

PERCEPTION OF COLOUR IN UNILATERAL TRITANOPIA

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SUMMARY

1. The unilateral tritanope described in the previous paper (Alpern, Kitahara & Krantz, 1983) was able to match every narrow-band light presented to his tritanopic eye with lights from a tristimulus colorimeter viewed in the adjacent field by the normal eye.

2. In two regions of the spectrum (called isochromes) physically identical lights appeared identical to the observer's two eyes. One isochrome was close to 'blue' for the normal eye, the other was in the long-wave spectral region seen by the normal eye predominantly as 'red'. Between these isochromes the normal eye required less than spectral purity to match, dropping to near zero purity at 560–570 nm.

3. A mixture of the two isochromes that appeared purple to the normal eye appeared neutral to the tritanopic eye. Hence dichoptic matches grossly violate Grassmann's additivity law.

4. For the normal eye colour naming conformed to typical normal results. For the tritanopic eye the results were coherent with those found by dichoptic matching: the spectrum was divided into two regions by the achromatic neutral band. To the short-wave side, only the colour names 'blue' and 'white' were ever used. To the long-wave side the predominant colour names were 'red' and 'white' with some 'yellow'. Spectral lights appeared neither 'red-blue' nor greenish. Surrounding the test with an annulus either 430 nm, 650 nm, or a mixture of these, fails to induce any greenish appearance, although the achromatic band shifted in the expected directions.

5. It is concluded that there must be exactly three functionally independent, essentially non-linear central codes for colour perception, and that these codes are different from those suggested in existing theories of colour perception.

INTRODUCTION

The previous paper (Alpern *et al.* 1983) gives results of colour matching and colour discrimination for each eye separately of a subject who acquired tritanopia in his left eye while remaining a normal trichromat with his right one. We report here

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experiments in which the colour perceptions from his two eyes were compared, either directly (by dichoptic matching) or through a common standard (by colour naming).

A dichromat fails to distinguish stimuli that, to a normal person, look strikingly different in colour. For example, a tritanope sees as identical a gamut of mixtures of 420 nm and 530 nm lights at constant brightness. Such mixtures vary in appearance from violet through blue and pale blue-green to green for a normal observer. It is natural to ask what colour is perceived by the tritanope for such a gamut: is it one of those perceived by the normal observer, some other colour in the normal repertoire, or something entirely outside normal experience? Such a question is prompted not merely by curiosity: its answer would tell us how the central perceptual mechanisms respond to drastically altered peripheral input, such as the loss of one visual photopigment, and this in turn could provide an important clue to the organization of colour coding in normal as well as abnormal observers.

Unilateral dichromacy offers a particularly favourable opportunity for investigating this question. The unilateral dichromat can attempt to adjust the inputs to his two eyes separately so as to equate the outputs of the central perceptual mechanisms driven by each eye. In the colour perception literature, such data have been relied on heavily for inferences about the central colour mechanisms of both bilateral dichromats and normal observers (von Hippel, 1880; Holmgren, 1881; von Kries, 1919; Dieter, 1927; Judd, 1948; Sloan & Wollach, 1948; Walls & Mathews, 1952; Graham & Hsia, 1958, 1967; Graham, Sperling, Hsia & Coulson, 1961; MacLeod & Lennie, 1976). These inferences depend on the assumed normality of the central colour mechanisms of the unilateral dichromat. This crucial but heretofore implicit assumption will be evaluated in the Discussion.

METHODS

Dichoptic matching

A binocular colorimeter was assembled around a mirror haploscope, with a Badal optical system and a 3 mm (diameter) artificial pupil in the eye's spectacle plane mounted on each arm. The left (tritanopic) eye viewed a $4.2^\circ \times 1.4^\circ$ horizontal rectangle whose dominant wave-length (the independent variable) was changed by placing one of twenty-nine Baird-Atomic 10 nm half-bandwidth (h.w.) interference filters in a beam of parallel light. The haploscope arms were converged to abut the right edge of this field with the left edge of a $1^\circ \times 2.6^\circ$ vertical rectangle seen by the normal eye. The light making up this field comprised a Nutting (1913) colorimeter. The three degrees of freedom in this device were: *i*, the wavelength of monochromatic (2 nm h.w.) light from a double monochromator of Czerny-Turner design with two 1200 grooves/mm diffraction gratings; *ii*, the luminance of this light, varied by adjusting a calibrated neutral wedge in the path of the monochromator beam; and *iii*, the luminance of a desaturating 'white' (4200 K) light (mixed with the monochromatic beam), varied by adjusting a counterbalanced 'neutral' wedge in the 'white' beam. The radiances of all monochromatic lights were obtained *in situ* with a calibrated PIN 10 silicon photodiode (United Detector Technology). The transmission of the monochromator wedge was similarly calibrated. The luminance of the desaturating white light was measured in the usual way with an S.E.I. photometer by allowing the light passing through the artificial pupil to fall on a white standard test plate ($r = 0.82$) at a distance of 10 cm.

