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PHOTO-LABILE CHANGES AND THE DIRECTIONAL SENSITIVITY OF THE HUMAN FOVEA

By H. RIPPS* AND R. A. WEALE

From the Institute of Ophthalmology, University of London, Judd Street, London, W.C. 1

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Analysis of the changes in retinal transmissivity effected by the bleaching of light-sensitive pigments has yielded important correlations between photochemical events and visual responses. Measurements in the human eye have demonstrated that the bleaching and regeneration of these pigments bear a relation to the subjectively determined spectral sensitivity and dark-adaptation functions (Weale, 1959; Rushton, 1961, 1963; Ripps & Weale, 1963*a*, *b*). Attempts to establish the precise relation that obtains for the normal eye have, however, met with both theoretical and experimental difficulties (Wald, Brown & Gibbons, 1963; Weale, 1964*a*). For example, in the study of rod function where presumably only one pigment subserves scotopic vision, difference spectra measured during the regeneration of visual purple exhibit spectral variations which have yet to be explained (Weale, 1962*a*). And in the case of the cones, the presence of at least two pigments with broadly overlapping photosensitivities (Weale, 1959; Ripps & Weale, 1963*b*) obscures the absorption properties of the individual pigments (Dartnall, 1957). It was thought, therefore, that objective study of another property of photopic vision, the directional sensitivity of the cones, might give useful information concerning the linkage between the absorption of light and its ultimate effect, the visual response (Weale, 1961*a*).

The sensation of brightness evoked by a pencil of light is found to depend on the part of the pupil through which it enters the eye. Stiles & Crawford (1933), the discoverers of this effect, found that rays were maximally effective when they passed near the centre of the pupil, and that their efficiency decreased with an increase in distance from this point. For light of a given wave-length, the relative visual efficiency (η) may be defined by the expression:

$$\log\eta = \log(I_c/I_p)_\lambda, \qquad (1)$$

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where I_c is the luminance required to produce a given visual effect when the rays traverse the pupil centrally, and I_p is the luminance required to produce the same effect when the rays enter at a given distance from the centre of the pupil. Although it is convenient to relate the change in luminous efficiency to the point of entry in the pupillary plane—a procedure that will be adhered to throughout—the effect is attributable to the obliquity with which rays entering peripheral parts of the pupil are incident at the retina (Stiles & Crawford, 1933; Weale, 1961*b*).

In the present experiment, subjective values of η were obtained for a constant apparent brightness, and analogous values for photolytic effects were measured by the method of fundus reflectometry. The subjective and objective data were compared for similar stimulus conditions.

METHODS

Since the apparatus was essentially the same as that used in earlier studies (Weale, 1959; Weale, 1964*b*; Ripps & Weale, 1963*b*), its operation need not be described here in detail Figure 1 shows the two main optical systems: one for measurement of fundus reflexion, the other for bleaching of retinal pigments.

As before (Ripps & Weale, 1963*b*), a Xenon-arc (S) provides the source for both the measuring and bleaching beams. The former is passed sequentially through a series of twenty-six interference filters mounted on a wheel (W) rotating at about 4 rev/sec. The beam enters the test eye through the dilated pupil (P_t), passes through the retina, is reflected at the fundus, again traverses the retina, and emerges through the pupil. A reflecting prism (M_1) picks up some of the emerging rays and directs them to a sensitive photocell (E in the elevated plan of Fig. 1), the output of which is displayed on a cathode ray oscilloscope and photographed. The procedure is such as to obtain a complete spectral scan of the fovea—first in the dark-adapted state, and again after it has been exposed to an intense bleaching light for 30 sec. For each measuring wave-length, the changes in density $\Delta D\lambda(2)$ are then computed from measurements of the corresponding oscilloscope deflexions (Weale, 1959). In practice, a schematic eye (P_c) receives the measuring beam alternately with the test eye (controlled by the position of the relay-operated shutter H_2) and its spectral reflectivity is similarly recorded. Stability of the tracings from this control eye ensures that the source and electrical components have not varied during an experimental run.

