of working with illuminations which are only just perceptible, we used an illumination which, though well below the color threshold, is still bright enough to be seen easily by the dark adapted eye. We then measured the relative energy at the various frequencies which is necessary to produce this degree of brightness. Our method is therefore a photometric one, in which one of the lights is kept at a constant brightness. In this way there is at once removed the uncertainty and strain of looking for lights that are not there. Moreover, there are eliminated the effects of variation in sensitivity of the visual system during the course of the experiments. The subject is required to match photometrically the constant light which serves as a standard. If the eye varies, it does so both for the standard and for the experimental light at the same time. With this method, the results took on at once a gratifying smoothness and regularity which will be apparent in the data to be presented.

2. The arrangement of the apparatus will be made clear with the help of Fig. 1. A 500 candle power Pointolite lamp in a light-tight box has its incandescent target focussed on the slit of a Hilger monochrometer. This is a spectrometer of the constant deviation type with a slit and thermopile groove in place of the eyepiece. In these experiments both slits of the spectrometer were kept at a width of 0.1 mm. The monochromatic light coming from the spectrometer spreads out gradually into a broad beam. Before it has sensibly diverged, however, it is passed through a pair of nicols, taken with

their mountings from a Hilger spectrophotometer. The beam then spreads out, and 150 cm. from the slit it is made to impinge on the end of a viewing box.

Here it passes through openings in an otherwise opaque cardboard. The shape of this cardboard is shown in Fig. 1. It is the pattern of a Lummer-Brodhun photometer made so as to be 10×10.5 cm. Since the

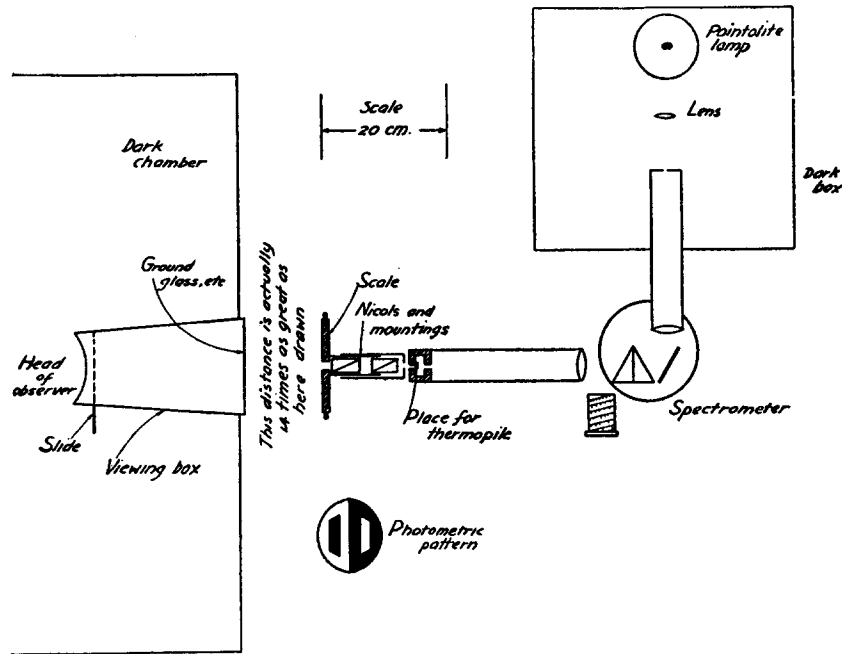


FIG. 1. Diagram of apparatus. The subject sits in the dark chamber curtained off from the rest of the dark room. Note that the front wall of this chamber is actually fourteen times as far from the spectrometer as shown in the drawing.

subject's eyes at the ocular end of the viewing box are 25 cm. from the pattern end, the pattern subtends a visual angle of 22° . The white portion of the pattern represents the parts cut out of the cardboard, through which the monochromatic light passes. In the viewing box and close up against this pattern are two sheets of ground glass which serve the double purpose of diffusing the light and reducing its intensity. The ground glasses are, however, so near the pattern that

though the light which comes through is diffused, it still possesses the shape given to it by the pattern.

This takes care of the variable monochromatic light. The constant comparison light is incorporated into the pattern of the viewing box. It consists of a layer of radium paint which covers the portion of the pattern represented as black in the figure. The layer of radium paint gives a constant and continuous illumination for long intervals of time (several years) provided it is not exposed to light. The brightness of this constant light was so adjusted as to be equivalent to an intensity of 2.7 times the threshold of visibility after complete dark adaptation. This was accomplished first by the two sheets of ground glass already referred to, and second by sheets of translucent paper cut into the proper shape and placed between the paint and the ground glass. The papers and the cardboard are held together by being mounted between two plates of ordinary glass.

The pattern end of the viewing box forms part of the wall of a dark chamber, curtained off from the rest of the dark room, in which the subject sits. In this way flashes of light used by the experimenter in taking readings and making adjustments are not seen by the subject, and hence do not spoil his dark adaptation. Moreover, a slide at the ocular end of the viewing box excludes even the experimental lights from the eyes of the subject between actual observations.

The intensity of the variable monochromatic beam is controlled by a coarse and a fine adjustment. The coarse adjustment consists of two neutral filters made of uniformly fogged photographic film, each reducing the intensity to $\frac{1}{10}$, and together to $\frac{1}{100}$. The fine adjustment between the range of the filters is made with the pair of Nicol prisms. The intensity which the nicols transmit is proportional to $\cos^2\theta$, where θ is the angle between the prisms. At $\theta=0^\circ$ the transmission is the maximum; at $\theta=90^\circ$ the transmission is zero. The function $\cos^2\theta$ varies slowly near 0° , and very rapidly near 90° . In order, therefore, to have a nearly constant rate of adjustment, the nicols were used between 70° and 20° . This is a range of approximately $\frac{1}{10}$, and thus covers the interval between the filters. By using the nicols always, first without any filter, then with Filter 1, and finally with Filters 1 and 2, it is possible to cover by a fine adjustment a range of intensities from 1 to $\frac{1}{1,000}$ of the light transmitted by the nicols alone. This was more than ample for the experiments.

The position of the nicols is indicated in Fig. 1. The filters were placed directly in the path of the monochromatic beam immediately on its emergence from the slit of the spectrometer, in the groove built for the thermopile. The filters were mounted in wooden cases which were so arranged as to fit this groove, thereby insuring a constant and accurate position of the filter.

3. The apparatus as set up requires the calibration of the transmission of the filters, of the settings of the spectrometer, and of the energy distribution in the spectrum. The filters were calibrated photometrically three times, using two sources of light 2 meters apart, and a Lummer-Brodhun photometer. The results were practically the same each time. Filter 1 transmits 0.0977, and Filters 1 and 2 together transmit 0.00954 of the incident light.

The spectrometer, having once been set up, was not moved or readjusted during the experiments here recorded. It was calibrated¹ ten times during the investigation by means of the three hydrogen lines obtained from a hydrogen discharge tube. The results varied comparatively little from time to time, so that we may take their averages as indicating the correct values. In recording the wave-lengths, we use the values obtained graphically from the calibration curve made by plotting the actual values of the hydrogen lines against the drum readings.

