Separation of the ‘blue’ and ‘green’ mechanisms of foveal vision by measurements of increment thresholds

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The curve relating the smallest perceptible intensity of a blue test stimulus with the intensity of an orange conditioning field against which it is viewed shows a characteristic division into low- and high-intensity components, indicating the operation of two mechanisms of cone vision at the fovea. The justification for calling these ‘blue’ and ‘green’ mechanisms is taken from an earlier investigation (Stiles 1939). While most subjects show this division clearly, for some the low-intensity component is masked by the intrusion of rod vision. The correctness of this view is established by measurements made while the eye is recovering from an intense light adaptation. The individual variations of the sensitivities of the ‘green’ and ‘blue’ mechanisms in twenty subjects are assessed. Further evidence is obtained of an anomalously low threshold for the ‘blue’ mechanisms at very high conditioning fields of orange light.

INTRODUCTION

The operation of three receptor mechanisms in rod-free foveal vision can be demonstrated, and some of their properties, e.g. their spectral sensitivity curves, can be determined to a first approximation by measurements of the liminal brightness increment (l.b.i.) under suitable conditions (Stiles 1939).* This conclusion rests mainly on measurements for one eye. A key feature of the results was the form of the curve relating the l.b.i. to the intensity of the conditioning stimulation for a test stimulus of short wave-length (below about 510 mµ) and a conditioning stimulation of long wave-length (above about 530 mµ). All such curves were found to show a ‘change of law’ enabling them to be represented as the resultant of two component curves, associated respectively with the ‘green’ and ‘blue’ cone

* This paper is referred to as I throughout.
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mechanisms, the former coinciding with the experimental curve at low-conditioning intensities, the latter at high. This association is justified by the way the component curves are displaced with respect to the co-ordinate axes when the wavelengths of test stimulus and conditioning stimulation are independently changed. From the observed displacements it appeared that the low intensity component curve was attributable to a mechanism having maximum sensitivity at a wavelength of 540 mμ approx., and the high intensity component curve to one having maximum sensitivity at 445 mμ approx.

In the present work the variation of the l.b.i. with conditioning intensity has been determined with a blue test stimulus and an orange conditioning stimulation for a group of twenty subjects. The results show a high-intensity 'blue' component in every case and in about half the cases the low-intensity 'green' component appears much as in investigation I. For some subjects, however, abnormally low values of the l.b.i. are obtained at low-conditioning intensities, suggesting that rod vision is playing a part. To test this point, the recovery of the eye after adaptation to an intense white light was determined by measurements of the l.b.i. for the blue test stimulus on a dark background. The recovery curves for the subjects in question show the characteristic two stages which Hecht (1937) and others have found to be associated with retinal areas where both rod and cone mechanisms are operative. With the aid of these recovery curves, the 'green' component curves can be determined approximately for all subjects, with one doubtful case. While confirming strongly the conclusion that the 'green' and 'blue' cone mechanisms can be separated by measurements of the l.b.i., the results reveal considerable variations among individuals both in the absolute and the relative sensitivities of the two mechanisms. In I it was observed that at a sufficiently high intensity of an orange or red conditioning stimulation further increase produced no corresponding increase in the l.b.i. of the 'blue' cone mechanism. From the present results it appears that this limited conditioning effect of orange or red light on the 'blue' mechanism occurs for most subjects.

By measurements of the l.b.i. with a different choice of colours for the test and conditioning stimuli, the 'green' and 'red' mechanisms can also be separated, although with more difficulty (I). Under the conditions of the present work, the 'red' mechanism is not in evidence and need not be referred to again.

2. Experimental details

The subject applied his eye to an artificial pupil and saw a circular patch of orange light of diameter 18° (the conditioning stimulation), containing at its centre four black fixation dots defining a square of 2° side (figure 1a). The test stimulus, a square patch of blue light of 1° side, was superposed on the orange background at the centre of the fixation square in flashes of 0-2 sec. once in every 1·4 sec. Its intensity was variable by the subject. The latter fixated carefully at the centre of the four black dots, and after several minutes' adaptation to the
orange field adjusted the test stimulus to be on the limit of visibility. Four or more settings were made. The intensity of the conditioning stimulation was then raised and the process repeated. For the special case of zero conditioning intensity, the dark fixation dots could not be seen and were replaced by four feeble points of orange light. A complete set of observations at 12 intensities from zero upwards occupied about 2 hr., including a preliminary period of about 20 min. dark adaptation.