The light presented to the dichromatic eye originated from a horizontal tungsten ribbon filament and was attenuated by each one of a set of interference filters. The radiance of monochromatic light entering the eye varied from one run to the next. In the experiment yielding the results in Fig. 1 it had the smallest value ($9.13 \log \text{ photons sec}^{-1} \text{ deg}^{-2}$) at 400 nm and the largest value ($10.16 \log \text{ photons sec}^{-1} \text{ deg}^{-2}$) at 700 nm; between 410 nm and 530 nm the radiance values were more or less

constant ($\pm 0.1 \log_{10}$ unit) at around $9.38 \log \text{ photons sec}^{-1} \text{ deg}^{-2}$, except at 450 nm ($9.56 \log \text{ photons sec}^{-1} \text{ deg}^{-2}$). For wave-lengths longer than 530 nm log radiance increased approximately linearly with increasing test wave-length at a rate of $0.0036 \log_{10}$ units per nm.

Colour naming

The field consisted of a circular monochromatic (2 nm h.w.) disk 1° in diameter surrounded by a 3° (outside diameter) annulus of the monocular colorimeter (Alpern *et al.* 1983). The surround was the 'white' light of the xenon arc (about 5200 K) attenuated by inconel 'neutral' filters and wedges to 1000 trolands for most of the spectrum. A heterochromatic match between surround and centre was achieved by adjusting the intensity of the centre for all monochromatic lights of $\lambda \geq 450$ nm. For $\lambda \leq 440$ nm constraints on the intensity of the light emerging from the monochromator required the latter to be set at its full intensity and the luminance of the surround reduced accordingly to achieve the heterochromatic brightness match. At the short-wave spectral extreme this was 100 trolands, with intermediate levels in the wave-length region between.

For each spectral wave-band tested, the subject first made a left-eye brightness match between the monochromatic centre and the 'white' surround, then adapted to the surround alone, and finally reported left-eye colour names, viewing the entire pattern (surround plus centre). This process was then repeated for the (normal) right eye, before moving on to another wave-length.

Brightness matches were made by adjustment, with the surround field steady and the centre field exposed repeatedly for 2 sec, with an inter-stimulus interval of 6 sec. After completing the brightness match the subject adapted for at least 20 sec to the surround, and then began naming colours, with the central field again exposed one or more times for 2 sec, with 6 sec between exposures.

The colour-naming method was as follows. First the subject selected one or more names from the following five: 'red', 'yellow', 'green', 'blue', 'white'. After his initial choice, he was asked explicitly whether or not 'traces' of the omitted qualities were present. Finally, he divided ten total points among the selected qualities, with 'trace' not counting in the total. For example, a response might be: "'red', 5; 'white', 5; trace of 'yellow'"; or again, "'red', 5; 'white', 4; 'yellow' 1"; or again, "'red', 5; 'white', 5". (In this last case we scored 'yellow' as 0, as well as 'green', 0 and 'blue', 0.)

In this fashion, the spectrum was covered in a haphazard order, in 10 nm intervals from 410 nm to 630 nm, plus 650 nm and 670 nm, for both eyes, in a single session. Two repetitions a week apart yielded essentially identical results.

RESULTS

Dichoptic matching

Three general findings from dichoptic matching justify comments before the details are examined:

First, a match of this kind was feasible for each wave-band, from 400 nm to 700 nm, presented to the left eye. Such a match would likewise be possible for any mixture of wave-lengths presented to this eye (since, by dichromacy and Grassmann's laws, any such mixture is metameric to some single wave-length). Therefore, the entire gamut of colour perceptions attainable through left-eye stimulation corresponds to colour percepts attainable through stimulation of the normal right eye. This fact excludes certain theories of colour coding; for example, straightforward versions of the Young-Helmholtz theory predict that the tritanope, lacking the short-wave receptors, should perceive a green more saturated than any attainable by a normal eye under the same viewing conditions.

Secondly, adjustment of all three variables was usually necessary to attain a match. No previous study of unilateral dichromats has used a three-variable dichoptic match. Yet the use of only two controls is impractical unless the matching right-eye lights fall on a particularly convenient surface in the right-eye tristimulus space, for

example on a plane (which would mean Grassmann's additivity laws held dichoptically). Studies with only two controls may end up with only approximate colour matches unless the controls generate precisely the right surface.

Thirdly, the matching lights, in the trichromatic eye, were predominantly 'red', 'white' and 'blue'. In two spectral regions, around 485 nm and 660 nm, the wave-bands in the left eye were matched by approximately the same light presented to the right eye (i.e. same wave-length, purity and luminance). We call such a light, perceived the same by either eye, an *isochrome*. Mixtures of the blue and the red isochromes presented to the normal eye look purple, but the same mixtures look desaturated, and, in the correct proportion, white, to the dichromatic eye. This shows, among other things, that Grassmann's additivity law is grossly wrong for dichoptic matches, though it holds for monocular matches within either eye. Grassmann's law of scalar multiplication apparently also fails for dichoptic matches, (see below).

In all, three sets of dichoptic colour matches were attempted. The first used only a two-variable colorimeter, omitting a desaturating channel. Approximate matches obtained in this way gave rough agreement, in wave-length of the matching light, with subsequent data. The two later runs used three variables. Because the other run was not done at exactly the same intensity level and because some experience was required in making precise matches, the results of only the final run are shown in Fig. 1. These results differ from those of the first three-variable run only in being more saturated (\log_{10} purity higher by about 0.4, an effect which was not wave-length-dependent).

