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SPECTRAL SENSITIVITY CURVES AND THE ABSORPTION OF LIGHT BY THE OCULAR MEDIA*

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THE inter-relation of sensory, electrophysiological, and photochemical data in vision requires a knowledge of the behaviour of the retina in the absence of the ocular media. As far as the human eye is concerned, such knowledge is very inadequate in the case of the enucleated eye, and non-existent in that of the eye *in situ*. While light absorption by the pre-retinal and intra-retinal media cannot affect any mode of colour-vision, it modifies the sensitivity to light. The sensitivity of the eye to radiations of different wavelengths is usually defined as the reciprocal of the spectral energy required to produce a given constant sensation. It is immaterial whether the constancy means equality of brightness, threshold of vision, or absence of flicker; in all instances the experiment involves the measurement of energy. Since the photo-receptors are adjacent to the pigment epithelium, light reaching them must have travelled through the cornea, aqueous, lens, vitreous, and a major part of the retina proper. Every one of the structures acts as a light filter, thus reducing its intensity, and necessitating a larger supply of energy for the production of a given sensation than would otherwise be required. The energy is measured at the cornea. It follows that the sensitivity as measured at the cornea, S_W, is less than the receptoral sensitivity S_{REC} (Thomson, 1951). If the pre-receptoral structures were neutral, *i.e.*, if the percentage absorption of light were the same for all wavelengths, a knowledge of their characteristics would be important only in connection with measurements of the absolute sensitivity. All the scanty available evidence, however, indicates that they absorb selectively in different spectral regions (see Ludvigh and McCarthy, 1938, for data on human and animal eyes), the predominant absorption taking place at shorter wavelengths.

The unequivocal measurement of all the absorption characteristics in an intact human eye *in situ* is impossible. If enucleated eyes are used (Ludvigh and McCarthy, 1938), autopsy may mask the results, especially if the eyes are kept at 38° C., as should be done in all such cases. The application of animal data to human results is a doubtful remedy: in any case the intra-retinal absorption cannot be determined in this or in any other manner. This depressing outlook is somewhat mitigated by the circumstance that the spectral absorption of the pre-retinal media at long waves (green to red parts

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of the spectrum) is very nearly constant, so that in this region the shape of the spectral sensitivity curve as measured at the cornea agrees substantially with that of the receptoral sensitivity. This is deduced from a comparison between the human scotopic sensitivity curve and the absorption spectrum of visual purple (Wald, 1949). The pre-retinal media thus provide a convenient scape-goat for the wide discrepancies observed in the blue part of the spectrum for both photopic and scotopic sensitivity curves. These are usually ascribed to lens pigmentation or excessive macular pigment. The latter has occupied a key position in the question of pre-receptoral filters. Wald (1949) has measured the spectral absorption characteristics of human macular extracts, and found that they exhibited certain shape irregularities. Brindley and Willmer (1952) obtained a value for the macular absorption *in situ*, but the method is equivocal (Weale, 1953a).

However, while the first-order variations were of great interest a few years ago, recent measurements of the spectral sensitivity have focused the attention of visual physiologists on second-order effects, such as small inflexions and similar shape irregularities, superimposed on the general trend of the absorption curve. The reason for this is as follows:

The foveal photopic spectral sensitivity curve, measured with relatively large fields (Fig. 1*a*), subtending at the eye an angle of 1–2°, is smooth, with the exception of a slight modulation at short wavelengths (Thomson, 1949). But when the angular subtense is reduced to well below 1° (Fig. 1*b*), there appear secondary inflexions (Stiles and Crawford, 1933; Wright, 1946; Crozier, 1950; Thomson, 1951; Weale, 1951b) which are reproduced by most observers.

There arises the problem of the origin of these inflexions. Are the troughs (Fig. 1) caused by selective light absorption by pre-receptoral media, or are the peaks caused by an enhancement of the sensitivity in the relevant spectral region ?