The lay-out of the apparatus and its mode of operation are made clear by figure 1b and the following key:

- **E**: Artificial pupil of diameter 2.7 mm.
- **S₁**: 500 W opal lamp run at a colour temperature of approximately 2700° K.
- **X**: Sheet of plain glass carrying four opaque spots of white paint which appeared as black dots when silhouetted against S₁. When S₁ was extinguished, the spots were faintly illuminated by a small lamp placed above the filters F₀, Fₙ (not shown).
- **F₀, Fₙ**: Chance's light orange glass and gelatine neutral filters (as required).
- **C**: Composite glass cube of 3 cm. side with half-reflecting diagonal surface.
- **L₁**: Lens imaging the fixation points and diaphragm D at infinity; power to suit subject's refractive error, 4D for emmetropic eye.
- **S₂**: Ribbon filament lamp run at colour temperature of approximately 2450° K.
- **L₂, L₃**: Lenses of power 6.5 and 4D respectively giving a real image of S₂ on diaphragm D.
- **Fₐ, Fₙ**: Ilford's spectrum blue and gelatine neutral filter (if required).
- **H**: Rotating sector passing the light from S₂ for 0.2 sec. in every 1.4 sec.
- **Wₓ, Wₑ**: Opposed neutral wedges for varying continuously the intensity of the test stimulus.
- **D**: Diaphragm containing a square aperture covered by the image of S₂.

(The screening of the apparatus is not shown.)

The approximate relative energy distributions Eₐ of the lights used for test and conditioning stimuli are plotted in figure 1c. Their colours approximate to those of monochromatic lights of wave-lengths 470 and 615 mμ respectively.

For tests on the recovery of the eye, a rectangular panel (5 × 12.5 cm.) of diffusing glass illuminated to a brightness of 770 candles/ft.² (white light) was mounted by the side of the main apparatus. The subject stared at this panel with both eyes from a distance of about 8 cm. for 10 min. At a given moment the panel illumination was extinguished and the subject quickly transferred his eye to the aperture E and signalled as soon as the test stimulus, set at a suitable intensity, became visible. The test stimulus intensity was then considerably reduced, by the experimenter, and again the subject signalled when he could just see it, and so on. In
the later stage of the recovery process the subject himself made settings to the liminal intensity. Throughout, lamp \( S_1 \) was kept extinguished so that the test stimulus appeared on a field of zero intensity.

The simpler apparatus and technique, compared with those used in I, were adopted mainly to make the tests less tiresome for the subject and to reduce the call on his time. The use of colour filters and non-Maxwellian view gives a ‘cleaner’ conditioning field than before, but, setting by the subject, the use of a material artificial pupil and the abandonment of the dental impression method for fixing the subject’s head make for less satisfactory measurements. Details of the subjects are given in table 1.
Table 1

<table>
<thead>
<tr>
<th>subject</th>
<th>sex</th>
<th>age</th>
<th>eye used in measurements</th>
<th>colour vision (normal unless otherwise indicated)</th>
</tr>
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<td>—</td>
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<tr>
<td>B</td>
<td>F.</td>
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<td>—</td>
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<tr>
<td>C</td>
<td>M.</td>
<td>53</td>
<td>right</td>
<td>—</td>
</tr>
<tr>
<td>D</td>
<td>M.</td>
<td>38</td>
<td>right</td>
<td>—</td>
</tr>
<tr>
<td>E</td>
<td>M.</td>
<td>37</td>
<td>left</td>
<td>—</td>
</tr>
<tr>
<td>F</td>
<td>M.</td>
<td>53</td>
<td>right</td>
<td>—</td>
</tr>
<tr>
<td>G</td>
<td>M.</td>
<td>38</td>
<td>right</td>
<td>—</td>
</tr>
<tr>
<td>H</td>
<td>M.</td>
<td>43</td>
<td>left</td>
<td>—</td>
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<tr>
<td>I</td>
<td>M.</td>
<td>33</td>
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<td>—</td>
</tr>
<tr>
<td>J</td>
<td>F.</td>
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<td>—</td>
</tr>
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<td>M.</td>
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<td>—</td>
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<tr>
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<td>F.</td>
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<td>left</td>
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</tr>
<tr>
<td>T</td>
<td>M.</td>
<td>23</td>
<td>right</td>
<td>—</td>
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</table>