Owing to the nature of the experiment, the bleaching system incorporates several modifications, and will be described more fully. Lens L_8 forms an image of the arc in the plane of a small circular aperture I_2, the irradiance and spectral composition being controlled by neutral density and colour filters at M_1. The light is then collimated by lens L_9 and brought to a focus at P_t by lens L_{10}, thus forming an image of I_2 in the pupillary plane of the test eye. M_3, M_4 and M_5 are reflecting prisms, the last being movable so as to admit the measuring beam into the eye. The position of the image of I_2 in the pupillary plane is obviously of importance, and was controlled in the following manner. By suitable adjustment of the various reflectors, the measuring and bleaching beams were made to coincide at P_t. The subject's head was then appropriately positioned (*a*) objectively: the pupil being viewed along a line just above M_4, and (*b*) subjectively: by means of the rotating prism R_r. This 1^{Δ} prism could be turned about a horizontal axis collinear with the optical axis of the bleaching optics. It deviated the bleaching beam by 3 mm to the left or the right at P_t. Consequently, if for a fixed position of gaze, light succeeded in entering the eye without cut-off in either position, the point of entry for the undeviated beam was not far off 'centre'

(see below for the size of the image in the pupillary plane). The situation was rendered precise by the provision of a comparison beam of light, its source being placed effectively at *Y* (see inset). When the subject was correctly positioned, a match between this beam and the bleaching beam passing through R_r in one position had to hold also when R_r was rotated through 180 degrees. Once this was achieved R_r was removed. The prism R_p moved the image in the pupil through 3 mm only. In the position shown, entry was central. (The two-position match was made when the bleaching beam 'straddled' the point of maximum sensitivity. Although this point may not coincide exactly with the geometric centre of the pupil (Stiles & Crawford, 1933), it will be referred to as the point of central entry. Turning R_p through 180° about a vertical axis moved the image some 3 mm to the nasal edge of the right pupil. The bleaching light was either blue (Ilford 621) or orange (Ilford 607); transmissivities of the respective colour filters are shown in Fig. 2.

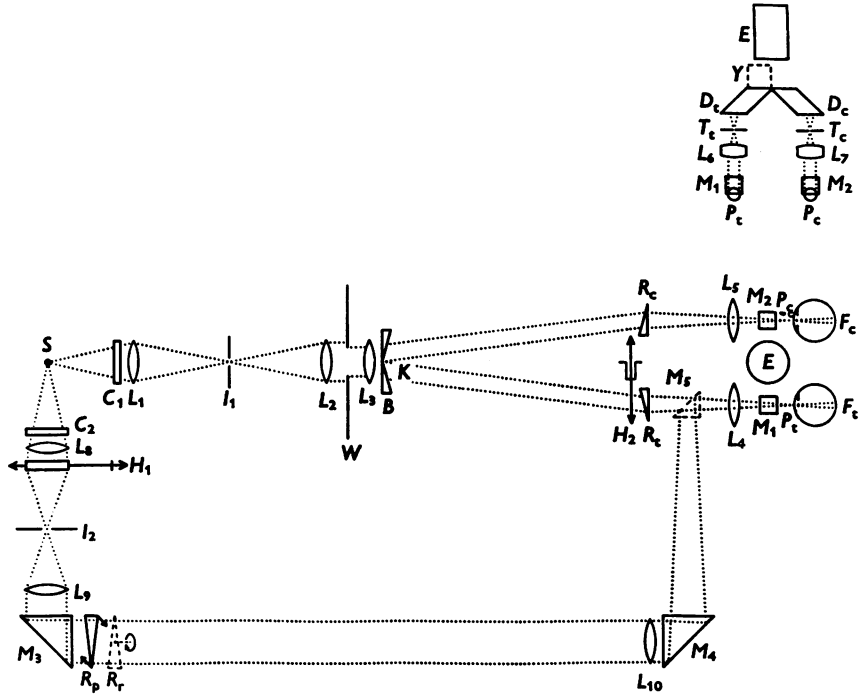


Fig. 1. Plan of apparatus. Inset: elevation of the part shown underneath in plan. Not to scale; for details see text.