The question why the mere reduction in the size of the test-field should produce filter effects which are absent when the field is large has never been squarely faced. Two of the inflexions (at 450 and 470 mμ) appear, admittedly, also in large-field data (cf. Fig. 1*a*). Thomson (1951) failed to eliminate their counterparts in the small-field data by applying corrections corresponding to various amounts of macular pigment and Ludvigh and McCarthy's data for extra-retinal absorption. Moreover, such corrections, including one for haemoglobin, have only a small " smoothing-out " effect. The majority of the inflexions remain or become accentuated. Two facts have, therefore, to be admitted if the effects are wholly due to pre-receptoral filters: first, since large test-fields fail to detect the inflexions, the responsible filters must be concentrated nearly exclusively in the centre of the fovea, their extent subtending at the posterior nodal point an angle of less than 1°. Secondly, we are wholly ignorant of the spectral characteristics of such filters. The latter statement cannot surprise if the former is true. Assuming that the filters are present only in the central fovea, it is remarkable that they

should be found in that part of the human retina which is thinner than any other. Moreover, it is doubtful what function they should fulfil. Granted, as suggested by Dartnall and Thomson (1949), that a respiratory pigment is required for the foveal region because of the obstacles encountered in this region by the choroidal blood supply; the areal extent of such a pigment would have to exceed 1°. It would thus appear that the inflexions cannot be accounted for exclusively on the basis of local filtering actions.

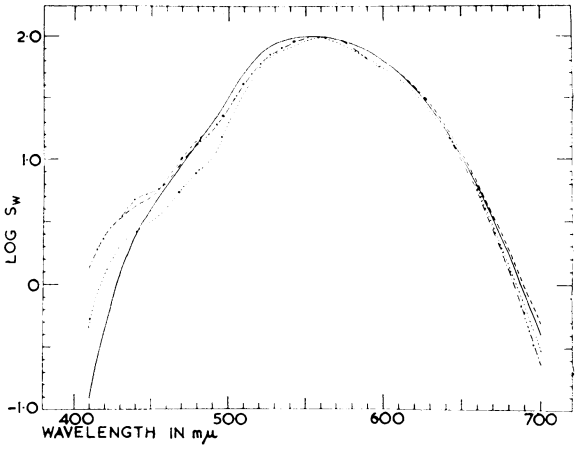

FIG. 1(*a*).—Photopic spectral sensitivity curves measured with a medium sized field (1-2°).
Full line : CIE;
dashed line: Gibson and Tyndall's mean value;
dotted line: observer L.C.T.;
dash-dot line: observer W.D.W.

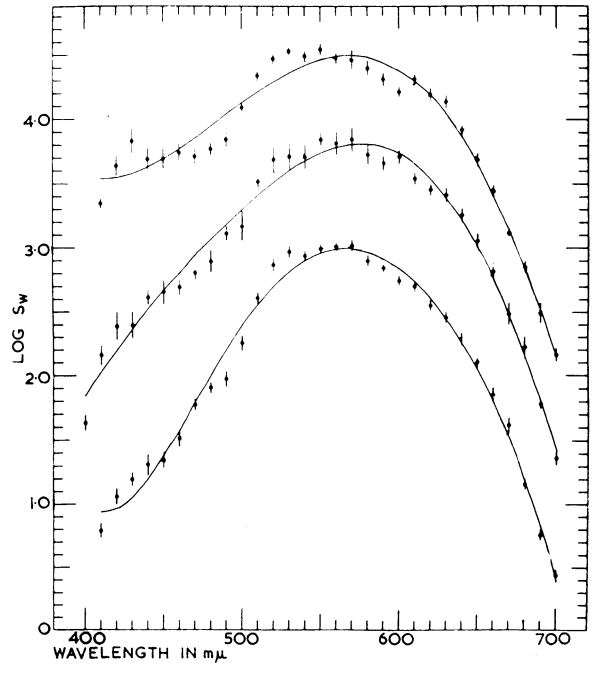

FIG. 1(*b*).—Photopic spectral sensitivity data measured with a small field (15–20′) in the foveal centre.
Full lines represent best-fitting calculated functions of the 4th degree (B.H.C.) and the 5th degree (W.D.W. and L.C.T.).
The vertical bars represent the standard errors of the mean.
In this and all other Figures the violet part of the spectrum is on the left, the red on the right.

