VISUAL ACUITY IN THE BLUE CONE MONOCHROMAT

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SUMMARY

1. To isolate the blue cones of the normal eye, blue sine-wave gratings were superimposed on a bright yellow background. Threshold contrasts for resolution of the gratings were then determined.

2. Under these conditions visual acuity for high contrast gratings on four normal subjects was on the average 0.31 min^{-1} . This is about a factor of ⁶ lower than grating acuity under optimal conditions.

3. The contrast sensitivity of two subjects who lack the normal red and green receptor mechanisms was measured using blue sinusoidally modulated gratings. Visual acuity was found to be greatly reduced from normal. The low acuity of these individuals is due to both a reduction in contrast sensitivity and a reduction in resolution.

4. The spatial resolving characteristics of these subjects resembles the vision of the normal eye under conditions which isolate the blue sensitive mechanisms.

5. The vision of the cone monochromat differs significantly from that of the more typical rod monochromat. The rod monochromat has even lower acuity than the blue cone monochromat for high contrast gratings but has much greater contrast sensitivity for gratings of low spatial frequency.

INTRODUCTION

The spatial resolving properties of the normal eye are relatively poor when measured using blue test stimuli superimposed on bright yellow or green adapting background. These experimental conditions are known to isolate blue sensitive mechanisms which seem likely to be the blue sensitive cones of trichromatic vision. Consequently, these findings have been interpreted as indicating that the blue cones are spatially organized rather differently than the other two colour mechanisms. In particular, it has been argued that the blue cone mechanism has a lower visual acuity (Stiles, 1953; Brindley, 1954; Green, 1968), greater spatial summation (Brindley, 1954) and reduced contrast sensitivity (Green, 1968).

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To measure the properties of the blue cones in the normal eye the sensitivity of the red and green sensitive systems must be depressed with a suitably chosen adapting field. This is not the case, however, for the rather unique inidividuals who the Blackwells (1961) called blue cone monochromats. These individuals appear to have a genetically determined colour vision defect wherein they have lost the normal red and green cone mechanisms. In the dark-adapted state the blue cone monochromat has ^a more or less normal scotopic spectral sensitivity curve. When their eyes are light adapted they exhibit a reverse Purkinje shift. Rather than showing the usual long wave-length shift in spectral sensitivity they become even more short wave-length sensitive. Alpern, Lee & Spivey (1965) have shown that this photopic luminosity curve which peaks at $\lambda = 440$ nm is the same as the spectral sensitivity curve of the blue mechanisms of the normal eye as measured by Stiles (1959) using two colour increment thresholds. In addition, the above authors found that the absolute cone threshold of the blue cone monochromat was the same as that of the π_1 cone mechanism of the normal fovea.

One further aspect of the blue cone monochromat's vision which agrees with the properties of the isolated blue channels of the normal eye is their low visual acuity. At photopic levels of illumination the visual acuity for Snellen letters of the blue cone monochromat is reported to be about 0.3 min^{-1} . This acuity is substantially higher than the 0.13 min^{-1} for blue cone acuity reported by Brindley (1954) but agrees well with the 0.3 min^{-1} found by Green (1968). Using sinusoidal gratings on backgrounds of ^a different colour, Green (1968) found that in addition to having low acuity the blue cones of the normal eye have a contrast transfer function which is reduced by a factor of about ten as compared with the red or green mechanisms.

The studies reported here were undertaken to determine the spatial resolving properties, as measured by gratings with sinusoidal modulation, of the photopic system in the blue cone monochromat. The determinations of threshold contrast at various spatial frequencies show that these individuals have a contrast transfer function which is the same as that of the blue cones of the normal eye.

METHODS

A sinusoidal grating pattern was formed upon the face of ^a cathode-ray oscilloscope (Tektronix type 544) using the technique described in detail by Campbell $\&$ Green (1965). In the case of the normal subjects the spatial arrangement of the background and the test fields was the same as in ^a previous study (Green, 1968). A $4^{\circ} \times 1.5^{\circ}$ striped visual acuity target was superimposed on the larger 12° circular background field. A Kodak Wratten filter (type 21) was used to colour the background field. This background was obtained by imaging the filament of a tungsten source into the subject's pupil by reflexion from the beam-splitting cube.

