THE MONOCHROMATISM OF THE CENTRAL FOVEA IN RED-GREEN-BLIND SUBJECTS

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The tritanopia of the central fovea of the normal subject was first described by König in 1894, but the observation passed relatively unheeded. This happened very largely because of an unfortunate confusion in nomenclature and through a misunderstanding of the unsatisfactory term 'blue-blind'. Perhaps, also, the observation was allowed to fall into oblivion because it was difficult to reconcile with the part which cones were supposed to play in the perception of colour, according to the current trichromatic theory; for, if cones were the only elements responsible for colour discrimination and three types were required in order to satisfy the data from experiments on colour mixing, then it was difficult to see how an area believed to consist entirely of cones should not have the complete trichromatic mechanism. König's detailed account, however, was completely and independently confirmed a few years ago (Willmer, 1944; Willmer & Wright, 1945) when it was found that the errors which are made in matching colours on very small fields were not random errors but followed a systematic pattern, and were, in fact, practically identical with those which have been described as characteristic of the tritanope (Pitt, 1944); moreover, it was again shown that the normal subject could match all the spectral colours with mixtures of red and violet, provided that the fields fell within the central foveal area and that central fixation was maintained.

For most normal observers, fields, which subtend about 1° at the eye and are centrally fixated, theoretically fall within the so-called 'rod-free area' of the fovea. In practice, however, three factors make it desirable to use a considerably smaller field than this in investigations of the behaviour of this area. In the first place, recent observations (Lord & Wright, 1948; Barlow, 1949) have shown that small eye movements frequently occur, and these may be sufficiently large to bring margins of the 1° field on to parts of the retina outside the central fovea. Secondly, the field size should be kept small and its intensity low, because sufficient light may otherwise spread to neighbouring areas and cause stimulation of extra-foveal receptors. In the dark-adapted eye, for example,

the low-threshold rods may be about one thousand times more sensitive than the elements in the central fovea, so that a very small amount of scatter from the central spot may involve these receptors also. Thirdly, there may be some lateral spread of excitation within the retina itself and this should not be allowed to reach the extra-foveal elements. It may be difficult, or in some cases even impossible, to prevent the surrounding areas from becoming involved, but the smaller the field and the more carefully it is centrally fixated the less inter-ference is likely to be caused. The ganglion cells which are stimulated by the rods 'cover' relatively large areas of the retina and their shape and connexions make it not unlikely that their behaviour may be determined by other elements besides the low-threshold rods. Clearly, then, it is very important in investiga-tions of the properties of the central fovea to use considerably smaller fields than the dimensions of the so-called rod-free area suggest. Preferably such fields should not subtend more than 30' at the eye. Moreover, Thomson & Wright (1947) have shown that the foveal area is not uniform, and that progressive differences in apparent hue occur as a small (15') field is moved from the position of central fixation to positions 20' and 40' eccentrically.

When a normal subject examines a divided field, or two small separate fields, with his central fovea he may at first notice nothing curious about the colours subjectively, and he may be able to distinguish between colours in apparently the normal way. As he becomes firmly fixated, however, and after a measurable delay, which gets less with practice, then the subjective impressions change, and, what is more important, he makes definite confusions.

Even under these conditions, however, the normal subject can *subjectively* distinguish a very wide variety of colours with his central fovea, though his hue discrimination is very much reduced (Willmer & Wright, 1945). Red and blue-green are the colours most characteristically registered by the normal central fovea, though a curious saturated violet is also seen. Yellow tends to be indistinguishable from white and may be called either yellow or white. Similarly, violet, blue and blue-green are all confused to some extent. A bright violet may appear to be blue or blue-green, though the converse does not seem to be true, i.e. when a blue-green (say $\lambda = 480$ mμ.) is reduced in intensity it does not appear violet but tends rather to a greyish hue. However, these subjective impressions are open to all manner of suggestions and are notoriously unreliable; the main *objective* fact about the normal central fovea is that, within that area, all spectral colours can be matched by mixtures from two colours only, provided that these are chosen from the spectral extremes. The mixtures are specific for each wave-length and the matches only hold within definite limits. This suggests the presence of only two separate pathways, with different spectral sensitivities, between the retina and the brain. Moreover, the fact that particular mixtures of the spectral extremes match particular wave-lengths shows that the matches are genuine matches and not random errors made by

