Evidence for the existence of colour mechanisms producing unique hues as derived from a colour illusion based on spatio-chromatic interactions

Alexander D. Logvinenko a,*, Sara J. Hutchinson b

a Department of Vision Sciences, Glasgow Caledonian University, Glasgow G4 0BA, UK
b School of Psychology, Queen’s University, Belfast BT7 1NN, UK

Received 22 October 2004; received in revised form 13 October 2006

Abstract

When its spatial frequency is high enough, a grid of grey horizontal strips presented on a coloured background may change its neutral colour. It was found that some background colours induce a strong illusion and some no illusion at all. The effect of the background colour on the illusion was studied for the spatial frequencies of 0.5, 2.5, 4, and 8 c/deg. Thirty chromaticities (evenly distributed across the colour gamut triangle) of the backgrounds in the equiluminant plane, and 24 in the ML plane (where S-contrast was zero), were tested. Five matches were made for each frequency and each background chromaticity. Viewing was binocular. For the low (0.5 c/deg) frequency strips, the backgrounds were found to induce the colour, if any, approximately complimentary to that of the background (i.e., chromatic simultaneous contrast). For the high (8 c/deg) frequency, most backgrounds induced only illusory colours close to unique hues (yellow, blue, and green), with a few backgrounds inducing a mixture of green with blue. Then, the method of adjustment was used to determine the unique hues for the same three observers. A remarkable similarity was found between unique hues and illusory loci, suggesting that the illusion is due to a difference in the spatial resolution of the post-receptor channels producing the unique hues.

Keywords: Colour vision; Colour illusion; High-spatial-frequency tritanopia; Unique hue; Colour channel

1. Introduction

Human colour vision implies the combination of the outputs from three types of photoreceptors (cones), with peak sensitivities in the short-, medium-, and long-wavelengt (S-, M-, and L-, respectively) regions of the visual spectrum (e.g., Kaiser & Boynton, 1996; Packer & Williams, 2003; Wyszecki & Stiles, 1982). Since S-, M- and L-cone mosaics interleave each other on the retina, such combining of the outputs of the adjacent cones of different types implies, in turn, a sort of spatial integration on the retina (Williams & Roorda, 1999). Therefore, some spatio-chromatic interaction lies at the heart of colour vision, being its essential feature.

One important consequence of this is that if the size of a light spot is so small that it stimulates just a single cone, the spot either appears hueless, or its hue is uncertain, that is, it invokes various hues at different presentations (Hofer, Singer, & Williams, 2005). In order to use their trichromatic vision, trichromats should be presented with objects that are big enough to stimulate all three cone types. Therefore, the same light spot might look different depending on its size. There is abundant evidence for the effect of the size and other spatial dimensions (e.g., spatial frequency) of an object on its colour. In particular, when one reduces the size of an object to less than 25' but keeps it well above the level of visual acuity, a change in colour appearance may occur (König, 1894; Willmer, 1944). This phenome-
non was called tritanopia of the central foveola (Mollon, 1982; Williams, MacLeod, & Hayhoe, 1981) as the test stimuli were projected onto the central foveola where there are no S-cones (Curio et al., 1991). Interestingly, a similar change in colour appearance (so-called small-field tritanopia) can still be observed providing the stimulus size is small enough, even when the stimulus is projected onto an area of the retina outside the central foveola, where S-cones are available (Hartridge, 1945; Mollon, 1982). Small-field tritanopia is usually accounted for by the poor spatial resolution of the S-cone channel (Brainard & Williams, 1993).

More recently, varying the spatial frequency content of stimuli (square wave gratings), Wandell and collaborators found that the stimuli changed their colour appearance with spatial frequency (Bauml & Wandell, 1996; Poirson & Wandell, 1993). They argued that this direct evidence of the effect of spatial dimensions on colour appearance emerged from the difference in the spatial frequency characteristics of the post-receptor mechanisms, the spectral characteristics of which were found to be close to the yellow–blue (YB) and red–green (RG) opponent mechanisms as suggested by Jameson and Hurvich (1955).