The normal observers viewed ^a cathode-ray tube with ^a P ¹¹ phosphor. The P ¹¹ has ^a radiant energy peak at ⁴⁵⁰ nm and ^a dominant wave-length of ⁴⁷⁸ nm. The blue cone monochromats viewed ^a cathode-ray tube having ^a P22B phosphor without an adapting background. This phosphor has ^a radiant energy peak at ⁴⁴⁵ nm and a dominant wave-length of 455 nm.

Unless otherwise noted the subject's head was fixed relative to the ³ mm artificial pupil by means of ^a bite bar or chin-head rest combination. The subject's accommodation was paralysed by instilling one or two drops of ¹ % Cyclogyl (cyclopentolate hydrochloride) into the conjunctival sac. Spectacle lenses were used to bring the image of the oscilloscope, which was viewed from several distances, into focus on the retina. All the observers viewed $10.2 \text{ cm} \times 3.8 \text{ cm}$ field of stripes, the normals from a distance of 145 cm, the blue cone monochromats from 114 cm, one rod monochromat $(R,H.)$ from a distance of 72 cm and the other $(J.G.)$ from 46 cm. The contrast of the grating pattern was varied by changing the magnitude of the voltage reaching the brightness control grid of the cathode-ray tube. The subject adjusted the magnitude of the modulating voltage until he was satisfied that the grating could just be detected.

RESULTS

In the first group of experiments the spatial resolving properties of the blue sensitive mechanisms of the normal eye were determined (Fig. 1). The observer adjusts the contrast of a blue sinusoidal grating $(\lambda = 478 \text{ nm})$ until it can be resolved against a yellow adapting background ($\lambda = 594$) nm). The grating produced a retinal illumination of 2-7 log td on the background of 5-6 log td. Different symbols are shown in Fig. ¹ for each of the normal observers on whom measurements have been made. A continuous curve in the Fig. 1, obtained by averaging across observers, defines the contrast transfer function of the normal blue cones. The dashed curve in the Figure shows the average contrast transfer function for ten normal subjects viewing a green sinusoidal grating without an adapting background. It is included in the Figure to emphasize the difference between the ordinary resolving power of the eye and this capacity when subjects use their blue cones only.

Fig. ² shows the results of having two blue cone monochromats adjust the contrast of sinusoidally modulated grating for threshold visibility. No adapting background was used. The dominant wave-length of the striped field was $\lambda = 455$ nm and it produced a retinal illumination of 2.1 log td. The continuous curve was obtained by averaging the measurements from the two observers. Fig. ³ shows the contrast transfer function of the blue cone monochromat and the comparable function for the normal redrawn from Fig. 1. The agreement between the two sets of measurements is quite good. Nonetheless, one might wonder whether the similarity was fortuitous.

The conclusion that the photopic vision of the blue cone monochromat is like the isolated blue mechanism of the normal eye would be strengthened if there were some differences between the contrast sensitivity of the blue

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cone monochromat and that of the rod monochromat. Fig. ⁴ shows contrast sensitivity determinations from two rod monochromats. The measurements in the Figure were obtained using gratings having ^a mean luminance of 200 cd/m² and a radiant energy peak at $\lambda = 530$ nm. This is just one of several different luminances at which measurements were obtained. Since

Fig. 1. Contrast sensitivity for normal observers viewing ^a blue grating on a yellow background. Measurements from four observers are indicated as follows: \Box D.G., \triangle F.M., \bigcirc M.A., \bigcirc T.C. Each point is the average of four measurements. The continuous curve shows the results averaged over the four observers. The dashed curve indicates the average contrast sensitivity obtained on ten normal observers viewing sinusoidal gratings without ^a superimposed adapting field.

the contrast transfer functions were essentially independent of luminance above about 0-2 cd/m2 only the data for the brightest condition are shown in Fig. 4.