the subject because the matching fields are too small to allow of precise judgement. Furthermore, it may be concluded that no more than two pathways are involved, for, if they were, then the matches and confusions which are characteristic of the central fovea would not be made, since the third or other pathways would give the information required for distinguishing the colours. For example, a mixture of red (R) and violet (V) can be used to match green (G) in the central fovea because green in that area is seen when receptor A responds with intensity a and receptor B with intensity b (Fig. 1). Wave-lengths V, stimulating receptor A to the extent v, and R, stimulating receptor B to the extent r, can thus be chosen and used in sufficient intensities to stimulate receptor A to the extent a and receptor B to the extent b. Thus $vx = a$ and $ry = b$. If, however, a third receptor C were involved, whose spectral sensitivity was different from
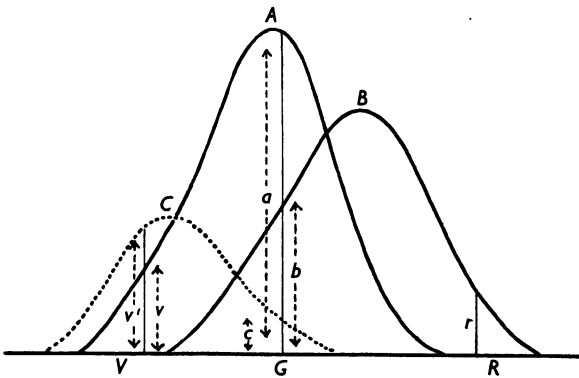

Fig. 1. Diagram to illustrate the difference between dichromatic vision and trichromatic vision. A and B, sensitivity curves (hypothetical) for the two receptors present in the central fovea; C, sensitivity curve, also hypothetical, for a third receptor. V, violet; G, green; R, red; a, sensitivity of receptor A to green; b, of receptor B to green; c, of receptor C to green; v, of receptor A to violet; v', of receptor C to violet; r, of receptor B to red.

those of A and B and was not uniform through the spectrum, then wavelength V would stimulate it to the extent v' and it would be extremely unlikely that, if $vx = a$, $v'x$ should also equal c, where c represents the extent to which receptor C is stimulated by wave-length G when this wave-length is stimulating receptors A and B to the extents a and b respectively. It is clear, therefore, that if more than two receptors are involved it would be almost impossible to make matches with all the spectral colours by means of two primary colours only.

The central fovea of the normal subject therefore behaves as though it possessed two independent pathways, and there are very strong indications that it has only two pathways. It does not follow that structurally there are only two pathways, though the evidence for this is strong, but, functionally, two pathways are the necessary and sufficient requirements to satisfy the data

with respect to colour matching, etc., in the central fovea, when such data are obtained under conditions which minimize the possibility for interaction from other retinal elements. In this connexion it may be again emphasized that the foveal matches described are only made after a perceptible lapse of time after the image has apparently been fixated. The reason for this delay is unknown, but it can be reduced by practice. It may be due to the interference by some third pathway being 'inhibited' out, or it may simply be necessary to wait till the information, derived from other parts of the retina during the process of fixation, has faded from memory before a pure central foveal observation can be made.

If, therefore, the normal subject has only two instead of three pathways from his central fovea and the missing path is the so-called 'blue path', then it is pertinent to inquire how the red-green-blind observer behaves with respect to his central fovea. He may be lacking his red receptor if he is a protanope, or, if he is a deuteranope he may lack his green receptor, or if Pitt's (1944) interpretation is correct, he may have his red and green receptors combined into a single pathway. At this point it must again be stressed that the 'blue' receptor does not mean the receptor which necessarily gives rise to the sensation 'blue', but it means the receptor which 'covers', more than the other two, the blue end of the spectrum. Similarly, the green receptor has its maximum in the green region of the spectrum, though it probably covers most of the visible range, and there is no evidence that greenness is the result of stimulation of this receptor alone. Red, green and blue receptors are the terms given to denote the regions of the spectrum in which the receptors have their maximum sensitivities and their stimulation should not be correlated with any particular sensation, for the latter are much more likely to arise as the result of different proportional responses from two or more of the receptors. The original failure to accept König's observations on the tritanopia of the central fovea was caused because he described the condition as one of blue-blindness, meaning absence of the receptor mechanism covering the blue end of the spectrum, and not the inability to have the sensation of blue aroused by stimulation of this area. The sensation of blue can be aroused from the central fovea, though this area is relatively insensitive to the blue end of the spectrum and behaves as if it were lacking a receptor covering this region.