3. Curves showing the variation of the liminal brightness increment with the conditioning intensity

The circle points of figure 2 show the observed variation of the l.b.i. with conditioning intensity for the writer’s left eye. The cross-points are observations for this eye obtained in I* and refer to monochromatic test and conditioning stimuli of nearly the same colours as the present filtered lights. The two-component form is clearly shown by both sets of points, and the positions of the component curves along the axis of abscissae are in satisfactory agreement. Their positions along the ordinate axis would not be expected to agree precisely for three reasons:

(i) the exposure time of the test stimulus has been increased (0.063–0.2 sec.);
(ii) the effective wave-length of the test stimulus is slightly shorter (480–470 mµ approx.);
(iii) the ‘subject-setting’ method gives slightly higher values for the l.b.i. than the 50 % probability method used in I (difference estimated at about 0.1 or 0.15 log unit).

The quantitative effects of (i) and (ii) can be estimated approximately, (i) from the Blondel-Rey law (1911), (ii) from the shapes of the spectral sensitivity curves of

* The l.b.i. $U_\lambda$ and conditioning stimulation $W_\mu$ were then expressed in energy units but have been converted to photons by multiplying by $2.18 \times 10^8 V_{480}$ and $2.18 \times 10^8 V_{410}$ respectively, where $V_\lambda$ is the C.I.E. relative visibility function. The photon is a unit of retinal stimulation: 1 photon is equivalent to 1 candle/m.² or 0.003 candle/ft.² seen through an artificial pupil of area 1 sq.mm.
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the 'blue' and 'green' mechanisms. Including the effect of (iii), the circle points would be expected to fall below the cross-points by about 0.2 log unit ('green' component) and 0.3 log unit ('blue' component). Thus the agreement here is also very satisfactory.

![Graph](http://rspb.royalsocietypublishing.org/)

**Figure 2.** Observations for left eye of subject A (W.S.S.).

The (l.b.i./conditioning intensity) curves for the remaining nineteen subjects fall into three groups:

(a) those which can be represented as the resultant of two component curves (circle points of figure 3);*

(b) those like (a), except that at zero intensity the l.b.i. is abnormally low (circle points of figure 4);*

(c) those with abnormally low l.b.i. values at several of the low intensities (circle points of figure 5).*

By the resultant is to be understood a curve whose value at each intensity is equal, at least to a first approximation, to the lesser of the values of the two component curves.

For several subjects in each group the l.b.i. is anomalously low at one or two of the highest conditioning intensities. The discussion of this feature of the results is postponed to § 5.

The low values of the l.b.i. obtained at low intensities in groups (b) and (c) are almost certainly caused by the intrusion of rod vision. From the measurements of the recovery curve of the eye given below an approximate estimate of the l.b.i. of true cone vision at zero intensity can be made, and the values obtained are plotted as the square points in figures 4 and 5. Observations of the l.b.i. falling materially below the square-point value are to be attributed to rod response, and

* In figures 3–5 the scale of ordinates is correct for the top curve but must be shifted down 1 log unit for the second curve, 2 for the third, and so on.
if such observations are excluded the results for the subjects in groups (b) and (c) can be represented by two component curves as shown. In figure 5 the excluded points may be regarded as forming a third, rod component curve.

![Graph showing logarithmic plots](image)

**Figure 3.** Observations for subjects in group (a).

All the cone component curves drawn in figures 2–5 are obtained from a curve of fixed shape which is displaced (without rotation) to different positions in the diagram to give for each subject the best fit with the experimental points in the high- or the low-intensity range. The basic curve of fixed shape is the one derived
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in I for the writer’s left eye ($-\log \xi(x) \text{ v. } \log x$, shown as curve 2 in figure 36 of I). On the whole this shape, when applied to the present measurements, is satisfactory for all subjects, but because of the comparatively short range of points on each component the test is not a critical one. However, the results are consistent with the view that the curve relating the l.b.i. of cone vision to the conditioning intensity is the resultant of two component curves of similar shape, the same for all

Figure 4. Observations for subjects in group (b).
subjects, whose positions relative to the co-ordinate axes vary considerably from one subject to another. It is apparent from figures 3–5 that the changes of position are in general different for the two components, i.e. the resultant curve is not displaced bodily without change of shape.