Before the alternative is considered, namely that the irregularities superimposed on the general trend of the curves are due to a spectrally restricted receptor activity, it may be as well to assess their significance. Thomson (1951) and Weale (1951b 1953b) have done so by fitting to the data orthogonal polynomials (Fisher and Yates, 1943). The basis of this procedure is that any continuous single-valued function $y = f(x)$ can be expressed as a power series:

$$y = a + bx + cx^2 + dx^3 \ldots (1)$$

The method of orthogonal polynomials consists in the determination of the co-

efficients a, b, c, etc. from known values of y. A perfect fit can always be obtained when the number of coefficients is equal to the number of values of y. In practice, the labour involved is unfeasible and unnecessary because the problem of photopic spectral sensitivity curves reduces to the question of whether or no a relatively simple expression, *i.e.*, one consisting of a few terms only, will describe all the experimental points to an accuracy comparable with that of the data themselves. When this was done for sensitivity curves (y was identified with log S and x with the wavelength λ), it was possible to evaluate the residual discrepancy Δ which was found to differ from zero in a statistically significant manner (Fig. 2). There are three regions in which Δ is positive: here the measured sensitivity is greater than would be expected if the experimental curve were smooth and single-humped.

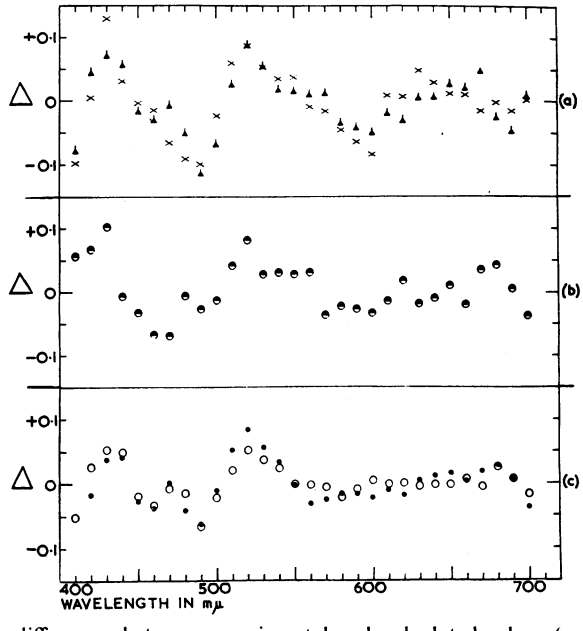

FIG. 2.—Δ, differences between experimental and calculated values (such as those shown in Fig. 1*b*) of log S_{11}.
(*a*) Two normal observers (15′ field),
(*b*) a protanope (15′ field),
(*c*) a cone-monochromat (O . . . 1° 20′ field, ● . . . 15′ field).
Note that there are three " humps " in (*a*) but only two in (*b*) and (*c*).

Moreover, the three regions are respectively located in the red, green, and violet parts of the spectrum, which has led to the suggestion that the three colour-mediating mechanisms, postulated by the tri-stimulus theory, add their weights to that of a dominant mechanism responsible for the perception of brightness. While the presence of the peaks and troughs in the spectral variation of Δ can be shown to prove that (1) is a function of a high order, no physiological significance can be ascribed to their spectral location.

Measurements of the photopic spectral sensitivity in the extra-foveal

regions throw further light on the possible origin of the shape irregularities and also on the contribution of light absorption by the macular pigment. The most remarkable feature of such measurements is the considerable increase in sensitivity to light of short wavelengths. This is illustrated in Fig. 3, where the foveal sensitivity is plotted side by side with the data obtained at a perimetric angle of 25° (Weale, 1953*c*). These values were obtained in the presence of a white surround which controlled the state of adaptation of a large part of the retina, the luminance level corresponding approximately to 1 *e.f.c.* both in the fovea and at 25°. The trends of the values of the sensitivity S_W, whose logarithm is plotted along the ordinate, are substantially alike between green and the long-wave end of the spectrum (520–660 mμ) but diverge considerably at shorter wavelengths. This difference means that the relative sensitivity at 440 mμ is about 15 times higher at 25° than it is in the fovea. A similar, though minor, increase has been observed at smaller perimetric angles, namely at 5° (Stiles and Crawford, 1933), and at 10 and 15° (Weale, 1951b). The facts that this increase continues at perimetric angles outside the generally accepted extent of macular pigmentation (10° surrounding the fixation area), and also that it depends on the luminance level at which the experiment is carried out (Fig. 4), render it unlikely that it can be due solely to the absence of macular pigment from those retinal locations. The indentation at 490–500 mμ has become much more pronounced in the 25° data, suggesting that the portion corresponding to wavelengths shorter than this is produced by a mechanism, particularly sensitive to spectral lights of this region.