A red-green-blind subject may therefore be expected to become totally colour-blind if his vision is restricted to the central fovea, because he has only one pathway where the normal person has two. Such an observer should be able to match any colour with any other colour provided that the intensities were also matched, and the following experiments describe a simple technique for showing that this is so.

METHODS

Essentially, the apparatus has been designed to illuminate two small fields, each subtending 10′ at the eye and with their centres separated by a distance equivalent to 20′, with light from Ilford
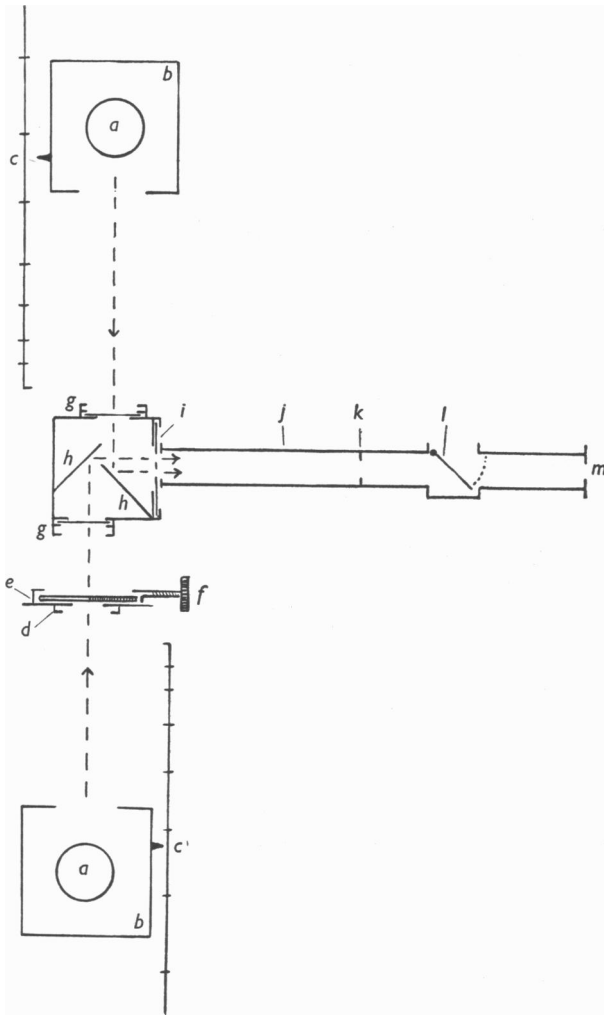

Fig. 2. Plan of apparatus (not to scale). *a*, 100 W. tungsten filament frosted lamp; *b*, lamp-house mounted on runners; *c*, scale of intensities, relative to unity at the end of the scale; *d*, filter-holder for neutral filters, etc., in front of 2·5 cm. aperture; *e*, holder for blue and red dipartite filter; *f*, micrometer screw with scale for moving dipartite filter across aperture; *g*, filter-holder and ground-glass screen; *h*, front-silvered mirrors; *i*, stop for regulating dimensions and shapes of viewing fields; *j*, viewing tube; *k*, stop for preventing internal reflexion; *l*, holder for mirror or glass plate which can be used to reflect fixation spots, adapting lights, etc., and which can swing out of line when not required; *m*, artificial pupil.

spectral filters. The left-hand field was illuminated by light or a single wave-band, obtained by using one of the Ilford filters, 601–609, whose intensity could be varied by the insertion of neutral