The effect of the spatial frequency content of a pattern on its colour can also be observed in Fig. 1. As the spatial frequency of the grid of physically neutral strips increases (this can be achieved by either receding the page or tilting it), the strips become tinged blue, yellow or green depending on the background colour.

This colour illusion is different to tritanopia of the central foveola since it does not need a gaze fixation and can be experienced throughout the retina except the extreme periphery (Logvinenko, 2001). The illusion is also different to small-field tritanopia as it is observed with quite large patterns. In fact, it is the spatial frequency, rather than the angular size of the pattern that is involved in this type of spatio-chromatic interaction. The illusion was called high-spatial-frequency tritanopia, since, first, the illusory colours were found to be close to those experienced in small-field tritanopia, and second, it could be observed only when the spatial frequency of the background strips was rather high (Logvinenko, 2001).

While there is every indication that the illusion results from the spatial frequency attenuation (filtering-out) of the output of some colour mechanisms (Logvinenko, 2001), it is not clear whether this happens at the level of the receptor or post-receptor mechanisms. It was found recently that patterns as in Fig. 1 with the same S-cone contrast between the strips and the background (i.e., differing only in luminance) could produce different strengths of the illusion (Logvinenko & Hutchinson, 2005, 2006). This implies the post-receptor site of the illusion in accord with the finding by Wandell and collaborators (Bauml & Wandell, 1996; Poirson & Wandell, 1993). Still, studying the same colour illusion, Monnier and Shevell (2003, 2004) suggested that it can be accounted for by spatio-chromatic interactions within the S-cone mechanism.

In the first experiment, we test the receptor and post-receptor accounts, providing further evidence for the post-receptor explanation of the illusion.

2. Experiment 1 the effect of the background’s chromaticity on illusory colours

Assume that the strips in Fig. 1 became tinged at high spatial frequencies because the response of some chromatic mechanism to the strips and the background is attenuated due to the poor spatial resolution of this mechanism as compared to the other chromatic mechanisms, as previously suggested (Logvinenko, 2001; Logvinenko & Hutchinson, 2005, 2006). For example, if the yellow–blue (YB) mechanism has narrower spatial frequency characteristics than the red–green (RG) and luminance mechanisms (e.g., Cavonius & Estevez, 1975; Green, 1968; Hess, Mullen, & Zrenner, 1989; Kelly, 1974), then the colour of the strips will be contaminated by a dc response of this mechanism at spatial frequencies above its spatial resolution. In other words, illusory blue (or yellow) will be the result of the “leakage” of the background’s blue (respectively, yellow) component into the strips because of the poor spatial resolution of the YB-mechanism. Therefore, observing the illusory colours one can ascertain, at the first approximation, what chromatic mechanism “leaks”. If it is the YB-mechanism then the illusion colours should be tritan colours. If it is the YB-mechanism then these should be yellow and blue colours which this mechanism supposedly “secretes”. Another possibility is that the YB- and RG-mechanisms have nearly the same spatial resolution which is nevertheless lower than that of the luminance mechanism (e.g., McKeefry, Murray, & Kulikowski, 2001; Sekiguchi, Williams, & Brainard, 1993). In this case the prediction will be a shift of the strips’ chromaticity toward the background’s chromaticity, that is, a sort of chromatic assimilation, as Shevell and collaborators suggested (Cao, Pokorny, & Smith, 2005; Hong & Shevell, 2004; Shevell & Cao, 2006).

Fig. 1. The high-spatial-frequency tritanopia effect. As viewing distance increases, the neutral horizontal strips become coloured. Neutral strips on the pink, green, and yellow background become blue, yellow, and green, respectively.

1 It must be mentioned, however, that Xian and Shevell (2004) recently showed that the degree of assimilation in similar spatio-chromatic patterns was affected by perceptual grouping. It implies that the illusion they studied might have been more complicated than high-spatial-frequency tritanopia.
Therefore, knowing how the illusory colours depend on the background colour could, in principle, allow one to distinguish between these hypotheses. However, in the previous studies only specific background colours (which induced the maximum illusion) were used (Logvinenko, 2001; Logvinenko & Hutchinson, 2006; Monnier & Shevell, 2003, 2004). So, we have undertaken the following experiment to study the influence of the background’s chromaticity on illusory colours for patterns depicted in Fig. 1.