The Pointolite lamp which we used runs on 230 volts and 4.5 amperes. We calibrated its energy content in the visible spectrum by means of a Hitchins thermopile and a Broca galvanometer. The resistance of the thermopile is 14.9 ohms, and that of the galvanometer 9.02 ohms. The results are shown in Fig. 2, in which each point is the average of four separate measurements. The energy content of the wave-lengths used in the experiments have been determined by graphic interpolation from this curve.

4. The method of taking observations is very simple, and requires no previous training or experience on the part of the subject. It merely requires him to be intelligent and interested. The subject is brought into the dark room, and 10 minutes are spent in explaining

¹ During the calibration of the spectrometer and of the energy content of the lamp, we had the help of Mr. R. A. Woodeson, to whom we wish to express our thanks.

the object of the experiment, the apparatus, and the procedure. He is then seated in the curtained off, dark chamber in front of the ocular end of the viewing box. Special precautions are taken to make the subject very comfortable, to have his back supported all the time,

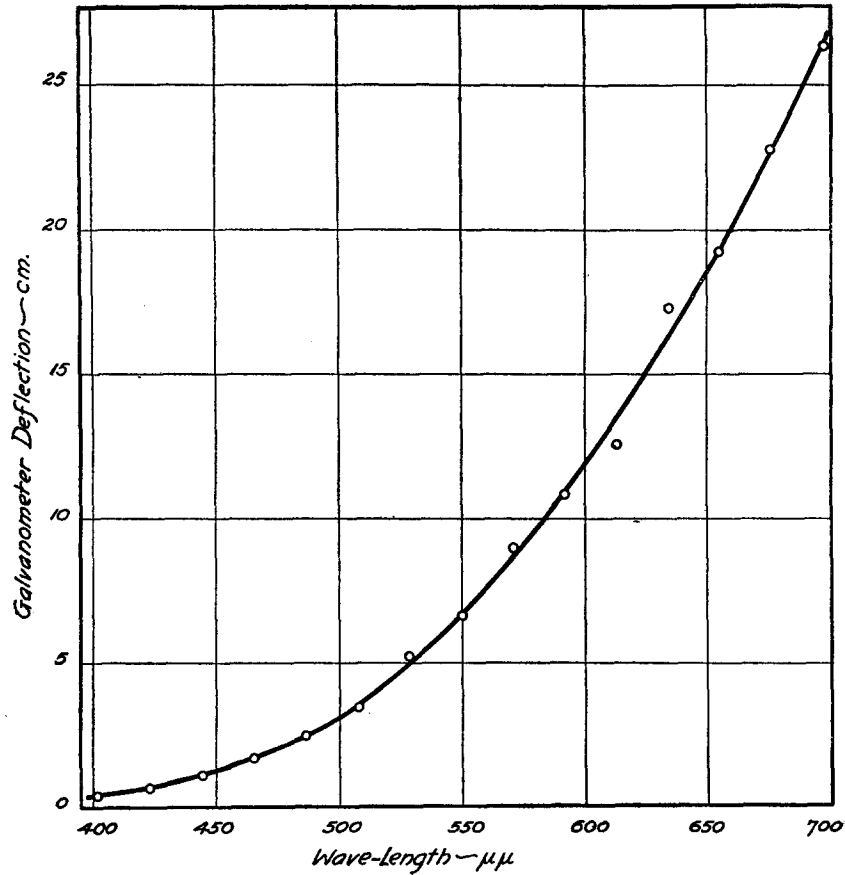


FIG. 2. Energy distribution in spectrum of a 500 candle power Pointolite lamp. Each point is the average of four determinations of the galvanometer deflection obtained from a thermopile placed in the position indicated in Fig. 1.

to have the chair the right height, etc., so that the act of sitting for an hour and a half or more will involve as little physical strain and discomfort as possible. The positions of the chair and the subject

are so adjusted that in order to look into the viewing box he is required to move his head forward only about 5 cm. We mention these details because we are convinced that the personal comfort of the subject has a decided influence on the smoothness and accuracy of the results.

The light from the spectrometer is cut off by placing the nicols at right angles, and the subject is allowed at least half an hour for dark adaptation. During this half hour the subject is kept interested by allowing him to watch the gradual appearance of the pattern formed by the radium paint, indicative of the increase in the sensitivity of his eyes. This pattern usually becomes faintly visible after 10 or 15 minutes. During the next 15 minutes it increases in brightness and clearness, so that the subject becomes familiar with its shape and learns how to find it when looking into the viewing box and pulling out the slide. The appearance of the pattern at this stage is that of an oval field of light with vertical dark bars in it representing the places where there is no radium paint and where the experimental light will come through later. The edges of the pattern are not sharp, because of the ground glass diffusion and the use of rod vision.

The subject is now given a few practise trials in the methods of making observations. The spectrometer is set for $412\mu\mu$, the nicols being still at right angles. The subject looks in and observes the shadows and the pattern. This takes a few seconds only; the slide is immediately replaced in the viewing box, and the subject remains in complete darkness. The movable nicol is then turned to admit some of the experimental light. The subject again observes the pattern and notices whether the vertical shadows are still as strong as they were before. More illumination is admitted, and the subject again examines the pattern. This is continued until the shadows have completely disappeared, and the field has become uniformly illuminated; the last observations are made slowly and in steps of about $10'$ of arc. The final judgment of uniformity is always checked after a rest of a minute or so.

It should be emphasized that the errors and troubles of heterochromic photometry do not exist here, because the field is uniform not only in lack of brightness contrast, but in lack of color as well.

The entire process of making a uniformity judgment is repeated after a few minutes of rest. The same wave-length is used, and the subject is aware that this is a repetition. These preliminary measurements with the same wave-length are continued until two successive determinations agree within a degree of arc. In most cases only two or three such practise readings are necessary, the facility with which the technic is acquired being really surprising. Out of the 48 subjects with whom we made the final measurements, 22 required only 2 determinations to produce the desired duplication; 13 required 3 determinations; 10 required 4 determinations; and 3 required 5 determinations. It is therefore apparent that the method is a simple one, and justifies our assumption that we could apply it to a large number of people, who, though intelligent and to a large extent scientific, yet possess no special training in visual work.

At the end of the practise tests the subject has had at least 45 minutes of dark adaptation, which is more than enough. The measurements are then carried out with lights of chosen wave-length one after the other, allowing about 8 minutes for each determination. After the last portion of the spectrum has been measured, the first measurement is repeated. This observation usually checks well with the first ones; occasionally it is 1° or 2° higher. A complete experiment takes the greater part of a morning or of an afternoon. An example of the type of observations made is given in the record of an experiment in Table I, exactly as it was noted in the record.

III.

Results.