filters or by appropriate movements of a 100 W. tungsten lamp along a scale graduated in intensity units relative to the ground-glass screen which formed the basis of the visible field, and which was in a constant position relative to the eye. The right-hand field was illuminated by light from another similar 100 W. tungsten lamp passing through a divided filter of which one half was blue (Ilford 602) and the other red (Ilford 608), and falling on a second fixed ground-glass plate. This filter could be moved by a micrometer screw across the beam of light so that the small right-hand field could be illuminated with pure red light, pure blue light or with mixtures of the two in any proportion. The light falling on the ground-glass plate had passed through a square aperture of side 2·5 cm. and the micrometer scale indicated the number of millimetres of the aperture occupied by the red filter. Separating the red and blue filters was a narrow (1 mm.) band of black. The intensity of the mixed field could also be varied if necessary by neutral filters or by movement of the light source along a graduated scale. The light from the two ground-glass plates was reflected by front-silvered mirrors in such a way as to illuminate the two fields which were formed by means of two 2 mm. holes in a brass plate which was viewed from a distance of 70 cm. By the use of alternative brass plates as 'stops' various other field sizes up to and including two adjacent semicircular fields subtending 2° at the eye could be obtained. A 2 mm. artificial pupil was used throughout. It was placed at the end of a viewing tube fitted with a suitably placed stop to prevent internal reflexion along the tube, and the tube itself prevented interference by extraneous light. The general plan of the apparatus is shown in Fig. 2. Observations were made in a darkened room illuminated only by stray light from the apparatus which was reduced to a minimum by enclosing as much as possible of the apparatus within black screens. Readings were taken only after the subject had been in the dark for at least 10 min., by which time 'cone adaptation' is nearly complete. The subject was asked to fixate on the space between the two fields or on the left-hand edge of the right-hand field. He held his head relatively firm by biting on an adjustable dental impression clamped to the bench. Owing to the chromatic aberration of the eye, the light from the red and blue filters is apt to separate when the eye is not viewing the fields directly. The correct position of the head can therefore be checked by ensuring that the blue and red fields overlap on the right-hand small field. Observations were only made and readings taken when the subject considered that he was fixating the fields centrally. A blue filter was chosen rather than a violet since the pure violet filter transmits so little light that many of the matches would have to be made at a very low intensity, with consequent inaccuracy. The two filters did not transmit equal quantities of red and blue and in any case the relative brightness of the two filters was different for different observers, particularly if the latter were colour-blind. The scale readings for the amounts of red and violet light thus represent purely arbitrary values and it must be borne in mind that as the amount of red increases, so the amount of blue declines, and vice versa. The quantitative data for the amounts of red and blue which match other spectral colours for the normal central fovea have already been published (Willmer & Wright, 1945).

<div align="center">RESULTS</div>

In preliminary experiments the subjects were asked simply to find the position of the dual filter so that the field illuminated by it matched in hue the other field which was illuminated with a single wave-band. The light source for the mixture of red and blue was maintained at a fixed position throughout the experiments. The brightness of the single field could be adjusted to match the brightness of the dual field. It was soon found that this method led to great variability in the readings obtained, and if adjustments were made to the brightness then several positions could be found over which a match could be obtained. In later experiments, therefore, the subject was asked to add as much red to the mixture as he could and still preserve a match for the single field which he was allowed to vary in brightness as much as he liked. Having

found the extreme red position he then tried to find the extreme blue position, again being allowed to vary the intensity of the single field. Between these two positions it was therefore possible to match the single field at some brightness level with mixtures of red and blue. Outside these limits it was impossible to make a match, however the intensity or proportions were altered.
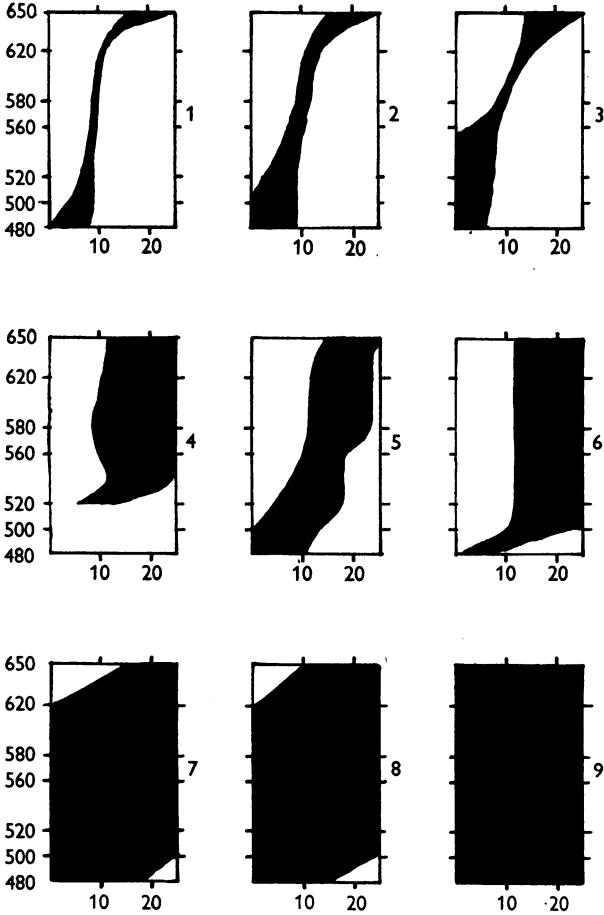