2.1. Method

An asymmetric colour-matching technique was used to measure illusory colours. Three female observers (DR, TL, and SH) participated in this experiment. Observer SH wore her corrective eyewear throughout experiments. In contrast with the two other observers, SH (an author) was aware of the purpose of the experiment. She had a history of participating in experiments on this illusion. Observer DR was well experienced in psychophysical experiments but not in this illusion. Observer TL was completely unexperienced.

2.1.1. Apparatus and stimuli

Stimuli were created by a PC equipped with a video card (VSG 2/5) and displayed on a Sony colour monitor calibrated using an Oriel spectroradiometer. Luminance calibration and gamma correction were done separately for each of the three colours guns of the monitors using the standard software from Cambridge Research Systems. Also the spectral distribution of the light emitted by each colour gun under its maximum luminance was measured with the spectroradiometer. Then, using the CIE 1931 colour matching functions amended by Judd (Wyszecki & Stiles, 1982, p. 331, Table 1 (5.5.2)), the CIE chromaticity coordinates and luminance of each colour gun were derived from the measured spectral distributions. The averages of five consecutive measurements are shown in Table 1.

After these chromaticity coordinates were entered into VSG software, we measured the chromaticity coordinates and luminance for the stimulus patterns used in the experiments. While the set-up chromaticity coordinates (i.e., which were entered via the keyboard of the PC into which the VSG was installed) and luminance for the patterns and the actual coordinates as measured by a spectroradiometer were in good correspondence, we adjusted the set-up chromaticity coordinates for each stimulus pattern employed in the experiment so as to achieve desirable actual coordinates. To make sure that the actual coordinates did not deviate essentially from the set-up coordinates over time, we repeated these measurements on a monthly basis.

The monitor was viewed by observers sitting at a distance of 4 m. On the monitor, a matching bar was presented underneath the pattern which was used by the observers to match the perceived colour of the test grid. A keyboard allowed observers to change the hue, saturation and intensity of the colour of the matching bar.

Neutral \((x = 0.314, y = 0.331)\), horizontal, equally spaced test strips, were presented on coloured backgrounds. Spacing of the strips was varied at four levels. Specifically, the vertical distance between the strips was 9, 18, 28 and 110 mm, that made the spatial frequency of the test grid 8, 4, 2.5 and 0.5 c/deg, respectively. The width of the strips was a quarter of the distance between them. The dimensions of the stimulus layout were as follows: the whole display was 5.5° by 4.3°, the 8 and 4 c/deg gratings were 5.2° by 3.2°, the 2.5 c/deg grating was 5.2° by 3.0°, the 0.5 c/deg pattern was 5.2° by 2.1°, the matching bar was 5.3° by 0.4°. The matching bar and pattern were both surrounded by a neutral \((x = 0.314, y = 0.331)\) background, the luminance of which was set equal to the luminance of the test grid (25.0 cd/m²).

Distributed across the colour gamut border of a Sony monitor, 30 chromaticities in the equiluminant plane and 24 chromaticities of the backgrounds in the \(ML\) plane were tested. The cone coordinates were evaluated in terms of the normalised Smith and Pokorny fundamentals (Smith & Pokorny, 1975; Wyszecki & Stiles, 1982, p. 615, equation 35 (8.2.5)). The background chromaticities were chosen so that the background colours were more or less evenly distributed, when presented in the CIE 1931 chromaticity diagram.

2.1.2. Procedure

In a single trial, one pattern was presented on the monitor screen, and the observer was asked to adjust the colour of the matching bar so that its colour matched the colour of the test grid. The start-up colour of the matching bar was randomly shifted by a small vector from the neutral position. In each trial, the observer controlled the colour of the matching bar via three pairs of keys on a keyboard. One pair of keys allowed the observer to alter the colour of the matching bar so that the point in the CIE 1931 chromaticity diagram, corresponding to this colour, moved towards (or from) the neutral point, thus changing the saturation of the matching bar’s colour. Another pair of keys allowed a point in the CIE 1931 chromaticity diagram, corresponding to the matching bar’s colour, to move in a circle around the neutral point, controlling the hue of the matching bar. The third pair of keys changed the intensity of light from the matching bar.