After many preliminary experiments involving modifications of apparatus and technic, we carried out 48 sets of measurements; 43 were with men, and five with women. The average age of the subjects was about 25 years. The subjects were mostly graduate students in the University of Liverpool, but some of them were older people of the teaching staff in Chemistry and Physics. Two were school boys of 15 years, whose results are just as good as those of the others, illustrating the simplicity of the method.

Of the subjects used in these final measurements, three were kind enough to come twice. Fig. 3 gives their data. The points show

the type of result which we obtained, and at the same time give an idea of the degree of reproducibility of the results under the experimental conditions.

In Fig. 3 the ordinates are the logarithms of the relative energy necessary to match the radium paint in brightness. A logarithmic scale is used because a direct plot covering so large a range of values minimizes the finer changes which occur at the lower intensities, and exaggerates the large changes at the higher intensities. Because of

TABLE I.

Data of an Experiment.

W. D., male. Jan. 7, 1922. Lights out at 10:40.

Wave-length.	Time.	Filter.	Nicol reading.
$\mu\mu$			
412	11.20	0	50° 23'
412	11.38	0	50° 43'
455	11.48	1	60° 36'
486	12.05	1 + 2	43° 22'
496	12.15	1 + 2	47° 18'
507	12.22	1 + 2	54° 43'
518	12.30	1 + 2	55° 12'
529	12.40	1 + 2	57° 12'
540	12.50	1 + 2	55° 0'
550	12.58	1 + 2	53° 36'
582	1.12	1 + 2	36° 30'
613	1.16	1	53° 18'
666	1.19	0	49° 50'
412	1.25	0	50° 17'

the construction of the apparatus (decimal filters and nicols) the degree of accuracy is nearly the same at all values of energy content, a fact which can be brought out only by a logarithmic plot.

In Fig. 3 the points for 666 $\mu\mu$ are omitted simply to enable one to get the three sets of results in one figure. The energy required in this region is very high indeed, as will be apparent from Fig. 4.

In order to secure the average results, the following method was used. The data for each subject were computed individually and a graph made of them. From this the minimum point in the curve was found, and an arbitrary value of 10 assigned to it. The experimental results at the other wave-lengths were then computed in terms

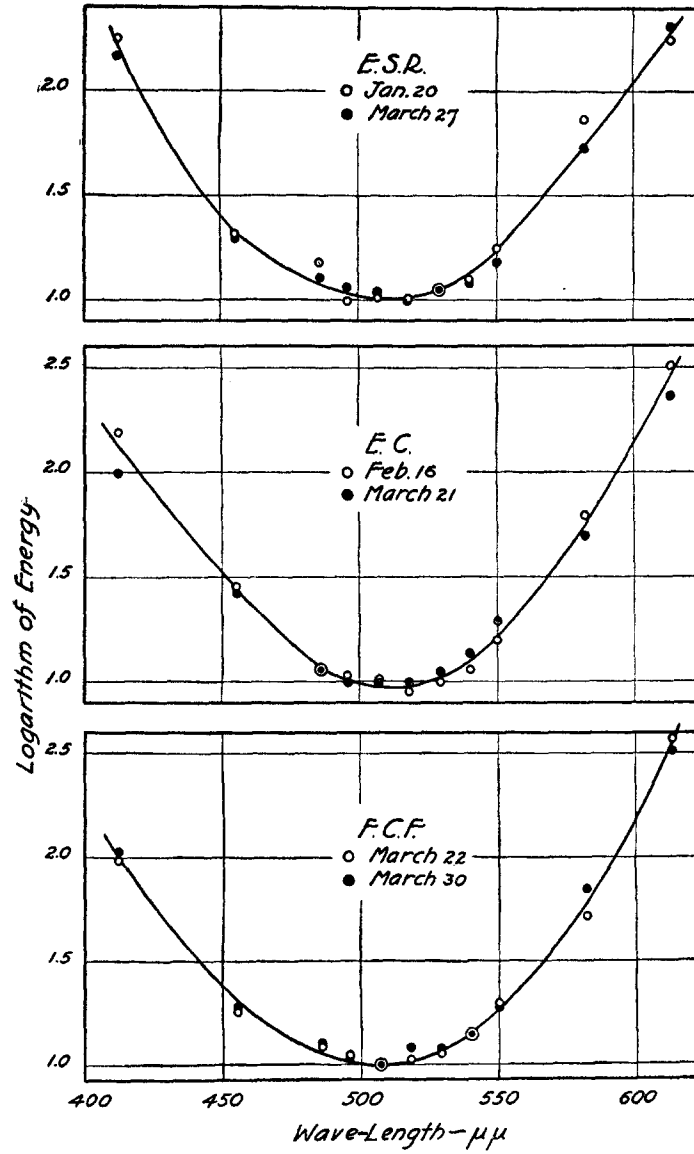


FIG. 3. Results with three subjects who came twice. The points are single readings. The results are reproducible for the same subject at different times, and are practically the same for the three subjects.

of this minimum value of 10. This served to get the data for all the subjects into a similar order of magnitude. The results for each wave-length for the 48 observations were then averaged. These averages are given in Table II, second column. In order to show them graphically, they are plotted logarithmically in Fig. 4.

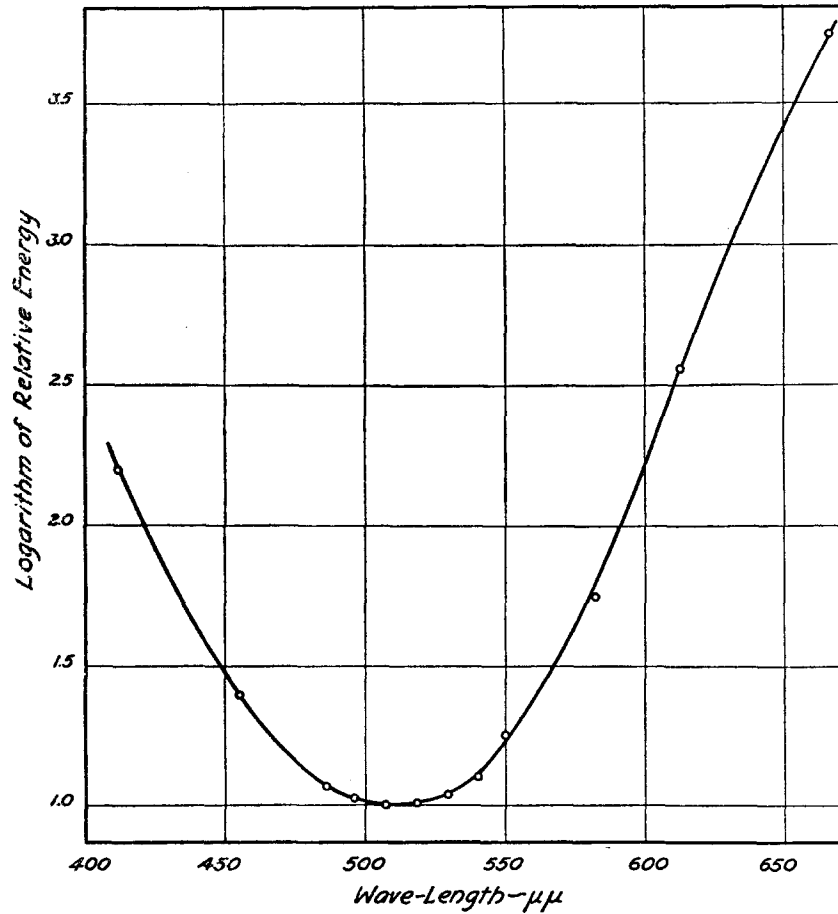


FIG. 4. Relation between energy for achromatic vision and wave-length. Each point is the average of 48 determinations.