The colorimeter settings are plotted in Fig. 1 in terms of the dominant wave-length, colorimetric purity, and luminance of the right-eye field (moving respectively from the top to the bottom of the Figure). Dominant wave-length and purity are measured relative to the 4200 K desaturating beam; thus, the former is just the wave-length setting of the double monochromator, the latter is the ratio of the luminance in the monochromatic channel to the sum of the luminances in the monochromatic and the desaturant channels.

In the top graph of Fig. 1 the central point of the wave-band presented to the tritanopic eye is plotted on the lower horizontal line and connected to the matching dominant wave-length for the right eye, plotted on the upper line. (This kind of plot was used by Graham *et al.* 1961.) It is striking that a wide span of left-eye wave-bands, from 400 nm to 550 nm, are all matched close to 485–490 nm in the right eye. In particular, 485 nm itself is an isochrome – matched by the same dominant wave-length (top), at nearly 100% purity (middle graph), and at the same radiance (zero luminance difference, shown in the lower graph).

The middle and bottom graphs of Fig. 1 show that while matching wave-length varied little, the purity and relative luminance of the matching field varied greatly from 400 nm to 550 nm. At both extremes of this range the matching purity was low, indicating that the stimulus presented to the left eye looked very pale. At the short-wave end, the total luminance of the right-eye field needed for a match was considerable, relative to the test luminance in the extreme violet; the opposite was true near 550 nm.

The small variations in matching wave-length shown in the top graph (475–495 nm) are hard to interpret in view of the large variations in the intensity and relative amount of the not-quite-neutral desaturant (4200 K) and in view of some shift in adaptation level from one match to another. Colour-naming data, presented below,

indicate that the predominant colour appearance of wave-lengths in this region for the normal eye is 'blue'; rough determinations of spectral unique 'blue' and 'green' for this eye, around 475 nm and 515 nm, are consistent with later colour-naming data; but the latter reveal that the actual 'blue-green' band is around 495–500 nm under neutral adaptation.

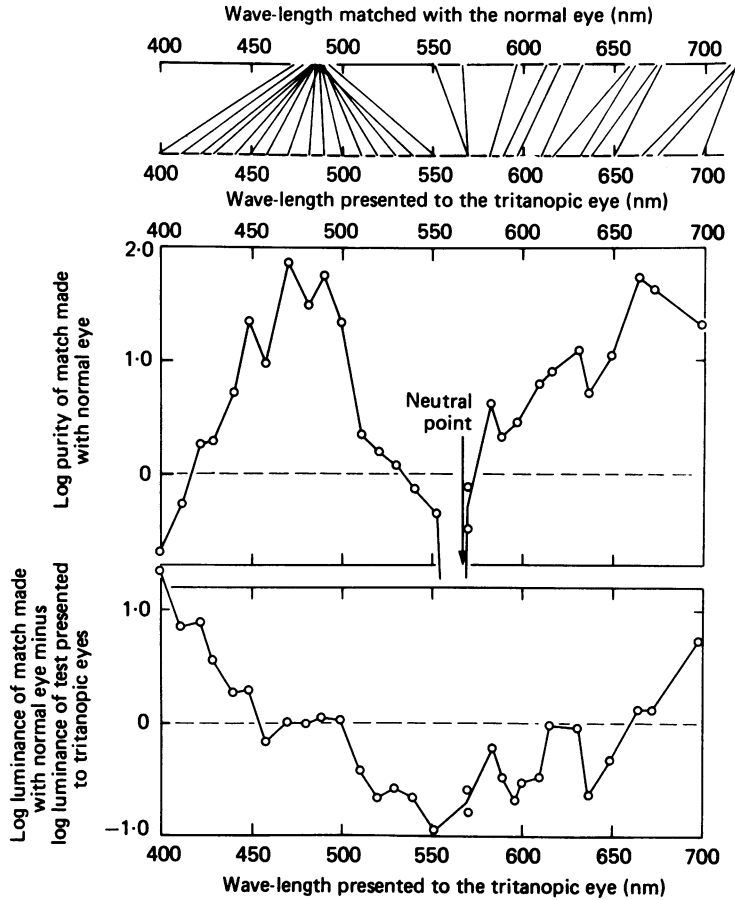


Fig. 1. Results of the final set of dichoptic colour matches. The abscissa scale (for all three graphs) is the peak wave-length of the narrow-band spectral distribution presented to the tritanopic eye with the radiances as described in the text. At the top (also on the abscissa) is the peak wave-length of the distribution with which these respective lights were matched in the trichromatic eye. The middle graph shows the log of percentage colorimetric purity (p_c) of the dichoptic match ($p_c = (100)L_\lambda/L_w$, where L_λ , L_w are the luminances of the respective monochromatic and white lights of the Nutting colorimeter at the match). The bottom Figure shows the ratio $\log [(L_\lambda + L_w)/L']$, in which L' is the test luminance of the monochromatic light presented to the tritanopic eye.