Fig. 3. Diagrams illustrating the ranges within which matches between spectral wave-bands and mixtures of red and blue lights are valid for normal, colour-anomalous and colour-blind subjects, when using two 10′ fields separated by 10′ and centrally fixated. Black areas indicate the range. 1, 2 and 3, normal subjects; 4–8, subjects with varying degrees of colour-blindness; 9, protanopes and deuteranopes. Ordinates, wave-lengths; abscissae, scale readings of dipartite filter position; 0 = blue; 25 = red.

When a normal subject matches the various wave-bands with mixtures of red and blue the results can be plotted as in Fig. 3. For each particular match there is a definite and often considerable range over which the match holds provided

that the subject is allowed to alter the intensity of the field to be matched. This range is least in the yellow region of the spectrum but progressively increases towards the spectral extremes. The width and the exact pattern of the area on the diagram which records the limits within which the match holds, vary somewhat from individual to individual but for normal subjects they are roughly the same (Fig. 3, subjects 1–3).

When some degree of colour anomaly is present, the pattern changes and probably assumes characteristic shapes according to the type of anomaly, though this has not, in fact, been tested systematically. With protanopes and deuteranopes, however, as these are determined by the Ishihara test or by their ability to match red and green on a 2° field, the pattern changes to a simple black rectangle because such subjects can match any colour with either red or blue or with any mixture of the two provided that central fixation is maintained and that they vary the intensity of the field to be matched.

In other words, protanopes and deuteranopes are completely colour-blind when their vision is confined to the central fovea. In this region they behave as monochromats and require only one primary colour, to match all other colours and also white.

Some subjects can match all the spectral colours between red and blue-green with red but they detect a difference between these colours and blue and, similarly, there have been found several subjects who can match red with all colours as far as blue but they detect violet as something different. The reason for this is not yet determined. It may be that the 'blue' receptor which is usually absent from or only very sparse in the central fovea may be present to a greater extent than usual in these subjects. Alternatively, it may be that such subjects have more difficulty than most in maintaining fixation with the requisite accuracy so that the match is therefore frequently 'breaking' because information is obtained from the foveal slopes or parafovea. Under these conditions the subject may not be able to separate the information obtained from the central fovea only, from that obtained from surrounding areas.

With regard to the normal subject and the subjects who have colour anomalies the results are clearly of a preliminary character. With a modification of the apparatus which would allow better control of the separate intensities of red and blue it should be possible to obtain important data on the relationship between intensity and hue discrimination. Since the normal fovea has only two pathways, experimental results obtained from this area alone should give data of a simpler kind than those derived from the usual triple system for the whole eye.

A few subjective observations may be noted. Most of the colour-blind subjects report the fields when matched as having lost all colour; others describe them as grey-blue; and in one case, which happened to be that of a deuteranope, who would, in earlier days, have been described as green-blind, all the spectral colours when matched on the central fovea were described as appearing green.

SUMMARY

1. A simple method is described for matching spectral colours, obtained by filters, with mixtures of red and blue, on small fields and with central fixation.

2. Provided that central fixation is maintained and that the intensities of the fields are properly adjusted, normal subjects show a characteristic range in the amounts of red and blue in the mixtures which match the particular wave-bands; colour-anomalous subjects show significant variations in this range; protanopes and deuteranopes can match all wave-bands with one primary only.

3. It is concluded that while the central fovea of the normal subject is dichromatic, that of protanopes and deuteranopes is monochromatic.

4. This monochromatism of the central fovea of red-green-blind subjects is thought to follow logically from the dichromatic character of the same area in the normal subject and suggests that a simple trichromatic theory is both necessary and sufficient to account for the facts of colour vision. It is unlikely that more than three types of receptor are involved, but it is possible that one or even both of the receptors of a diodic system (i.e. a system having two independent receptors and pathways) might show variations in sensitivity in different parts of the eye in such a way as to be capable of providing the necessary third variable.

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