It is apparent from Table II and Fig. 4 that the wave-length at which the minimum energy is necessary to produce a given brightness is very near $510 \mu\mu$. The energy values for the wave-lengths on both

sides of this point rise quickly, and in the orange and the violet are more than a thousand per cent greater than at the minimum.

Both the position of this minimum and the shape of the curve relating energy for vision with wave-length are of significance for an understanding of the photochemistry of visual reception. We shall therefore devote the remainder of this paper to these two points and to certain other matters which arise in connection with them.

TABLE II.
Relation between Wave-Length and Energy for Vision and Visibility.

Wave-length.	Relative energy.	Visibility.
$\mu\mu$		
412	158.1	6.32
455	25.03	39.95
486	11.99	83.40
496	10.65	93.90
507	10.06	99.35
518	10.28	97.30
529	10.98	91.10
540	12.69	78.78
550	17.99	55.60
582	56.24	17.78
613	367.2	2.72
666	5,525	0.181

IV.

Shape of Visibility Curve.

It goes almost without saying that the rods must possess a photo-sensitive substance which has an absorption band in the visible spectrum. The effect of light on this substance is the initial event in its reception by the retina. Let us assume that in order to produce a certain sensation of gray in the eye the same amount of photochemical action must be induced in the sensitive substance, irrespective of the wave-length of the light. In terms of Grotthus' law, and its quantitative demonstration by the work of Lasareff (1907), this means that to produce the same visual effect the sensitive substance will have to absorb the same amount of energy regardless of the wave-length of the incident light.

Let us call this amount of energy E . At the position of maximum absorption λ_{max} of the sensitive substance, $\frac{E}{a_{max}}$ units of incident light will be sufficient to yield that amount of absorbed energy, a_{max} being the absorption coefficient at the maximum. At any other wave-length λ the absorption coefficient a_{λ} will be less than at λ_{max} , but the amount of light necessary so that E units are absorbed will always be $\frac{E}{a_{\lambda}}$. In short, the amount of light A_{λ} necessary to produce a given sensation at any wave-length λ will be given by the equation

$$A_{\lambda} = k \frac{E}{a_{\lambda}}$$

By solving this equation for a_{λ} we get

$$a_{\lambda} = k \frac{E}{A_{\lambda}}$$

which gives us the value of the coefficient of absorption of the sensitive substance for any wave-length. The term k is a constant, and E is a constant; therefore the absorption coefficient of the sensitive substance for any wave-length is proportional to the reciprocal of the amount of energy necessary to produce a given sensation of gray at that wave-length.

It should then follow that the reciprocals of our data in Table II, second column, should represent the absorption spectrum of the sensitive substance in the condition in which it is in the retina. The continuous (low intensity) curve in Fig. 5 shows the shape taken by the data when plotted in this manner. The values of the points are taken from the third column of Table II, and are the reciprocals of those in Column 2 arranged so that the maximum of the curve has a value of 100. It is at once clear that the shape of the curve corresponds to the shape of the absorption bands of numerous well known substances.

It would be highly desirable to demonstrate this exact correspondence by applying an equation for the shape of an absorption band to the results in Fig. 5. Unfortunately this cannot be done with any great assurance in the present stage of our knowledge of absorption.

spectra, because there exists no generally applicable equation for the shape of an absorption curve of a complicated substance in solution. In fact there exists no accepted interpretation of the shape of the absorption spectrum even of simple gases.

Several attempts have indeed been made to devise some formula for the shape of visibility curves (as the curves in Fig. 5 have been called) for high intensities (Nutting, 1908) as well as for low intensities

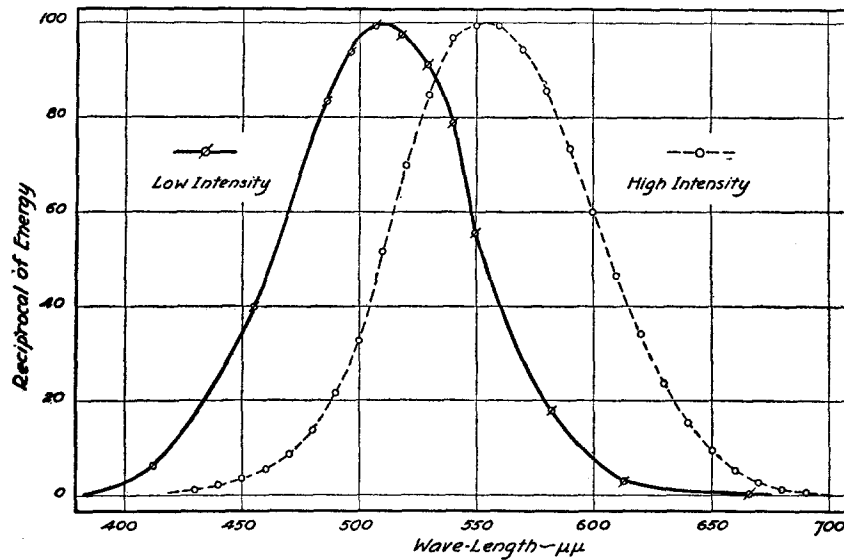


FIG. 5. Visibility curves for achromatic and chromatic vision. The ordinates are proportional to the absorption coefficients of the sensitive substances in the retina. The low intensity curve is therefore the absorption spectrum of the sensitive substance in the rods, while the high intensity curve is the absorption spectrum of the sensitive substance in the cones.

(Goldhammer, 1905; Renqvist, 1920). The best that may be said for these attempts is that they are amusing. They contribute little to the theoretical aspects of the matter, because they are all strictly empirical. Nutting's formula is based on a probability function, whereas Goldhammer's equation has not even that basis. Although nominally derived from Wien's formula for black body radiation, it is really an arbitrary relation between pure numbers possessing no dimensions, and as such it has not a trace of theoretical significance.

Renqvist has tried to apply Planck's resonance theory of light absorption in gases to a calculation of Trendelenburg's data for visibility at low intensities. Aside from the fact that Trendelenburg's data are valueless for this purpose because he took account neither of the adaptation of his eye nor of the energy distribution in the gas flame which he used, the application of Planck's equations in this connection is rather arbitrary and is far from possessing any general significance.