For test wave-lengths near the neutral point of the tritanopic eye, matching purity fell nearly to zero and the match wave-length is indeterminate. Above 580 nm all matching wave-lengths fell in a part of the spectrum perceived as reddish (above the unique 'yellow' point, roughly 590 nm). In view of the variability and poor hue discrimination of this (and every other) normal eye in this part of the spectrum, lights

from 640 nm to 700 nm are once more approximate isochromes. The perceived colour is predominantly 'red', though on some trials slight yellowness is reported as well.

Clearly it would have been desirable to replicate these dichoptic colour matches several more times; unfortunately, the observer was not available for a sufficient period of time to do this.

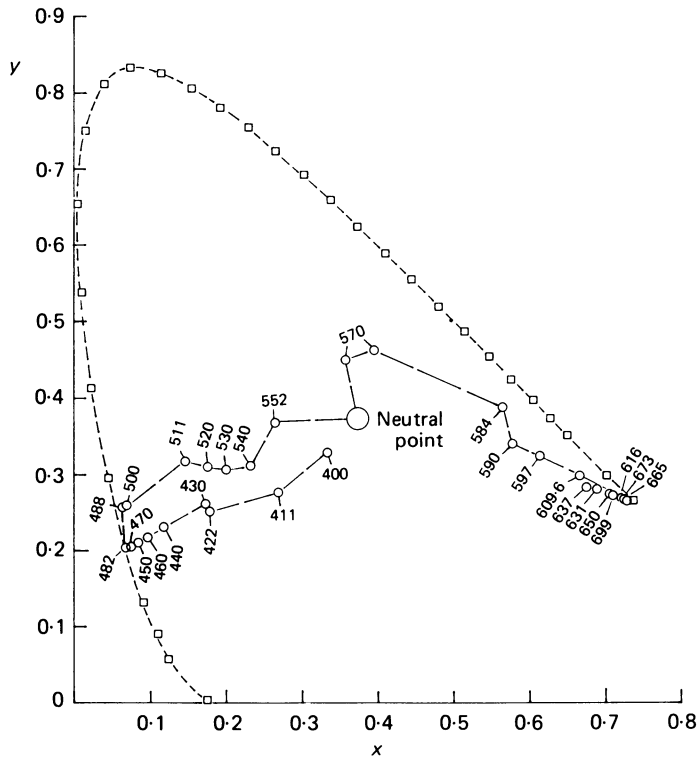


Fig. 2. Re-plot of the dichoptic matches shown in Fig. 1 in the chromaticity co-ordinates of the 1931 C.I.E. standard observer (open circles). Squares show the chromaticities of monochromatic lights at 10 nm intervals in the visible part of the spectrum as matched by the standard observer. The dichoptic matches are with respect to 'white' light of colour temperature 4200 K (large open circle: $x = 0.372$, $y = 0.372$) rather than for an 'equal-energy white' ($x = 0.333$, $y = 0.333$).

The results can be viewed another way by plotting the right-eye matching fields as chromaticity vectors (Fig. 2, open circles, labelled by the left-eye wave-band that was matched). Since a fixed-primary colorimeter was not used, chromaticity must be calculated from spectral colour-matching functions for a normal eye. In the Figure, the C.I.E. standard observer's colour-matching functions were used; the picture is essentially the same if they are replaced by the observer's own right-eye colour-matching functions (Fig. 2 of the preceding paper).

Near the isochromes, the match points fall on the spectrum locus; elsewhere, as is clear from the lower purity in the middle graph of Fig. 1, the results fall on a curve inside the spectrum locus.

If Grassmann's scalar multiplication law held for dichoptic matching, then the right-eye chromaticity would be determined by the left-eye chromaticity, independent of intensity. That this fails is shown by the failure of the short-wave end of the left-eye chromaticity curve to double back on itself around 455 nm. The previous paper showed that left-eye chromaticity is non-monotonic, attaining an extreme value at about 455 nm and doubling back for spectral lights less than the wave-length (Fig. 3 of Alpern *et al.* 1983). For example, 422 nm and 523 nm have the same left-eye chromaticity. Had these two lights been presented in the intensity ratio proper for a metameric match, they would necessarily have been matched by the same right-eye field. As it was, they were presented at about equal radiance in the dichoptic matches, i.e. the 422 nm stimulus was about one-sixteenth as intense as that needed for the tritanopic match to 523 nm. It is clear from the different right-eye chromaticities (interpolating between 520 nm and 530 nm for the latter one) that this intensity factor produces a substantial shift in the dichoptic match.

It must be emphasized, therefore, that the quantitative results in Figs. 1 and 2 are valid only for the radiances used. However, the qualitative features of these results are not very likely to change with overall radiance level, as can be judged from the colour-naming results, described below.

If the Grassmann additivity and scalar multiplication laws were valid dichoptically, then the results in Fig. 2 would fall on a straight line. The clear curvature shown in the Figure is thus further evidence against Grassmann's laws.

The failure of Grassmann's linearity laws shows that the dichoptic matches are not simply matches for the long- and middle-wave cone pigments, nor for any two channels whose responses are a function of a linear combination of cone pigment quantal absorptions (Krantz, 1975).