Before each experimental session the subject's pupil was dilated with several drops of 1 % homatropine. The size of the effective entrance pupil was measured as follows. Translucent paper was placed in the plane of P_t and an outline of the image of I_2 drawn. The surrounding part was then blacked in and the clear image area carefully excised. Together with a graduated scale, this aperture was projected on squared paper and measured; the area of the entrance pupil, slightly elliptical in shape, was calculated to be 1·5 sq. mm. Replaced in the appropriate position at P_t, the aperture served also as an artificial pupil when making heterochromatic brightness matches between the coloured bleaching lights and an illuminated MgO surface. The luminance of the diffuse surface was then measured with a calibrated Holophane–Edgcumbe Lumeter. The retinal illumination of the full orange beam was thus found to be $4{\cdot}18 \times 10^6$ photopic trolands, and that of the blue beam $3{\cdot}48 \times 10^6$ photopic

trolands. Only one (maximum) luminance I_p was used for peripheral entry: for central entry, however, the luminance was varied, the object being to discover the value, I_c, which gives rise to the same photolytic effect as I_p. It should be noted that whereas the bleaching beam entered the eye either centrally or peripherally, the measuring beam remained, of course, in a fixed position and entered through a central zone of the pupil irrespective of the bleaching conditions. The measuring field was rectangular (longer side vertical) and subtended an angular area of $1{\cdot}4° \times 0{\cdot}75°$ at the subject's cornea. The circular bleaching field had an angular diameter of 3°.

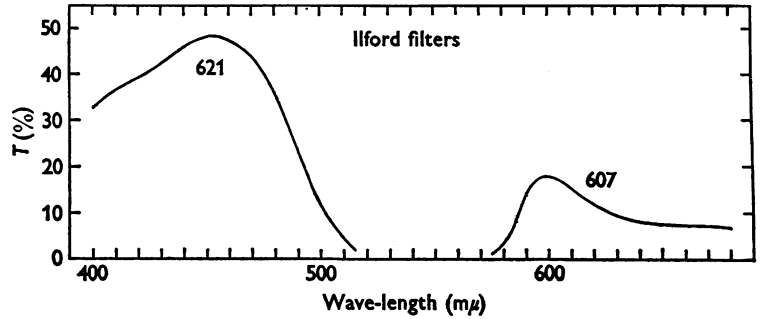
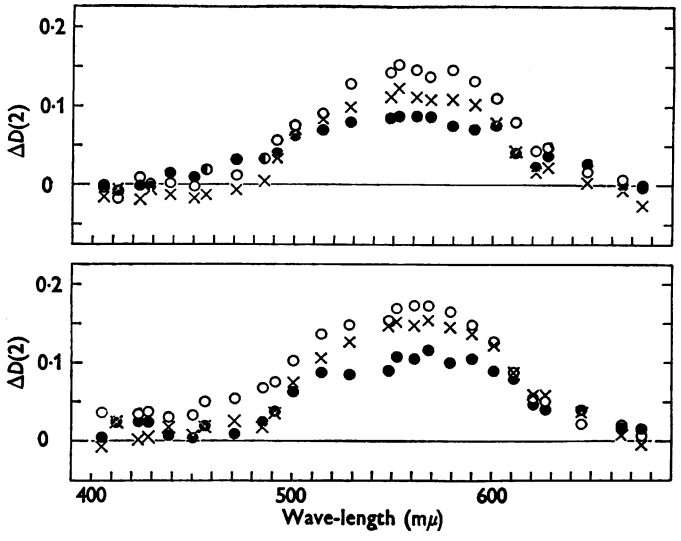


Fig. 2. The spectral transmission factor of the blue (621) and orange (607) filters employed.

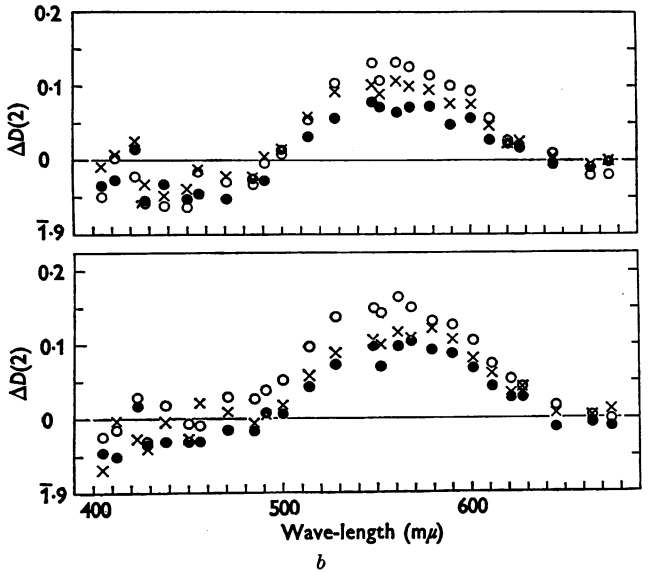
Subjective determinations of the Stiles–Crawford effect were made by the method of brightness matching. The source near Y, being appropriately filtered, illuminated the slit T_t, conjugate with the retina. A strip of opaque paper was then placed across a central part of L_{10} so as to coincide in the visual field with T_t. The bleaching field thus appeared to be bisected by the strip of light from the comparison field at T_t. Brightness matches were made for central and peripheral entry of the bleaching beam. As after-images impeded the match at the luminance levels used for bleaching, the luminance was reduced by a factor of about 4 below that used in the objective experiments.