The rod monochromat's vision is clearly quite different from that of the blue cone monochromat. For high contrast targets the rod monochromat's visual acuity is only half that of the blue cone monochromat. The rod monochromat, however, has much better low frequency contrast sensitivity. Consequently, the contrast sensitivity functions of these two types of colour blind observers cross at about ³ cycles/degree.

Fig. 2. Contrast sensitivity of two blue-cone monochromats. Each point $($ J.N., \bigcirc G.N.) is the average of four measurements, obtained without an adapting background at the indicated spatial frequency. The continuous curve shows the results averaged over the two observers.

Fig. 3. Comparison of the contrast sensitivity of normal blue-cone channels (continuous line indicates averages from Fig. 1) with that of the blue-cone monochromat (interrupted line indicates averages from Fig. 2).

Fig. 4. Comparison of average contrast sensitivity of blue-cone monochromat (interrupted line) with corresponding curves from two rod monochromats (\Box J.G., \bigcirc R.H.).

DISCUSSION

One of the very important consequences of the trichromatic theory of colour vision is its explanation of the common forms of dichromat vision in terms of the loss of one of three fundamental mechanisms. In this scheme the protanope lacks the red sensitive cone pigment and the deuteranope lacks the green sensitive cone pigment. The additional assumption that the receptor pigments which remain are the same as two pigments of the normal trichromat leads to a simple theory of colour blindness. Colour matching behaviour of dichromats (Nuberg & Yustova, 1961; Miller, 1970), the failure of chromatic adaptation with intermediate and long wave-length adapting lights to change the shape of their foveal spectral sensitivity curve (Wald, 1966), and the results of retinal densitometry (Rushton, 1964) all fit in nicely with this hypothesis.

There are two ways in which protanopia and deuteranopia could be reductions of normal trichromatic vision. One possibility is the cones and associated neural apparatus of one of the colour mechanisms could be missing or functionless. Alternatively, the receptors that are lost could be filled with one of the remaining pigments. For example, the missing red cones of the protanope might be filled with the green sensitive pigment.

The existence of ^a patient deuteranopic in only one eye who reported all wave-lengths greater than 502nm seen with the deuteranopic eye would match ⁵⁷⁰ nm seen with the normal eye is suggestive of the latter possibility, as is the normal visual acuity of the dichromat. On.the other hand, the colour defect of the unilateral deuteranope might be quite different from that of the ordinary dichromat. Moreover, it has become increasingly clear that visual acuity of the isolated red and green mechanisms of the normal eye is so high that it would be nearly impossible to detect any acuity loss even if one of the receptor systems were absent (Brindley, 1954; Green, 1968).

The blue cone monochromat is an even more extreme example of a reduction in normal vision. He has lost both the red and green receptor mechanisms. The single cone system operating at photopic levels has the spectral sensitivity of the normal blue cone pigment. Moreover, the agreement between his absolute visual sensitivity and that of the blue mechanism of the normal suggests that he has no loss or gain in the number of blue cones. The results reported here show that the blue cone monochromat's acuity is reduced by about ^a factor of six from normal due to the same kind of reduction in resolution and loss in contrast sensitivity that was found for the blue cones of the normal fovea. These observations taken together provide strong evidence suggesting that cone mechanism which remains in these patient's foveas is just the same as the blue channel of the normal trichromatic eye.

This, however, may only be approximately true. There still remains at least one unexplained aspect of blue cone monochromacy. Alpern, Lee, Maaseidvaag & Miller (1971) convincingly show that these individuals have rudimentary colour vision. They are dichromats with colour matching functions which are consistent with colour vision mediated by receptors having the spectral sensitivity of rods and blue cones. The available evidence suggests that this is not the result of ordinary rods and blue cones participating in colour matches but rather is due to the fact that some of their foveal cones are filled with rhodopsin. This being the case, it is not at all clear how these rhodopsin-filled cones can signal colour without adding to photopic luminosity or participating in the process of visual resolution.

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