Colour naming

For both eyes, 'red' and 'green' were used in opponent fashion, as were 'yellow' and 'blue'. That is, if any amount of one of these qualities was reported, even a trace, then no amount of the paired opponent quality was reported, not even a trace. There was no constraint in the method that forced this result, and indeed, care was taken not to suggest in any way that opponent pairs should exist. The subject was always prompted for all five colour names, in the invariable order 'red', 'yellow', 'green', 'blue' and 'white'.

For the tritanopic left eye, 'blue' and 'red' were also used in opponent fashion and 'green' was not used at all. That is, the only response combinations ever used were 'blue' with 'white', or 'red' with 'white', and sometimes with 'yellow' also. To put matters another way, the only two chromatic qualities that occurred together were 'red' and 'yellow'. The subject never reported 'green' and never reported 'purple' or 'violet' ('red' mixed with 'blue').

Quantitative colour-naming results are shown on the three graphs in Fig. 3. The ordinate scales give the average point score for each name for every monochromatic light. The graphs are arranged in a display consistent with the observed opponent pairs. In the upper right graph, large positive numbers indicate strong weight to 'red', large negative numbers to 'green'. In the upper left, positive numbers indicate 'yellow', negative numbers 'blue'. Plotted below (positive numbers only since 'black'

was not an option) is the weight given to 'white' in the responses evoked by these monochromatic lights. The responses evoked when the flashes were presented to the normal trichromatic (i.e. the right) eye are shown by filled circles. These responses are consistent with those found more generally with normal observers (Boynton, Schafer & Neun, 1964; Boynton & Gordon, 1965).

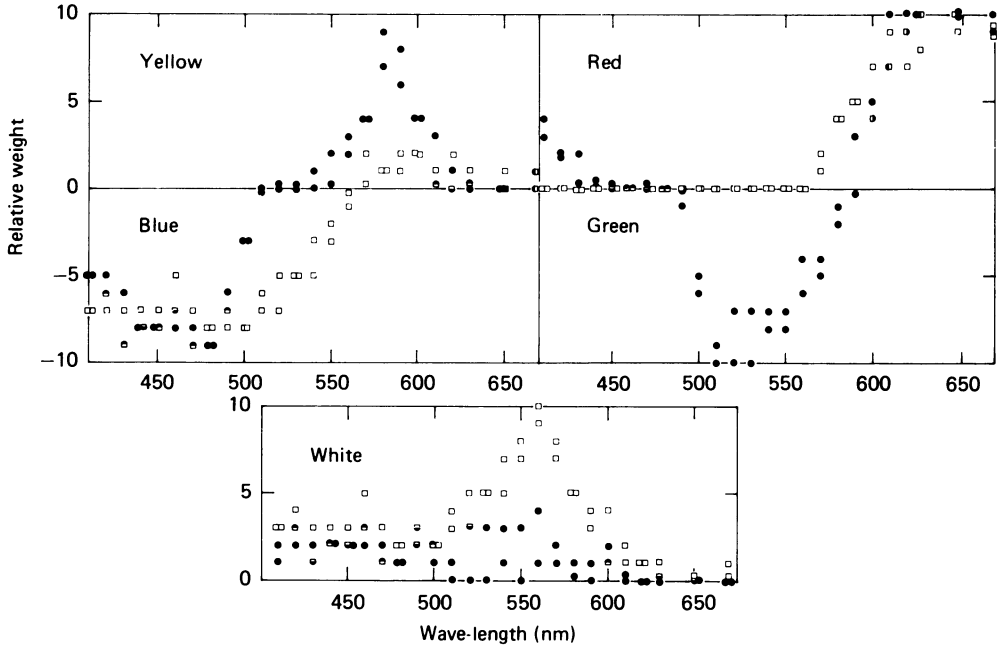


Fig. 3. Results of two repetitions of colour naming with neutral surround, as seen monocularly by the trichromatic (filled circles) and dichromatic (open squares) eyes respectively. The abscissae in each graph give the peak wave-length of the 'monochromatic' spectral distribution, the ordinates the relative weights (as defined in the text) in the 'red'/'green' (upper right), 'yellow'/'blue' (upper left) and 'white' (below) dimensions respectively.

The names obtained with the dichromatic eye are illustrated by the open squares in Fig. 3. These data are consistent with the inferences drawn from dichoptic matching even though the retinal illuminance (in photopic trolands) was very nearly constant in the naming experiment and varied over a range of slightly more than $3.8 \log_{10}$ units in matching. Once more, there is the suggestion that monochromatic lights very near, if not identical to, the short wave-length seen by the normal eye as neither 'red' nor 'green', i.e. unique 'blue', have the same appearance whether seen by the normal or by the tritanopic eye. Furthermore, naming experiments provide even better evidence for the existence of an isochrome in the long-wave end of the spectrum ($\lambda \sim 660$ nm). Monochromatic lights other than at these two isochromes generally appear more or less desaturated when presented to the tritanopic eye than these same lights exciting the normal retina alone.

Other features in tritanopic naming include absence of 'green', greatly reduced weight of 'yellow', and a psychological neutral point: 'yellow/blue' crosses the

horizontal axis at the same locus that 'red' goes to zero, just above 560 nm. This makes 'red' and 'blue' opponent in the same sense as 'yellow' and 'blue'. Most of these features can be identified in the spectral naming functions of the unilateral tritan observer of Ohba & Tanino (1976), though there are differences (notably the presence for their observer of some slightly greenish and slightly reddish blues and a lesser desaturation at wave-lengths other than the isochromes).