After the observer had made a match, a button on the keyboard was pressed to save it and the trial was over. The next trial appeared immediately after the trial was
saved. There were no timing restrictions, with the observer taking as much time as necessary to make a close match. At any time, the observer could alternate between the pattern and a blank screen by pressing a button.

2.1.3. Design

The experiment consisted of eight sub-experiments (two planes at four spatial frequencies). In one sub-experiment, stimuli of the same spatial frequency were presented in the same (either ML or equiluminant) plane. The sub-experiments were completed in random order. In each sub-experiment, each pattern was presented three times. In the sub-experiments that explored the ML plane, there were 72 trials in each. The random sequence of these 72 trials were divided into nine sessions (eight trials each). In the sub-experiments that explored the equiluminant plane, there were 90 trials in each. The random sequence of these 90 trials were also divided into nine sessions (10 trials each). One session was completed per day and each session lasted approximately 30 min.

2.2. Results

The mean matches for each observer are plotted in the MacLeod–Boynton chromaticity diagram (Figs. 2–9). (See also Figs. 10–15 where most of these data are presented on a larger scale.) As would be expected, at 0.5 c/deg there was no high-spatial-frequency tritanopia effect. More specifically, observers DR and TL did not exhibit any effect at all at this frequency. MANOVA showed that chromaticity of their matches at 0.5 c/deg did not significantly differ from that of the neutral point (p > .01). The patterns of matches by observer SH at 0.5 c/deg (Figs. 5 and 9) are, by and large, consistent with classical simultaneous chromatic contrast (i.e., each background induced a shift of chromaticity in a direction approximately opposite to its own).

Let us consider first the data obtained in the equiluminant plane. The high-spatial-frequency tritanopia effect was found to be strongest at 8 c/deg for all observers (Figs. 2 and 6). Notably, the whole variety of illusory colours produced by different backgrounds falls into three rather narrow bands of hues, verbally categorised as yellow, blue and green. The position of the illusory colours in the chromaticity diagram bears a resemblance to the unique hues loci (Burns, Elsner, Pokorny, & Smith, 1984; Webster, Miyahara, Malkoc, & Raker, 2000; Wuerger, Atkinson, & Simon, 2005). As with unique yellow, the illusory yellow loci form is fairly straight with the dominant wavelength falling within the range of unique yellow hues (570–580 nm). The illusory blue loci shape is curved in a manner similar to the unique blue loci, the dominant wavelengths being within the range of the unique blue hues (460–470 nm). As with the unique yellow and blue, the illusory yellow and blue are not collinear. Although the illusory green range is quite broad, the dominant wavelengths fall...
For 4 c/deg, illusory green practically disappears for observers DR and TL (Fig. 3). The range of yellows becomes shorter than at 8 c/deg but the range of blues is approximately the same. At 2.5 c/deg, the range of both illusory yellows and blues for these two observers become even more compressed than at 4 c/deg (Fig. 4).
of the illusory yellow and blue colours decreases when spatial frequency decreases, their dominant wavelength remaining approximately the same.

It should be noted that the results for observer SH are somewhat different from those for DR and TL. Specifically, at 8 c/deg (Fig. 2), the illusory blues for this observer do not join into the neutral point on the chromaticity diagram. While lilac backgrounds produce unique blue, pinkish backgrounds produce slightly greenish-blue. One inference is that this green component in the illusory colours from pinkish backgrounds is due to chromatic induction from the reddish component of the background.2 At 4 c/deg (Fig. 3), the range of yellow illusory colours is more compressed and shifted towards red. This red shift might be induced by the greenish backgrounds which produced the yellow illusory colours. Likewise, the blue illusory colours at 4 c/deg are less saturated and tinged with more green than at 8 c/deg.