RESULTS

Objective. Difference spectra obtained for several bleaching conditions are shown in Figs. 3*a* and *b*. The top parts represent data resulting from blue bleaches; the bottom parts illustrate measurements obtained for the orange bleaching light. The following points are noteworthy. The difference spectra obtained with maximum luminance at peripheral entry are systematically lower than are those for central entry. In addition, the data for orange bleaches show a spectral shift. Whereas the difference spectrum for light entering through the centre of the pupil is maximal approximately at 555 mμ, when the same bleaching beam enters the eye through the periphery of the pupil the maximum shifts to about 575 mμ. For central entry, a reduction in bleaching luminance likewise gives rise to a spectral shift toward longer wave-lengths, but the displacement is not as great ($\lambda_{max.} \simeq 568$ mμ) despite the nearly equivalent photolytic effect. Although the data for blue light are similar as regards the changes in density, there is no analogous spectral shift. These observations appear in the results for both subjects. To facilitate the determination of the value of I_c



a



b

Fig. 3*a*. Subject A. Vertical axis: Density difference for double transit through the retina. Horizontal axis: wave-length in mμ. No retinal illumination is given for entry of the bleaching beam through the pupillary periphery, this being obtained by interpolation as shown in Fig. 4. Upper panel: blue bleach; ○, pupil centre, $3{\cdot}48 \times 10^6$ phot. td; ●, pupil centre, $9{\cdot}58 \times 10^5$ phot. td; ×, pupil periphery, $3{\cdot}48 \times 10^6$ phot. td. Lower panel: orange bleach; ○, pupil centre, $4{\cdot}18 \times 10^6$ phot. td; ●, pupil centre, $1{\cdot}15 \times 10^6$ phot. td; ×, pupil periphery, $4{\cdot}18 \times 10^6$ phot. td.

Fig. 3*b*. Subject *B*. Details as for Fig. 3*a*.

by interpolation, intermediate bleaching luminances were also used with central entry but the data are not shown lest they confuse the picture. Owing to the differences in $\lambda_{max.}$ produced by varying the intensity or pupillary traverse of the orange bleaching beam, it was necessary to select arbitrarily a criterion wave-length at which to match the photolytic changes resulting from I_p and I_c. These measurements were made at $\lambda = 565$ mμ, midway between the extremes of the λ's$_{max.}$ (see above). Measurements of $\Delta D(2)$ for the blue bleaches were made at 560 mμ, as for this bleaching light the $\lambda_{max.}$ maintained this value in all bleaching conditions. The vertical ordinates so obtained, and corrected for the small oedema-effect where necessary (cf. Weale, 1962*b*) were plotted against retinal illumination for both bleaching lights and subjects and a free-hand curve drawn through them (Fig. 4). The $\Delta D(2)$ values pertaining to the peripheral-entry bleaches were entered on the curve and the corresponding retinal illuminations read off. It may be noted parenthetically that the correction for the oedema-effect did not significantly affect the values so obtained.