Nutting's attempt to use the probability function is commendable, though he does not seem to recognise the significance of visibility curves in terms of absorption spectra. The symmetrical or nearly symmetrical curves that represent simple absorption spectra resemble strikingly the distribution curves of errors, of populations, etc. which are familiar in the theory of statistics. It may be that the shape of an absorption curve represents the fact that the absorbing substance is composed not of a uniform series of resonators, but of a group of resonators whose free periods may be expressed by the common distribution curves of the statisticians.

It is, however, not in our province to proceed any further along this line of reasoning. For our purposes it will suffice to note the similarity of our curve with curves showing the shape of absorption spectra, leaving aside for the moment the exact theoretical interpretation of such curves. We may then proceed to a comparison of our results with those obtained in the study of the brightness values of spectral light at high intensities in which color enters as a factor.

v.

Chromatic and Achromatic Vision.

In recent years many careful measurements have been made of the relative brightness of different parts of the spectrum at high intensities by methods of heterochromic photometry. The results of all the investigators have been about the same, except, as Hyde, Forsythe and Cady (1918) point out, that the curves obtained with the flicker photometer have in general been somewhat wider than those obtained by methods of direct photometry. The method which we used in our own data on achromatic vision is one of direct photometric

comparison. Without therefore entering into a discussion of the relative merits of the two methods of heterochromic photometry, we have chosen for comparison with our own, those data, which like our own, have been made with a method of direct photometry.

It has never been possible to make this comparison before except in the roughest manner (*cf.* Nutting), because the data for achromatic vision was so inadequate. Now that the necessary data have been made available, we may compare them with the recently reported measurements of Hyde, Forsythe and Cady with 29 subjects. These authors give their data as the reciprocals of the relative energy necessary to produce a certain brightness using different spectral colors. The curve which they present is reproduced in the broken (high intensity) curve of Fig. 5. It is at once clear that the curve also resembles the absorption spectrum of a substance having a band in the visible.

Even a superficial comparison of the two curves in Fig. 5 shows their similarity. To make an accurate demonstration of this resemblance we have proceeded as follows: We have measured the horizontal distances between the two curves in twelve places. The average of these twelve measurements turns out to be very nearly $48 \mu\mu$. We have then moved the curve of Hyde, Forsythe and Cady $48 \mu\mu$ to the left, and have measured graphically the ordinates on their curve which correspond to the wave-lengths of the points on our curve. The two sets of points, theirs and ours, are plotted in Fig. 6. Their identity is shown by the fact that the same smooth curve passes through both sets of points. The agreement between the two sets of data is much better than the coincidence between the five or six visibility curves at high intensity which have already appeared from the careful work of different laboratories (*cf.* for example, the set of curves summarized in the paper by Hyde, Forsythe and Cady). It is therefore apparent that the two curves—one at high intensities involving color vision, and the other at low intensities involving only gray vision—are really the same curve in two positions on the spectrum $48 \mu\mu$ apart.

In order to make the comparison absolutely accurate, the data at high intensities should be corrected for the absorption of the macula lutea. The values for the high intensities are measured with the

fovea, whereas those at low intensities are measured with the periphery. To compare the two results as far as their receptive elements are concerned, the macular absorption should be considered. Unfortunately, however, no decent data are available for this correction. Sachs (1891) measured the absorption of the yellow spot using a double collimator spectrophotometer of the Vierordt type. The results he gives are few and irregular, and it would be an insult to the beautiful

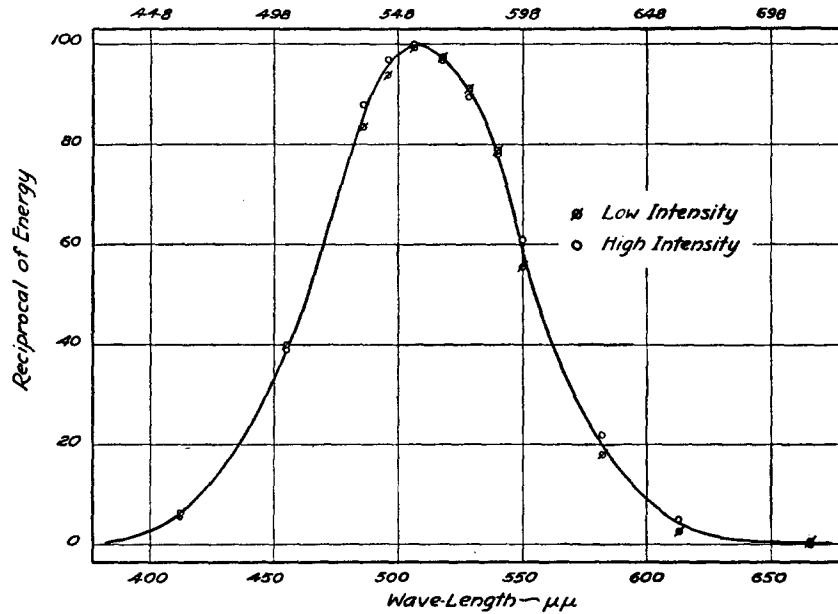


FIG. 6. Identity of high and low intensity curves of Fig. 5. The high intensity curve has been moved $48 \mu\mu$ to the left, but its scale of abscissæ is given at the top of the figure.

data of Hyde, Forsythe, and Cady to subject them to a correction in terms of the rough and unreliable measurements of Sachs.

Nevertheless we have made this correction for our own interest, simply to see what influence it has on the results. It changes the shape of the curve slightly so as to make it more symmetrical, and it moves the maximum from 554 to $540 \mu\mu$. That macular absorption really accounts for this difference in the position of the maximum is demonstrated by the fact that visibility curves for colored lights

made with the fovea and with a region just outside of the macular area differ in the same direction and order of magnitude (Abney and Festing). The corrected curve still coincides with our points, but the difference between the two becomes only 39 instead of 48 $\mu\mu$. Though this reduction is favorable to our interpretation, it possesses no theoretical significance, and leaves the fundamental fact secure that the two brightness curves—one for chromatic vision and the other for achromatic vision—are essentially the same curves in different positions on the spectrum.

VI.

Interpretation of Similarity of Visibility Curves.

1. There is one implication that follows at once from this identity of the shape of the two curves. No one has ever objected to the assumption that a *single* substance is concerned with the reception of stimuli which produce achromatic effects at low intensities. If our reasoning in an early part of this paper is correct, the low intensity curve in Fig. 5 represents the absorption spectrum of this substance in the condition in which it is in the retina. In the visibility of color at high intensities we find a curve which has exactly the same shape and size as that for no color at low intensities. It would therefore seem the most obvious thing to assume that in the brightness perception of color, we are dealing also with the photochemical properties of a *single* photosensitive substance. As far as we ourselves are concerned, we definitely accept this assumption of a single photoreceptive substance as the necessary conclusion from the above comparison.