**Figure 5.** Observations for subjects in group (c).
**Table 2. Sensitivities of the ‘blue’ and ‘green’ mechanisms for twenty subjects**

(Expressed in reciprocal photons)

<table>
<thead>
<tr>
<th>Subject</th>
<th>( g_{bl} )</th>
<th>( G_{or} )</th>
<th>( \log \left(\frac{G_{or}}{g_{bl}}\right) )</th>
<th>( b_{bl} )</th>
<th>( B_{or} )</th>
<th>( \log \left(\frac{B_{or}}{b_{bl}}\right) )</th>
<th>( M_{bl} )</th>
<th>( \log \left(\frac{b_{bl}}{M_{bl}}\right) )</th>
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<td>5.16</td>
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</table>

\( g_{bl} \) = sensitivity of the ‘green’ mechanism to the blue test stimulus.

\( b_{bl} \) = sensitivity of the ‘blue’ mechanism to the blue test stimulus.

\( G_{or} \) = sensitivity of the ‘green’ mechanism to the orange conditioning stimulation.

\( B_{or} \) = sensitivity of the ‘blue’ mechanism to the orange conditioning stimulation.

\( M_{bl} \) = sensitivity of the ‘blue’ mechanism to the blue test stimulus when the conditioning stimulation has produced its maximum effect.
According to I, the high- and low-intensity components are respectively the l.b.i. curves which would be obtained if the ‘blue’ and ‘green’ cone mechanisms acted alone. Thus differences in position of the component curves are to be interpreted as differences in the sensitivities of these mechanisms. Sensitivity of a mechanism to the test stimulus is defined as the reciprocal of the l.b.i. at zero conditioning stimulation, and sensitivity to the conditioning stimulation as the reciprocal of the intensity of the latter required to raise the l.b.i. to ten times its value at zero intensity. The derivation of these sensitivities for the green and blue mechanisms from the positions of the corresponding component curves is made clear by figure 6 and the values obtained for the twenty subjects are set out in table 2.

4. Results: recovery curves

If the intrusion of rod vision is responsible for very low values of the l.b.i. at low intensities, we should not expect these low values to be reached rapidly after the eye has been exposed to a high brightness because of the known slow recovery (dark-adaptation) of the rod mechanism. The recovery curves for subjects Q and I belonging to groups (e) and (b) respectively, are reproduced on the left in figures 7 and 8, and indicate that a time of the order of 20 min. is required before the l.b.i. value previously observed at zero intensity is reached. Moreover, the curves show an initial cone phase and a later rod phase and the final l.b.i. of true cone vision is clearly defined. These final cone values are transferred as the square points in the (l.b.i./conditioning intensity) curves shown on the right in the same figures. The recovery curves for the extreme types in group (a) (subjects B and G) show the more rapid single phase recovery curve appropriate to pure cone vision (figure 9).

The recovery curves for the remaining subjects were in general similar to those just discussed although in one or two cases (particularly for subject S), the cone to rod transition is less marked and the uncertainty in fixing the true cone l.b.i. at zero intensity is greater.

There are three reasons which could account for the intrusion of rod vision for some subjects:

(i) their foveas may contain rods or, at the least, the rod-free area may be smaller than the 1° square test stimulus;

(ii) they may have failed to maintain strict foveal fixation;

(iii) foveal fixation as normally understood may have been maintained but their rod-free areas may be displaced.

As regards (i), Abney & Watson (1916) found that three out of eight subjects showed characteristic rod properties at the fovea (test light, diam. 34 min.) and were emphatic that fixation errors were not responsible. In the present measurements, cause (ii) was certainly operating for some subjects. With the blue test stimulus used the ratio of rod to cone sensitivities reaches its highest value and every one had difficulty in fixing at zero conditioning stimulation. Subjects K
Figure 7. Recovery curve and (l.b.i./intensity level) curve.

Figure 8. Recovery curve and (l.b.i./intensity level) curve.
and O gave single phase recovery curves and did not repeat the abnormally low values of the l.b.i. at low intensities, obtained in the original (l.b.i./conditioning intensity) runs. On the other hand, one subject (N) gave a well-defined two-phase recovery curve, reaching lower values of the l.b.i. in the rod phase than had been obtained previously under steady conditions at zero intensity. These differences are attributable to varying success in maintaining fixation on different occasions.