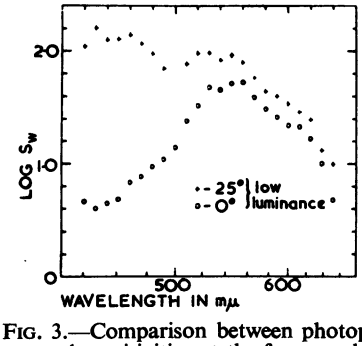

FIG. 3.—Comparison between photopic spectral sensitivities at the fovea and at a perimetric angle of 25°. Note vast relative increase in log S_W at short wavelength as periphery is reached.

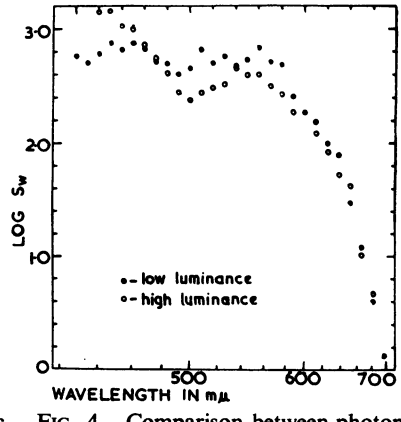

FIG. 4.—Comparison between photopic spectral sensitivities at 45°, measured at high and low luminance levels. Note how the latter gives rise to a flatter cufve at short wavelengths.

The origin of the indentation observed in foveal sensitivity curves at about 600 mμ is indicated by a comparison of high luminance data (90 *e.f.c.*) obtained at 25 and 45° respectively (Fig. 5*a*). In these data, plotted for an equal quantum spectrum, pre-retinal absorption has been compensated.

The trough at 600 mμ might well be due to a pre-receptoral structure selectively absorbing in this region. It is shown in the fovea (Fig. 3) and in the 25° data at both luminance levels (Figs 3 and 5*a*). At 45°, however, though still present, the dent is much less pronounced. Moreover, the accuracy of the results is not much lower than that of the 25° data, so that the appreciable difference between the two curves cannot be ascribed to experimental errors. If an orthogonal polynomial of four terms (cf. equation 1) is calculated for the points between 499·7 and 681·4 mμ, the results given by the small black dots are obtained. The odds that all the residual deviations are due to experimental errors are about 100: 1 against. However, an inspection of the data reveals that the large deviation at $\lambda = 651 \cdot 7$ mμ and its small standard error greatly contribute to the heaviness of the odds against the calculated curve giving an adequate description of the experimental results. There is still no evidence against the belief that the hypothetical pigment absorbing mainly at 600 mμ should extend beyond a perimetric angle of 25° but not as far as 45°. Indeed, if enhanced sensitivities of two or more photochemical mechanisms are not responsible for the peaks on either side of this trough, the existence of such a locally restricted pigment in the retinal tissues must be postulated: if pre-retinal media were responsible and the applied correction