Precisely what this involves one cannot say. Many questions arise at once. For example, is this single substance the receptive agent for only the brightness values of colors, or is it to be regarded as the receptive material for color vision as a whole? There is no definite answer to this question at present. A certain amount of suggestive data exists for supposing that the brightness function may be distinct from the chromatic function, and the reader is referred to an extended discussion of the possibilities of this separation in a recent review by Troland (1922). The similarity of the brightness curve to the absorption spectrum of a single substance might be taken as additional

evidence for such a separation if one adopts a three or four substance explanation of color vision. To us, however, this is not a necessary step. The field of retinal physiology has hardly been touched from the viewpoint of modern photochemistry; and in view of the meagreness of our quantitative knowledge of the retina and of the photosensory behavior of dyes, it would be premature to decide the matter. All that we wish to conclude at present is that judged solely by the visibility curves, there is as much evidence for assuming only one receptive substance for chromatic vision as there has been for achromatic vision. There the matter must rest until further quantitative information becomes available.

2. There are certain points with regard to this photoreceptive substance, however, a consideration of which will lead to a clarification of our ideas. We can usually reason about the color of a substance from its absorption spectrum. The substance represented by the high intensity curve in Fig. 5 should, like the one represented by the low intensity curve, be purple, but should also be slightly more violet because its maximum is farther toward the red. This substance is to be found in the cones of the retina.

It will be at once objected that no such colored substance, in fact, no colored substance, has ever been demonstrated in the cones. The objection carries its answer with it. There are limits to the visibility of colored solutions. Make them sufficiently dilute, and look at them in thin layers, and they fail to be perceptible. The terminal segments of the cones, where presumably this substance is localized, form an extremely thin layer. If in addition the concentration of the substance is low, the result will be an apparently colorless medium. One who is inclined to be skeptical on this point need only look at a thin layer of a not too dilute solution of hemoglobin, or at a crystal of hemoglobin under the microscope, to realise how limited is our capacity in this respect.

The objection will then be raised that when the solution is so dilute, and the layer so thin, the photochemical characteristics of the substance will have reached their vanishing point. Weigert (1920) has recently given the counter to such an objection by his beautiful work on the photochemical properties of thin layers of AgCl, and of dyes like cyanin. Far from losing their photochemical characteristics,

these dilute, thin layers of material apparently acquire a number of new ones, which, as Weigert has pointed out (1921), will be of significance in any consideration of the mechanism of color vision.

We may therefore accept the proposition that the high intensity curve in Fig. 5 represents the absorption spectrum of a dilute solution of a photosensitive substance in the condition in which it is in the cones. This substance is the receptive material concerned with the production of such quantitative relationships as given by the visibility curve. The recent work of Weigert has given us but a hint of the possibilities for a mechanism to accomplish such effects. But we must not jump, like the many lost souls already on record, into the realms of visual theory.

3. We have then apparently two photosensitive substances in the retina. One is in the rods, and has its maximum of absorption at $511 \mu\mu$, while the other is in the cones, and has its absorption maximum at $554 \mu\mu$ (or at $540 \mu\mu$, if we adopt the correction for the absorption of the macula). There are three logical possibilities for the relation between these two substances. They may be totally different substances; they may be similar substances differing perhaps in the position of the color-bearing groups in the molecule; and they may be identical.

The first possibility of complete diversity of structural relationship is made doubtful by the striking resemblance of the two absorption curves. Judging by the persistence of such substances as hemoglobin and chlorophyll in different groups of organisms, it might be argued that the organism would not produce two widely different substances located in the same sense organ and fulfilling very nearly the same function of brightness evaluation. The argument is admittedly weak; its significance lies in the plausibility of the other possibilities. Between the second and third possibilities there is little choice. The existence of two closely related substances would satisfy the situation, and there is something to be said for such an idea, as we shall presently see. We wish, however, to call attention to the possibility of complete identity.

The main point is the difference of $48 \mu\mu$ (or of $39 \mu\mu$ really) between the position of the two maxima. Such differences are, however, well known in spectroscopy, and we may be pardoned for calling attention

to them here. It had been known a long time that the same substance shows different positions for its absorption bands in different solvents; but it was Kundt (1878) who made the first systematic investigation of this phenomenon. Kundt wished to correlate the degree of refraction or of dispersion of a solvent with its effect on the position of the absorption bands of a substance dissolved in it. He was only partially successful, and the rule which bears his name, though having a number of exceptions, has been shown to hold true for many substances. In its most general form, Kundt's rule may be stated as follows. If one colorless solvent has a decidedly greater refracting or dispersing capacity than a second, then the absorption bands of a substance dissolved in the first will be nearer the red end of the spectrum than when dissolved in the second (Kayser, 1905).

Kundt's rule has had a particular field of support in the sensitizing properties of certain dyes on the photographic plate. Vogel (1874) found that the maximum of sensitivity of a photographic plate does not correspond with the maximum absorption of the added dye. The maximum of sensitivity is distinctly shifted toward the red. This work was later extended by Eder (1885) who showed that the shift is due to the actual position of the absorption maximum of the dye in the condition in which it is dissolved in the silver bromide grains. Eder obtained shifts toward the red varying from 15 $\mu\mu$ to as high as 65 $\mu\mu$, while shifts to the extent of 31, 47, and 48 $\mu\mu$ were fairly common. Eder has pointed out that this corresponds to Kundt's rule because the density of the AgBr grains is 6.5 as compared with 1.0 for water and 1.3 for dried gelatin. The still more recent work of Sheppard (1909) has amply confirmed the findings of Vogel and of Eder.

The matter may be illustrated beautifully in the case of cyanin. Cyanin has a band in the red—hence its blue color. Dissolved in a film of collodion which is still moist, cyanin is blue. If the film is allowed to dry, thereby increasing the density and refractive index of the collodion, the film becomes colorless, because the absorption band has been shifted into the infra-red (*cf.* Weigert, 1921).

Enough has already been said to show how the same substance could give the two curves in Fig. 5, 48 $\mu\mu$ apart, depending on the refractive index or density of the medium in which it is dissolved.

The Duplicity theory makes a sharp distinction between colored and colorless vision, the one being located in the cones, and the other in the rods. It is conceivable that the terminal segment of the cones is much denser and more refractive than that of the rods, and therefore that the same substance dissolved in the cones would have its absorption band shifted strongly toward the red in comparison to its position in the rods.

This matter, however, is not one for speculation, but can be put to experimental test; we are already engaged in preparing the experiments. There is, nevertheless, a test which may not be without significance, and for which the data are already available. To this we shall now turn.

VII.

Achromatic Brightness and Visual Purple.

1. We have so far not mentioned the relationship of these phenomena to visual purple, because we have wished to consider the matter in some detail and from a point of view somewhat different than the one which has usually been employed (Bayliss, 1918). In 1894 Koenig measured the absorption spectrum of visual purple, and compared it with the brightness value of the spectrum to a color-blind person and to color-sensitive people at low intensities. He concluded that the two sets of curves were coincident, and deduced therefrom the idea that visual purple is the receptor substance for achromatic vision. Trendelenburg in 1904 next measured the rate of bleaching of visual purple in different parts of the spectrum. After measuring in addition his own visibility curve at low intensities, he compared the bleaching rates with his and Schatarnikoff's visibility curves, and reached a conclusion similar to that of Koenig. Later (1911) Henri and Larguier des Bancelles, without adding any experiments, recomputed the data of Koenig and Trendelenburg and compared them with the results of Schatarnikoff and Pflüger on the visibility of the spectrum at low intensities. The conclusion they reached was that in order to produce a visual sensation, the incident light must be of such intensity that the visual purple in the rods will always absorb the same energy regardless of wave-length. This, as the authors point out, is the conclusion of Koenig and of Trendelenburg in a slightly different form.