Cause (iii) is certainly operative for one subject T for whose retina, it is known from other work, a rod-free response at low intensities can be obtained if the direction of fixation is about $\frac{1}{2}$ to the left of the test stimulus.

![Figure 9. Recovery curves.](image)

5. **LIMITED CONDITIONING EFFECT OF RED LIGHT ON THE ‘BLUE’ CONE MECHANISM**

In figure 2, upper curve, the l.b.i. for the highest conditioning intensity is about 0.3 log unit below the value expected from the ‘blue’ component curve. This is not just a bad observation but an example of an effect consistently observed in I, that as the intensity of an orange or red conditioning stimulation was increased it raised the l.b.i. of the ‘blue’ mechanism in the normal way to a certain value and thereafter produced no further increase. For green or blue conditioning stimulations this did not occur. The intensity available in the present apparatus was insufficient to reach the range of constant l.b.i. for the writer’s eye (see lower curve of figure 2),
but for several other subjects it appears to have been reached. Most of the observed l.b.i. values belonging to the high-intensity range in figures 2–5 differ from the ‘blue’ component curve as drawn by less than 0·1 log unit. Suppose the results of a particular subject are accepted as showing a limited conditioning effect if the observed l.b.i. at the highest intensity lies below the ‘blue’ component curve as drawn by 0·2 log unit or more. On this basis nine subjects show it, the effect being most marked for subject N. From the results for these cases, estimates have been made of $M_{bl}$, the reciprocal of the upper limiting value of the l.b.i. of the ‘blue’ mechanism (see figure 6). The log of this quantity and of the ratio $b_{bl}/M_{bl}$ are given in table 2. Log $(b_{bl}/M_{bl})$ takes values ranging from 0·53 to 0·97 with an average of 0·69 compared with the value 0·63 obtained in I as the mean from many curves for the writer’s left eye.

It appears therefore that limited conditioning sets in when the conditioning stimulation is sufficient to raise the log (l.b.i.) of the ‘blue’ mechanism by about 0·7 log unit. From the shape of the standard component curve it is readily determined that if $L$ and $N$ are the conditioning intensities required to raise the l.b.i. of the ‘blue’ mechanism by 1·0 and 0·7 respectively, then $\log N = \log L - 0·45$. We should not expect to observe limited conditioning if $\log N$ exceeds 4·00, the log of the maximum conditioning intensity used in the measurements. But by definition $\log B_{or} = \log (1/L) = -\log L$, so that $\log N > 4·00$ is equivalent to $\log B_{or} < 5·55$. From the values of $\log B_{or}$ given in table 2, it is seen that none of the subjects for whom $\log B_{or} < 5·55$ shows limited conditioning in the present tests, although two (A and K) are known from other work to show it at higher intensities. Of the thirteen subjects for whom $\log B_{or} > 5·55$, nine show the effect. In sum, therefore, $9 + 2 = 11$ subjects out of $13 + 2 = 15$ are known to show limited conditioning (about 3 in 4), while the remaining five subjects would not be expected to show it in the present measurements.

The anomalously low l.b.i. values at high intensities are regarded as a special property of the ‘blue’ mechanism and not as the initial part of the component curve of an additional mechanism. The reasons for this view are given in I.

6. Individual variations in the sensitivities of the ‘blue’ and ‘green’ mechanisms

In figure 10 the sensitivity to the test stimulus is plotted against the sensitivity to the conditioning stimulation for each subject and for the two mechanisms. The total range of variation and the standard deviations of the log sensitivities have the following values:

<table>
<thead>
<tr>
<th>log $g_{tl}$</th>
<th>log $G_{or}$</th>
<th>log $b_{bl}$</th>
<th>log $B_{or}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>total range</td>
<td>1·2</td>
<td>1·2</td>
<td>1·3</td>
</tr>
</tbody>
</table>
| standard deviation | 0·28        | 0·31        | 0·34        | 0·60
Figure 10

Figure 11
Separation of ‘blue’ and ‘green’ mechanisms of foveal vision

The spread arises in part from uncertainty in fitting the component curves to the observations, in part from a true individual variation which appears to be greatest for $B_{or}$. For the ‘green’ mechanism there is a weak correlation of the two sensitivities $\log g_{bi}$ and $\log G_{or}$ but for the ‘blue’ mechanism there is no correlation.