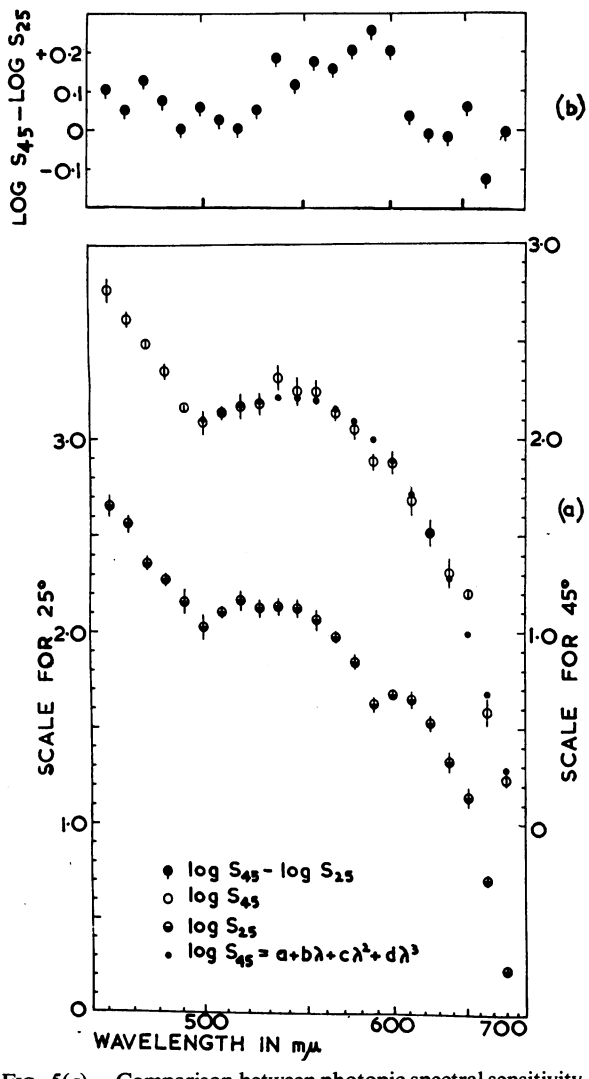

FIG. 5(*a*).—Comparison between photopic spectral sensitivity data at 25° and 45° corrected for pre-retinal absorption losses.

FIG. 5(*b*).—Log ratio (log S_{45}—log S_{25}) of (*a*) reveals a significant rise in sensitivity to light from yellow part of spectrum.

inadequate, the dent would have to appear to an equally marked extent at 45° also, unless their pigmentation is non-uniform.

It may be, of course, that after all this particular indentation is entirely due to an intra-retinal filter, and that the flattening observed at 45° is caused merely by a reduction in optical density, be it because the filter is becoming thinner or because the concentration of the pigment is reduced. The view that the disappearance of the irregularity is due to a modification of the photoreceptor system in the outer periphery is supported by a consideration of the wavelength discrimination data for these regions (Fig. 6). These were obtained in the usual manner by determining the just noticeable wavelength difference between two spectral lights under the same conditions as existed during the measurement of the spectral sensitivity, *i.e.*, the eye was adapted to similar luminance levels by means of a white surround (Weale, 1953c). Whereas the 25° measurements for both luminance levels exhibit trends characteristic of anomalous trichromatism, the data for 45 and 70° feature red-green confusion to a large extent: witness the large values of $\Delta\lambda$ between 500 and 600 mμ (when the ability to discriminate between lights of two adjacent wavelengths is poor, $\Delta\lambda$ is large and vice versa). Moreover, when the sensitivities for 25° and 45° are compared (Fig. 5*b*) a small but statistically significant increase is observed for the larger perimetric angle in this spectral region. If this fact is to be reconciled with the observed deterioration in wavelength discrimination, it must be postulated either that an independent peripheral mechanism, maximally sensitive to light of about 590 mμ, is adding its effect to that of the other mechanisms or that the " red " and " green " mechanisms, hypothesized by the tri-stimulus theory,