An additional tritanopic colour-naming study was performed a few weeks later, using a different apparatus, to examine the effects of simultaneous contrast on perceived colour. The configuration was a 1° central test field with a 0.5° annular surround (1° inner diameter, 1.5° outer diameter). The wave-length of the continuously exposed surround was either 430 nm ('blue') or 650 nm ('red'), at 150 trolands, or a mixture of those two ('pink'). The central 1° field was approximately 150 trolands (matched to the surround) and was exposed for 1.5 sec at a time, with 6 sec or more between stimuli.

With the 'pink' (nearly 'white', to the tritanopic eye) surround, the colour-naming data were very similar to those in Fig. 3, except no 'yellow' responses occurred. The 430 nm surround shifted the neutral point by about 30 nm down to 530 nm, but otherwise the results remained the same: no 'green', very little 'yellow', and the striking crossover between long-wave-length 'red' and short-wave-length 'blue'. Similar results were obtained with the 650 nm surround, except that the neutral point moved up to 570 nm and once more 'yellow' was suppressed completely. No 'green' appeared under any simultaneous contrast conditions. Of course, no 'purple' inducing field could be presented to the tritanopic eye.

DISCUSSION

Previous results

How do a unilateral tritanope's perceptions compare with those in other kinds of tritanopia? In 'transient tritanopia' they are different: a light normally seen as 'blue' is called 'green' (Mollon & Polden, 1977). But at perimetric angles where the sensitivity of short-wave-sensitive cones is depressed (Wooten & Wald, 1973) small flashes of monochromatic light exposed to the normal peripheral retina are named remarkably similarly to those reported by our unilateral tritanope (Gordon & Abramov, 1977).

'Foveolar tritanopia' (Willmer, 1949) falls between these extremes. Threshold ($1.3'$ subtense, 0.7 msec) flashes were named 'blue' and 'green' with a fixed ratio of frequencies independent of wave-length (Krauskopf & Srebro, 1965; Krauskopf, 1978); but 'green' was used about 3 times more frequently (J. Krauskopf, personal communication). Brighter foveolar fixated flashes were named by some normal observers in very nearly the same way as the one employed by the tritanopic eye studied here (Ingling, Scheibner & Boynton, 1970). One who did not (using 'green' and 'blue' discriminatively) became similar to the unilateral tritanope if the flashes were viewed on a bright *blue* background. Some normals match asymmetrically small $1'$ or $2'$ foveal fields similar to the dichoptic matches in Fig. 2 (Middleton & Holmes, 1949).

Even more striking is the similarity between the results for the dichromatic eye

in Fig. 3 and the names employed by a congenital tritanope (Smith, 1973). There are differences, of course, which is not too surprising given that cultural factors are bound to influence how congenital dichromats use colour names. Still, for this congenital tritanope 'Blue replaced green almost completely in the middle spectrum' (Smith, 1975, pp. 211-212). Finally, cerebral infarctions involving the medial and lingual occipitotemporal gyri bilaterally (8 years before testing) caused a defect labelled 'acquired tritanopia' (Birch-Cox, 1976). This patient named colours in a pattern nearly identical to the one followed by the present subject viewing with his tritanopic eye (Pearlman, Birch & Meadows, 1979).

Adaptation or suppression?

In everyday life, a unilateral dichromat views a coloured object binocularly and therefore passes different inputs from the two eyes to his brain. If the conflicting inputs are disturbing, they may be dealt with in two ways: by suppression of one of them, or by adaptation of the central mechanisms so that the two conflicting inputs each produce the same output, i.e. the conflict is abolished. In the literature on perceptual adaptation, striking instances of the second resolution occur (Kohler, 1962; Hochberg, 1971). But in strabismus, suppression is a common resolution (Crone, 1973; Burian & von Noorden, 1974). In the present case of conflicting inputs, resolution by suppression would lead to the assumption that the central mechanisms are substantially normal, and hence would permit inferences from the dichromatic results to the normal mechanisms; resolution by adaptation would greatly complicate such inferences.

One fact that might suggest adaptation was pointed out to us by J. D. Mollen: the short-wave isochrome roughly maximizes the ratio of absorptions of the middle-wave to the long-wave cone pigment. Thus, concurrent (or recent) conflict is minimized where the chromatic signal from the tritanopic eye is greatest. However, there are several lines of evidence suggesting that suppression is the main mechanism of resolution in this case. First, the subject approached us because he noticed differences in the colours perceived by his two eyes for the same object. Secondly, if the subject resolved the conflict such that the normal and abnormal eyes produced the same perceptual outputs, a degree of freedom would have to be lost centrally, and the subject would be dichromatic through both eyes. His excellent sensitivity through the trichromatic eye suggests that little, if any, such adaptation has occurred. Thirdly, there are remarkable similarities in naming between the tritanopic perceptions reported here and those acquired from bilateral cerebral vascular accidents (8 years before testing). Such persistence is the antithesis of adaptation, which regresses in time towards 'normality', and points to the possibility that this behaviour is characteristic of the normal colour code rather than a specific adaptation to minimize discrepancies between (recent or concurrent) signals from 'bad' and 'good' retinas. Finally, in an experiment designed to test directly whether suppression occurs, the subject was asked to fuse a monochromatic 'blue' light (481.9 nm) presented to one eye and monochromatic 'yellow' (590 nm) presented to the other and to match the mixture to a broad-band 'white' viewed in the adjacent field only by the normal eye. Every one of eleven normal subjects achieved this fairly readily, but the unilateral tritanope was unable to do so; instead he perceived only the colour