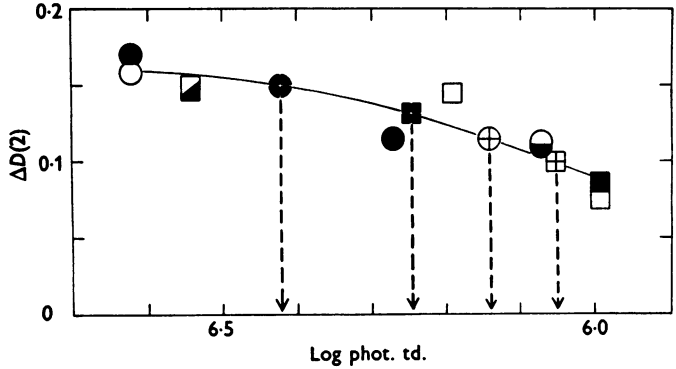


Fig. 4. Vertical axis: Density differences at $\lambda = 565$ mμ obtained from Figs. 3*a* and 3*b* after the application of corrections for the oedema effect. Horizontal axis: retinal illumination. The symbols with the crosses were read off the pupil periphery entry data in Figs. 3*a* and 3*b* (×), corrected for the oedema effect (subject A, blue) and placed on the free-hand curve of this figure. The retinal illumination corresponding to these measurements was then read off the horizontal axis and compared with those obtained subjectively in Fig. 5. Subject A, filled symbols; Subject B, open symbols. Circles Filter No. 607, squares Filter No. 621.

Subjective. The luminances for peripheral and central entry which yield equal apparent brightness, I_p and I_c respectively, were converted to $\log\eta$ values (eqn 1) and plotted as ordinates in Fig. 5. The standard errors other than that shown are smaller than the symbols. Aside from the inter-subject differences, it should be noted that for subject *A* (26-yr-old) the directional sensitivity for blue light is greater than for orange; for subject B (40-yr-old) the reverse is true (see below).

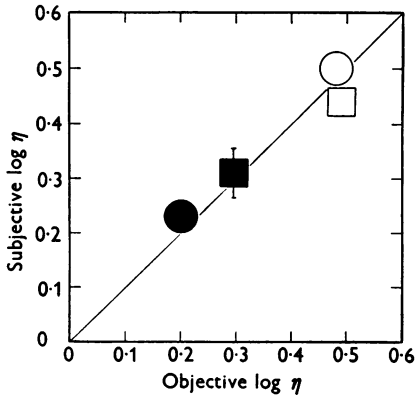


Fig. 5. Comparison of changes in effective retinal stimulation as measured by objective (horizontal axis) and subjective (vertical axis) means. For key to symbols see Fig. 4.

DISCUSSION

In order to achieve a valid comparison between objective and subjective data, it is stimulus rather than response relations which should be examined. Accordingly, as the subjective logη values represent luminance ratios, it is desirable to compute analogous values for the photolytic data. Interpolation in data such as those shown in Fig. 4 results in the log values plotted as abscissae in Fig. 5. This figure, then, suggests that the correlation between the objective and subjective data is high, the straight line representing almost perfect correspondence.

Although the spectral shift mentioned in connexion with the orange bleaches (p. 60) is not unexpected in view of the results obtained by Enoch & Stiles (1961), a discussion of this point is deferred to another occasion. But one or two remarks may be made on the magnitude of the changes shown in Fig. 5. The data of Enoch and Stiles would lead one to expect a greater directional effect for blue than for orange. Figure 5 shows this prediction to be fulfilled for subject A but not for B. It has to be emphasized, however, that the experiments with orange and blue bleaching lights differ in another material aspect. This relates to the spectral transmission factor of the human crystalline lens and to the relative pathlengths traversed therein by rays entering the pupil at its centre and periphery respectively. As the lens is pigmented *and* lens-shaped, the peripheral beam suffers less absorption than does the central (Weale, 1961*b*). Since the lens pigment is yellow, the orange beam is affected less by this difference in photometric density than is the blue beam. Thus while the retinal illuminations as due to the peripheral and central orange beams are approximately equal, the retinal illumination due to the peripheral beam is at least 0·12 log units higher than that due to the central blue

beam. The directional effect for blue light, therefore, is partially compensated by the increased illuminance of the more oblique beam (and more so for the eye of subject B who is older and consequently has a more densely pigmented lens).

SUMMARY

1. The method of fundus reflectometry has been used in the study of effects of oblique incidence of bleaching light on foveal cone pigments, an orange or blue bleaching beam being made to enter the eye either at the pupillary centre or near the periphery.

2. The peripheral beam is photolytically less efficacious than the central. Calibration of the latter enables one to show that the reduction in efficacy of the former bears a high correlation to the Stiles–Crawford effect measured subjectively in a conventional manner.

3. Differences between the results obtained with the orange and blue beams are attributed in part to the transmission characteristics of the crystalline lens and in part to the spectral variation of the directional properties of the foveal receptors.

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