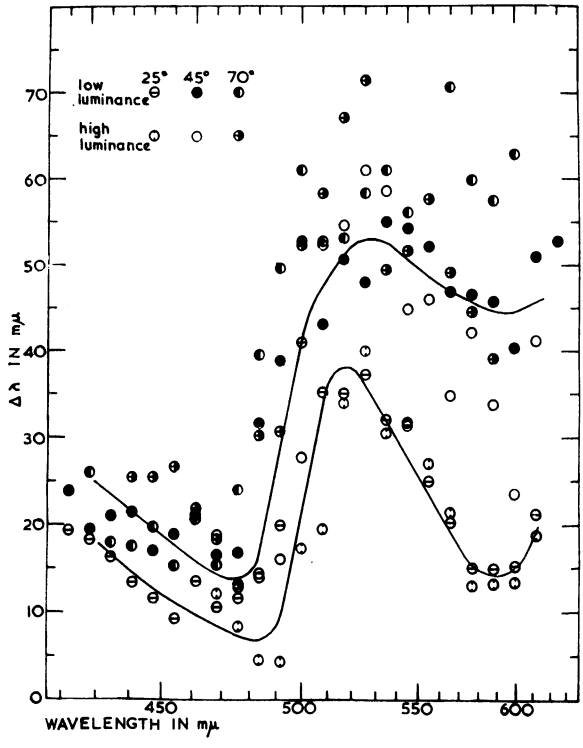

FIG. 6.—Wavelength discrimination in periphery. Note profound change in wavelength discrimination in region of 590–600 mμ as perimetric angle is increased from 25° to 45°. The curves are free-hand and merely serve to emphasize this change.

are being fused, or again that both the response curves representing the activity of these two mechanisms are reduced in amplitude and experience some broadening. When the relative increase in sensitivity to "blue" light is considered and it is borne in mind that this can be interpreted as a real reduction in the sensitivity of the "red" and "green" mechanisms, this third possibility appears to be the most plausible.

Although the above arguments indicate that some at least of the inflexions recurrent in the spectral sensitivity data of various observers are due to spectrally restricted enhancement in sensitivity, caused possibly by the presence of colour-mediating mechanisms, not all of them can be so explained. The outstanding example is afforded by the bifurcation of the humps in the central part of the spectrum (520–550 mμ). The evidence from data on wavelength discrimination that this, too, may be due to functional factors (Weale, 1951a) is slight. More convincing arguments are that the spectral location and the relative magnitudes of the prongs vary from one observer to another, and that they disappear with increasing field size.

Of the remaining inflexions, some appear only in isolated sensitivity curves. At the moment, no objective means can be envisaged which would determine whether they are due to individual differences in receptor mechanisms or to individual differences in pigmentation. One of the more promising lines of attack by subjective methods is spectral adaptation, which has so far been used only to a restricted extent (Wright, 1946). If adaptation by light of a wavelength at which the general trend of the curve shows a protuberance leads to its reduction, the enhancement must be due to functional factors. No data on this matter have yet been published.

The situation regarding the effect of the ocular media on the spectral sensitivity may therefore be summarized as follows. The foveal sensitivity curves for normal observers and for colour-defective observers of various kinds, measured with both small and medium size test-fields, consistently show two humps at about 450 and 480 mμ respectively. On the other hand, as the retinal area of measurement of the normal photopic sensitivity curve becomes more peripheral (10–70°), the curves obtained for a light-adapted eye exhibit an increase in sensitivity in these spectral regions. This cannot be due only to the absence of macular pigment from these retinal locations, since its total radial extent is approximately only 5° about the fixation area and the increase in sensitivity (relative to the long-wave regions) continues outside this limit. Moreover, the characteristics of Wald's macular extracts do not account for the inflexions found in the foveal curves. It can, therefore, be said with some confidence that the marked irregularities in this region are due both to selective pre-receptoral absorption and to a partial enhancement of the spectral sensitivity. The bifurcation observed in the medium wavelengths of the sensitivity curves of normal and colour-blind observers, while reported only in experiments carried out with fields smaller than 1°, persists in the peripheral data; there is some evidence, culled from results on

wavelength discrimination obtained at reduced luminance levels, to suggest that the twin peaks may be due to physiological rather than physical causes. But the presence of the bifurcation in the curves obtained for colour-deficient observers and for the normal light-adapted periphery suggests the opposite: the evidence is insufficient to decide which factor is responsible for this phenomenon.

Finally, the evidence that the dent at 600 mμ is due to the overlap of two photo-mechanisms is based on the facts that it is present in small-field data only, and that its gradual disappearance in the retinal periphery is accompanied by a deterioration in wavelength discrimination.

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