The following points are illustrated in figure 11:

(i) $\log b_{bi}$ v. $\log g_{bi}$. The sensitivities to the test stimulus tend to increase together and proportionally for the two mechanisms but subject S appears to be exceptional in this respect (figure 11a).

(ii) $\log B_{or}$ v. $\log G_{or}$. The sensitivities to the conditioning stimulation show a slight tendency to increase together but not proportionally (figure 11b).

(iii) $\log g_{bi}$ v. $\log B_{or}$ and $\log b_{bi}$ v. $\log G_{or}$. No correlation (not reproduced).

(iv) $\log \left( \frac{B_{or}}{b_{bi}} \right)$ v. $\log \left( \frac{G_{or}}{g_{bi}} \right)$. These log ratios tend to increase together but not proportionally (figure 11c).

(v) $\log \left( \frac{B_{or}}{b_{bi}} \cdot \frac{G_{or}}{g_{bi}} \right)$ tends to increase proportionally with $\log B_{or}$ (figure 11d) but shows no correlation with $\log b_{bi}$, $\log G_{or}$ or $\log g_{bi}$.

The quantity $\log \left( \frac{B_{or}}{b_{bi}} \cdot \frac{G_{or}}{g_{bi}} \right)$ is of some interest as for monochromatic test and conditioning stimuli it would remain unchanged if the subject made all his observations through a colour filter of arbitrary spectral transmission and this fact was ignored in working out the results so that the filter was treated as part of the eye. If such a colour filter had transmissions $t_{or}$ and $t_{bl}$ for the orange and blue lights, it is clear that the observed sensitivities would become $B_{or}t_{or}$, $G_{or}t_{or}$, $b_{bi}t_{bi}$, $g_{bi}t_{bl}$, respectively, but we should have

$$\log \left( \frac{B_{or}}{b_{bi}} \right) \cdot \frac{G_{or}}{g_{bi}} = \log \left( \frac{B_{or}}{b_{bi}} \right) \cdot \frac{G_{or}}{g_{bi}}.$$

The effective widths of the spectrum bands corresponding to the present non-monochromatic stimuli are small and it may fairly be concluded from the wide variation of

$$\log \left( \frac{B_{or}}{b_{bi}} \cdot \frac{G_{or}}{g_{bi}} \right)$$

that individuals differ in a way which cannot be assimilated to selective absorption by a pigment layer.

The outstanding feature in the above correlations, which are not of course all independent, is the large and dominating variation of $\log B_{or}$, the sensitivity of the ‘blue’ mechanism to orange light.

7. Conclusions

1. Measurements of the liminal brightness increment show for all subjects the operation of two cone mechanisms ('green' and 'blue') in foveal vision.

2. For some subjects, rod vision intrudes at low intensities, but this difficulty can be dealt with by determining the cone l.b.i. before the rods have had time to recover from intense light adaptation.
3. Individual variations are most marked in the sensitivity of the ‘blue’ cone mechanism to orange light.

4. Most subjects give evidence of a limited conditioning effect of orange light on the ‘blue’ cone mechanism.

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Experiments on the inactivation of bacteriophage by radiations, and their bearing on the nature of bacteriophage

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Three bacteriophages (S-13, C-36 and Staph-K) were irradiated by γ-rays, X-rays and α-rays. The survival curves were exponential, and the effect of a given dose was independent of the exposure time. For any given phage the inactivation doses of the three radiations increased in the order γ-rays, X-rays, α-rays, while for any given radiation the inactivation doses of the three phages diminished in the order S-13, C-36, Staph-K, which is the order of increasing size.

These observations lead to the conclusion that a single ionization suffices to inactivate a phage particle. In the case of the smallest phage investigated (S-13) this ionization is effective wherever in the particle it is produced, and reasons are given for concluding from this fact that S-13 is a macromolecular type of virus analogous to the crystallizable plant viruses.

In the case of the larger phages (C-36 and Staph-K), while a single ionization can inactivate a phage particle it is not sufficient for it to be produced anywhere in the phage particle; to be effective it must be produced in a more restricted region. It is suggested that this radiosensitive region constitutes the genetical material of the phage, and on the basis of this differentiation into genetic and non-genetic material these phages are regarded as primitive single-celled organisms rather than macromolecules.

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