of whichever light was presented to the normal eye, unless the intensity of the light to the dichromatic eye was increased about a log unit above the average value normals used to match the white. At that point, rivalry occurred; at higher intensities still, the dichromatic eye dominated; but normal fusion was never achieved.

On this basis we tentatively propose that central mechanisms of colour perception are normal in this observer, and ask what can be learned about their organization from the results detailed above.

Theoretical implications

The surprising facts are that although exhaustive attempts to uncover a short-wave cone pigment in this subject's tritanopic eye failed, this eye sees the entire spectrum on the short-wave side of the neutral point as 'blue' (with various degrees of saturation). The field-sensitivity spectrum (allowing for prereceptor colour differences in the two eyes) of $\Pi_4(\mu)$ is normal in his dichromatic eye; but he sees no 'green' anywhere in the spectrum with this eye!

Traditional colour theories do not easily deal with this enigma: in standard Young-Helmholtz interpretation (von Helmholtz, 1896) a tritanope missing short-wave cones is expected to see the spectrum as 'red', 'green' and 'yellow' and their combinations; neither 'blue' nor 'white' should be seen. In the modern view of the Hering theory (Hurvich & Jameson, 1955), tritanopia is regarded as a loss of the 'yellow-blue' sense; 'white', 'red' and 'green' should appear as for the normal eye, while the mixture of 'red' and 'green' would be achromatic. But, in fact, this tritanope sees the spectrum largely as 'red', 'white', and 'blue' with only a very small amount of 'yellow' and no 'green'.

Deleting the photopigment input that primarily drives the central mechanism for blueness does not thereby delete the perception of blueness; hence, this central mechanism must instead receive inputs mediated by other photopigments. At the same time, this change must result in the loss of perceived greenness: in the Appendix we outline a general mathematical framework in which this notion is expressed more precisely and discuss attempts to fill in details.

Another conclusion about normal organization derives from the very fact that dichoptic matches are possible. There must be a limitation to only three degrees of freedom at the level of central mechanisms, not merely at the level of photopigments. For if there were n functionally independent central mechanisms a dichoptic match would be an attempt to solve n equations in three unknowns, whence $n \leq 3$ (see Appendix).

Finally, it is noteworthy that the failures of Grassmann's laws in dichoptic matching point to essential non-linearities in the central mechanisms of colour perception.

APPENDIX

A theory of colour coding must specify the relationship between the outputs of the central neural mechanisms that correspond to the perception of colour (Stiles, 1967) and the receptor inputs and other parameters of visual stimulation. Let α , β , γ respectively denote the outputs (assumed monotonic with photon absorbance) of the

short-wave, middle-wave and long-wave cones of the normal central retina, and let y_1, \dots, y_n represent the outputs of n functionally independent central mechanisms that correspond to the perception of colour. Let Ω denote the parameter vector that specifies all the various conditions that modify the relationship between the y values and α, β, γ , including spatial and temporal configuration of stimulus presentation, preadapting light, contrast stimuli. The general input-output relation, which must be specified in a colour theory, consists of n functions f_1, \dots, f_n :

$$\left. \begin{aligned} y_1 &= f_1(\alpha, \beta, \gamma, \Omega) \\ &\vdots \\ y_n &= f_n(\alpha, \beta, \gamma, \Omega). \end{aligned} \right\} \quad (1)$$

Specific examples of such functions f_1, \dots, f_n are found in various quantitative developments of colour theory (e.g. Jameson & Hurvich, 1959).

The functional independence of f_1, \dots, f_n means that the value of y_n cannot be predicted from the values of y_1, \dots, y_{n-1} . (More precisely, the range of y_1, \dots, y_n is topologically n -dimensional) The fact that input is limited to α, β, γ does not entail that $n \leq 3$. For example, there is no necessary upper limit to the number of functionally independent y_i that can be defined by linear equations of the form $y_i = \Omega_{i1}\alpha + \Omega_{i2}\beta + \Omega_{i3}\gamma$, where the coefficients Ω_{ij} depend on the parameter vector Ω in a different way for each i . Nonetheless, most colour theorists, including Stiles (1967) and Jameson & Hurvich (1959), have assumed that $n = 3$. This assumption has been justified heretofore in two ways: on subjective grounds (colours vary independently only in hue, saturation and brightness) or on the grounds that asymmetric (cross- Ω) trichromatic matches are possible (Stiles, 1967). The data from dichoptic matching in unilateral colour blindness, as shown below, provide yet another argument that $n = 3$.