It will be noticed that these conclusions all depend on the coincidence of the curve of the absorption spectrum of visual purple with that of the curve for the visibility of the spectrum at low intensities. We have already pointed out at the beginning of this paper how unreliable are the data describing the visibility of the spectrum at low intensities. Indeed it was to supply this deficiency that our experiments were made. Now that we have secured these accurate data, it will be interesting to compare them with those of the absorption of visual purple in order to see whether this much discussed coincidence is real or only the product of insufficient data.

Before we do that, however, we wish first to say that, though we accept the conclusions of Koenig, Trendelenburg, and Henri and Larguier des Bancelles with regard to the relation of visual purple and achromatic vision, we cannot accept the evidence on which they are based. In fact, we believe that their evidence actually proves something quite different from what they thought. This paradox deserves an explanation.

2. The terminal segments of the rods are, from all observations and descriptions, fairly dense and highly refractive bodies—much more so, for example, than water (von Helmholtz, 1909). It is in these that the visual purple is dissolved in the living retina. If we may argue from Kundt's rule, which we explained in the previous section, the position of the absorption maximum of visual purple in the rods will not be the same as that in solution in water or in dilute bile salts solution. The absorption band of the visual purple in the rods should be shifted toward the red because the medium is much denser and more refractive than bile salts solution. The sensitivity of the rods to spectral light should, therefore, just as the sensitivity of a stained photographic plate, be farther toward the red than would be expected from the position of the absorption spectrum of visual purple as measured in bile salts solution.

If this were found to be true, not only would it strengthen our reasoning in this matter, but it would lend support to the possible explanation which we ventured for the difference in position of the maximum of sensitivity of the rods and the cones. Indeed, it was the idea of this explanation that first led us to examine the data from this critical point of view.

3. The absorption spectrum of visual purple has been measured on three occasions. The first was by Koenig in 1894. Koenig had built a new modification of the Vierordt spectrophotometer for just this work. But before he could acquire any technic with visual purple he came into the possession of a single human retina from a freshly extirpated eye. The temptation was too great, and even though the solution which he prepared was cloudy, he and Köttgen measured its absorption spectrum. The extended and fantastic theories which Koenig developed as a result of his measurements with this single retina are open for him to read who will. It is not for us to dwell too harshly on these lapses. If a datum is worth publishing it is worth interpreting to the limits of its capacity; and the criteria for publication are largely matters of taste, which are not in the realm of discussion. It will suffice to say that, though Koenig's curve for the absorption spectrum is none too regular, it is sufficiently so to show clearly that its maximum is very near $500 \mu\mu$.

After more practise with the new spectrophotometer and with the technic of preparing visual purple solutions, Köttgen and Abelsdorff (1896) took up the study of the absorption spectrum of visual purple in earnest. They made a large number of measurements with visual purple from a variety of animals, and their results are indicative of careful work. They found that visual purple prepared from the monkey, the cat, the rabbit, and the frog, gives the same absorption spectrum. We have studied their individual measurements in great detail and in every instance for every preparation the maximum of absorption is the same; that is, very near $500 \mu\mu$. The individual readings between 620 and $460 \mu\mu$ agree very well with one another, and may be accepted with confidence, short of course, of an error in the calibration of the prism. However, the last two readings in the red (660 and $640 \mu\mu$) and in the violet (420 and $440 \mu\mu$) are subject apparently to a large experimental error, because the individual values vary as much as 100 per cent from one another, besides occasionally yielding the theoretically impossible negative value for the absorption coefficient. We have therefore not included these four points in a consideration of their data.

The third determination of the absorption of visual purple was made by Trendelenburg (1904). He made no systematic measure-

ments, but on six occasions during his work on the bleaching of visual purple, he measured the absorption spectrum over short intervals now here, now there. The concentrations were never the same, and after making proper corrections, he averaged these irregular results. He then plotted them in comparison with those obtained by Köttgen and Abelsdorff. Though it is obvious that his curve lies consistently $5 \mu\mu$ farther toward the red, he makes no comment on the comparison. We fail to understand this difference, and must attribute it to the irregularity of the measurements; but we are surprised that the disagreement was allowed to pass without comment.

Of the three sets of measurements, those of Köttgen and Abelsdorff are therefore the only ones that can be considered as fulfilling the criteria of accuracy. Although all three sets of measurements show, without question, that the maximum of the spectrum visibility is distinctly farther toward the red than the absorption maximum of visual purple in bile salts solution, we can make reliable comparisons only with those of Köttgen and Abelsdorff. These are presented in Fig. 7. The solid curve with the small circles is the visibility curve at low intensity taken directly from Fig. 5., and according to our reasoning represents the absorption spectrum of visual purple in the condition in which it is in the terminal segments of the rods. The other points and the broken line are the data of Köttgen and Abelsdorff for the monkey and the rabbit, their original values having been recomputed so as to give the maximum a value of 100. Far from the two curves being coincident, it is apparent that the absorption spectrum of visual purple in the eye is definitely and consistently farther toward the red than in water solution. The two curves are, however, identical, and represent no doubt the same substance in two different media obeying Kundt's rule.

4. This having been established, it will be instructive to examine more closely the curves presented by the various authors in support of the coincidence of the two sets of observations. Koenig's figure shows beyond question that not only the maximum but almost the entire curves for the brightness perception of the spectrum of a color-blind person and of color-sensitive people at low intensities are distinctly farther toward the red than the maximum and curve for the absorption of visual purple. We have carefully replotted on a larger

scale the data given by Koenig, and find that the average difference between the two sets of data is about $5\mu\mu$.

We have already pointed out the discrepancy of Trendelenburg's absorption data. But even here, if one examines the curves in Fig. 7 of his paper, one sees that the *Dämmerungswerte* are distinctly shifted an average of $8\mu\mu$ farther toward the red than the calculated absorp-

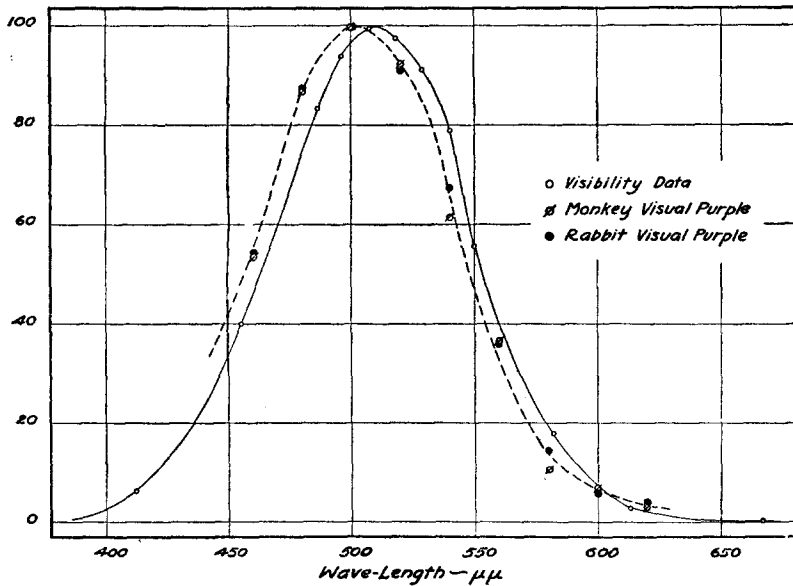


FIG. 7. Relation between absorption spectrum of visual purple in bile salts solution and absorption spectrum of sensitive substance in the rods as given by the visibility curve of Fig. 5. Though the two curves are identical, the visibility curve is shifted 7 or $8\mu\mu$ toward the red, as would be expected in terms of Kundt's rule.

tion of visual purple as determined by Trendelenburg. The main work of this author, however, is the bleaching effect of different wavelengths, which is probably quite accurate. If we compare the curve for the bleaching values with that for the dim values (*Dämmerungswerte*) of the same spectrum, we find here again that not only the maximum but the entire curve is displaced toward the red, an average distance of about 5 or $6\mu\mu$.

Finally, in the paper by Henri and Larguier des Bancels, if we compare the curve representing the energy necessary to produce the same absorption in visual purple with the curve for the energy necessary to see the spectrum at low intensities, we find exactly the same shift of the latter toward the red. The curves are quite irregular, and it is hard to estimate the exact extent of the shift, but it varies between 5 and 20 $\mu\mu$ in different parts. Any one who cares may see this for himself in the reproduction of Henri and Larguier des Bancels' figure in Bayliss' book on General Physiology.

In all the cases then, the shift, whether large or small, is consistently present, and is always in the same direction, toward the red. Therefore, as we pointed out, though we believe the conclusion expressed by these authors, we find that the evidence they present fails utterly to prove it. More than that, their data actually prove something else, which is quite as significant as what they were supposed to prove. This is that the absorption spectrum of visual purple in the rods, following Kundt's rule, is definitely shifted toward the red for a distance of 7 or 8 $\mu\mu$. It is to this shifted absorption spectrum that, we believe, the proportionality between visibility and absorption must be referred.

It is hardly necessary to indicate that this point too may be tested experimentally; but we do so in order to announce that we are preparing to perform the necessary experiments.

5. There is just one more point we wish to make about the absorption spectrum of visual purple and its relation to the visibility of radiation. We suggested the possibility that the two visibility curves of Fig. 5 are manifestations of the same sensitive substance, and that the difference in the position of the two curves is explainable in terms of Kundt's rule. This would assume that the visual purple which we can extract from the eye and whose maximum of absorption in bile salts solution is at 503 $\mu\mu$ is present in solution in the rods where its absorption maximum is at 511 $\mu\mu$, and in very dilute solution in the cones where its maximum is at 554 $\mu\mu$ (or more probably, as corrected for macular transmission, at 540 $\mu\mu$).

The shift between the rods and the cones is a pretty big one. Not that such shifts are uncommon in the sensitization of a photographic plate, as Eder's figures amply testify; but that such a shift has to be

produced by a pretty big increase in density and refractive index. It may be that the terminal segments of the cones actually possess this greatly increased density or refractivity; that is something that will have to be settled experimentally. There is however another consideration.

We pointed out that one possibility in this relationship is that there may be two closely related forms of the sensitive substance differing slightly in some detail of molecular arrangement, which would account equally well for the shift in the absorption spectrum. There do exist what appear to be two such forms of visual purple. Köttgen and Abelsdorff, in their study of visual purple, found a sharp distinction between the substance obtained from fishes and from all other vertebrates. The maximum for the visual purple of all other vertebrates is, as we have given it above, $503 \mu\mu$. That from fishes is definitely more violet, and its absorption maximum is at $540 \mu\mu$. This difference is too consistent for it to be anything but a real one.

This is all that is known. Whether the fish form of visual purple is the one that is present in the cones, or what this fish modification of visual purple is, are questions that cannot even be speculated on at the present time. We even refrain from the tempting, but probably quite futile, discussion of the evolutionary aspects of the situation. It is clear, however, that the field is ready for experimentation, and we hope that we may be fortunate enough to find some solution for these stimulating and provoking questions which strike at the basis of the mechanism of vision.

SUMMARY.

1. After a consideration of the existing data and of the sources of error involved, an arrangement of apparatus, free from these errors, is described for measuring the relative energy necessary in different portions of the spectrum in order to produce a colorless sensation in the eye.

2. Following certain reasoning, it is shown that the reciprocal of this relative energy at any wave-length is proportional to the absorption coefficient of a sensitive substance in the eye. The absorption spectrum of this substance is then mapped out.

3. The curve representing the visibility of the spectrum at very low intensities has exactly the same shape as that for the visibility at high intensities involving color vision. The only difference between them is their position in the spectrum, that at high intensities being $48 \mu\mu$ farther toward the red.

4. The possibility is considered that the sensitive substances responsible for the two visibility curves are identical, and reasons are developed for the failure to demonstrate optically the presence of a colored substance in the cones. The shift of the high intensity visibility curve toward the red is explained in terms of Kundt's rule for the progressive shift of the absorption maximum of a substance in solvents of increasing refractive index and density.

5. Assuming Kundt's rule, it is deduced that the absorption spectrum of visual purple as measured directly in water solution should *not* coincide with its position in the rods, because of the greater density and refractive index of the rods. It is then shown that, measured by the position of the visibility curve at low intensities, this shift toward the red actually occurs, and is about 7 or 8 $\mu\mu$ in extent. Examination of the older data consistently confirms this difference of position between the curves representing visibility at low intensities and those representing the absorption spectrum of visual purple in water solution.

6. It is therefore held as a possible hypothesis, capable of direct, experimental verification, that the same substance—visual purple—whose absorption maximum in water solution is at $503 \mu\mu$, is dissolved in the rods where its absorption maximum is at $511 \mu\mu$, and in the cones where its maximum is at $554 \mu\mu$ (or at $540 \mu\mu$, if macular absorption is taken into account, as indeed it must be).

The experiments for this paper were performed in the George Holt Physics Laboratory of the University of Liverpool. We take this opportunity of thanking Professor L. R. Wilberforce for his kindness in placing the facilities of the laboratory at our disposal. It is a pleasure also to record our thanks to Professor E. C. C. Baly for the use of apparatus from the Laboratory of Inorganic Chemistry, and above all, for the generous hospitality of his laboratory.

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