The results in the previous paper (Alpern *et al.* 1983) suggest that in the modified input-output relationship of the tritanope, the short-wave-sensitive input, α , is lost. But what does this mean in terms of eqn. (1)? It is meaningless, mathematically, to 'delete' α from a function which depends on α : the variable α must be replaced by something, e.g. by a constant such as 0 or 1 or, more generally, by a function $\alpha = T(\beta, \gamma, \Omega)$. One way simply to 'delete' α would be to assume that only certain of the outputs y_i have an actual dependency on α , and that those outputs are gone entirely in the tritanope. This, indeed, is the underlying assumption of the Young-Helmholtz approach and is also seen in the Hering approach in the assumption that the yellowness-blueness mechanism (one of the y values) is missing in tritanopia. But the present results suggest that this approach to deletion is utterly wrong: those central mechanisms which, in the normal observer, correspond to blueness (and, we assume, have heavy dependence on α), are most active indeed in the tritanope. We, therefore, assume that α is replaced in eqn. (1) by a constant or a non-constant function of β, γ and Ω :

$$\alpha = T(\beta, \gamma, \Omega). \quad (2)$$

This leads to the modification of eqn. (1): for $i = 1, \dots, n$,

$$y_i = f_{iT}(\beta, \gamma, \Omega) = f_i[T(\beta, \gamma, \Omega), \beta, \gamma, \Omega]. \quad (1_T)$$

In binocular viewing for a unilateral tritanope, the inputs α, β, γ from one eye and

β, γ from the other lead to conflicting values for y_i , via f_i (eqn. 1) and f_{iT} (eqn. 1_T); and the latter is suppressed, as we have argued in the Discussion. But in dichoptic viewing, each portion of the visual field receives input from only one eye, and there is no conflict. For any specified values of β, γ in the tritanopic eye, corresponding values α', β', γ' of the normal inputs can be found, such that a dichoptic match is made: for $i = 1, \dots, n$

$$f_i(\alpha', \beta', \gamma', \Omega) = f_{iT}(\beta, \gamma, \Omega). \quad (3)$$

The facts of dichoptic matching have two important consequences. First, $n = 3$; i.e. *there are exactly three functionally independent y_i values at the central level at which dichoptic matches are determined.* For if $n \geq 4$, eqn. (3) would require the solution of four or more equations in only three variables, α', β', γ' ; and, of course, $n \leq 2$ is impossible by trichromacy of normal vision. (A similar line of argument, for asymmetric colour matching, is implicit in Stiles, 1967.) Secondly, *the f_i values must be non-linear* in such a way as to produce a violation of Grassmann's laws for dichoptic matching.

To go further, one must suggest specific forms for eqns. (1) and (2) consistent with the known facts about normal colour perception and with the results of the present study. We have not succeeded in this task. The approach was to assume that y_1, y_2, y_3 correspond respectively to perceived redness/greenness, perceived yellowness/blueness, and perceived whiteness, and to specify non-linear colour-opponent forms for f_1, f_2 and f_3 that would both: (i) violate Grassmann's additivity law in eqn. (3) (the functions suggested by Jameson & Hurvich (1959), though non-linear, predict that additivity would hold) and (ii) be consistent with other linear and non-linear findings in colour perception (Purdy, 1931; Indow & Stevens, 1966; Larimer, Krantz & Cicerone, 1974, 1975; Moeller, 1976). For eqn. (2) we assumed a linear form, $\alpha = r\beta + s\gamma$, independent of Ω . Important constraints included the fact that the tritanopic redness/greenness function, f_{1T} , could be positive but never negative (no perceived green), and that f_{2T} must cross zero at the same spectral locus where f_{1T} reaches zero (see Fig. 3). But no functions fitting all these constraints have yet been found.

These difficulties are not easily circumvented by dropping the opponent-colours approach to central mechanisms. A Young-Helmholtz alternative, in which the output of each mechanism is a function of only a single cone absorption function, leads to the equations (replacing eqn. 3)

$$f_1(\alpha', \Omega) = f_1 [T(\beta, \gamma, \Omega), \Omega],$$

$$f_2(\beta', \Omega) = f_2 [\beta, \Omega],$$

$$f_3(\gamma', \Omega) = f_3 [\gamma, \Omega].$$

These have the solution

$$\gamma' = \gamma,$$

$$\beta' = \beta,$$

$$\alpha' = T(\beta, \gamma, \Omega).$$

If T has the form $r\beta + s\gamma$, then Grassmann's linearity laws are predicted to hold for

dichoptic matching, regardless of the non-linearities in the functions f_1, f_2, f_3 . So no such theory will do. A non-linear and/or Ω -dependent substitution T might be pursued within a Young-Helmholtz or an opponent-colour theory, but neither the data nor knowledge of physiology suggest an appropriate choice.

It is possible that the tritanopic vision of this observer is changed from the normal in more than one way; for example, α could enter each of the normal functions f_i in several ways (additively, multiplicatively, etc.) and each such occurrence could involve a different substitution of form (2). Because of the similarity to congenital tritanopia we are reluctant to accept such a complication and, in any case, to do so would open such a wide range of possibilities that it seems hopeless to narrow them down again with the constraints presently available. The present data resist a full explanation. They serve to place strong constraints on, and provide a challenge to, the formulation of theories of colour perception.

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