At 2.5 c/deg (Fig. 4) the apparent colours observed by SH contained almost no illusory yellow and blue, with the same induced green and red, observed at 4 c/deg, dominating throughout. In contrast with the DR and TL data for 2.5 c/deg, the cluster of matches obtained from SH for this frequency is more consistent with the notion of simultaneous chromatic contrast rather than high-spatial-frequency tritanopia.

It seems as if the illusion experienced by SH is determined by two different mechanisms, namely, high-spatial-

---

2 Alternatively, this may be a result of chromatic adaptation. However, as shown elsewhere the illusory effect for a homogeneous background (as in the present experiment) did not differ significantly from that obtained for a two colour square wave grating such that its colours were nearly complementary in terms of the S-component (Logvinenko & Hutchinson, 2006). If the illusion were (even partly) a result of chromatic adaptation then it should have reduced for the two colour square wave grating. But it was not the case.
frequency tritanopia and simultaneous chromatic contrast. With spatial frequency, the high-spatial-frequency tritanopia effect gets stronger, and the simultaneous chromatic contrast effect weaker. Therefore, at the high spatial frequency (8 c/deg) the illusory loci are mainly determined by the high-spatial-frequency tritanopia effect whereas at the low spatial frequency (0.5 c/deg) by the simultaneous chromatic contrast effect. Since observers DR and TL did
not experience the simultaneous chromatic contrast effect, their results give an opportunity to observe the high-spatial-frequency tritanopia effect as such (i.e., not contaminated by the simultaneous chromatic contrast effect).

Note that there are some background colours (marked with the black circles in Figs. 2–4) against which high-spatial-frequency tritanopia is not observed. Specifically, MANOVA showed that for each observer their matches made against these backgrounds did not significantly differ from the neutral point ($p > .01$). We will refer to these colours as a no-illusion background set. Curiously enough, the dominant wavelengths of these background colours fall into the short wavelength end of the spectrum. While the $S$-component for these colours is rather strong, they do not invoke any illusory colours—the fact which is hard to account for by any theory based on poor spatial resolution of the $S$-cone mechanism per se. This also shows that the role of chromatic aberration in the illusion is rather small, if any.\footnote{Moreover, since the impairing effect from longitudinal chromatic aberration might be compensated by monochromatic wave aberrations, the $S$-cone spatial image quality can be of much better quality than was previously thought (McLellan, Marcos, Prieto, & Burns, 2002).}

Indeed, it is for these backgrounds that the chromatic aberration effect would be expected to be highest because the major contribution into producing them is made by the blue colour gun the spectral power distribution of which is mainly located in the short wavelength part of the spectrum.

Generally, a similar pattern of results was obtained for the background colours lying in the $ML$ plane (Figs. 6–8). While the range of the matches to the test grid of 8 c/deg was compressed as compared to that observed in the equiluminant plane at 8 c/deg, the same illusory colours were observed (Fig. 6). Though, for observer DR, the stretch of blue colours is slightly shifted towards green. However, this green shift disappears at 4 c/deg for observer DR (Fig. 7), where only illusory yellow and illusory blue
were observed. At 2.5 c/deg (Fig. 8), this observer exhibited the same illusory yellow and blue only within a smaller range. As mentioned above, there was no significant effect whatsoever for DR and TL at 0.5 c/deg.

While the clusters of matches obtained for observer SH at 4 (Fig. 7) and 2.5 c/deg (Fig. 8) are more complicated than those for observers DR and TL, we believe this is because simultaneous chromatic contrast becomes more

Fig. 11. An enlarged version of Fig. 3 with averaged unique hue settings (black lines).

Fig. 12. An enlarged version of Fig. 4 with averaged unique hue settings (black lines).
pronounced at these spatial frequencies. In other words, we believe that her results for the ML plane can be accounted for as those obtained in the equiluminant plane, that is, they are a mixture of high-spatial-frequency tritanopia and simultaneous chromatic contrast. Again, as in the equiluminant plane, as spatial frequency increases, the high-spatial-frequency tritanopia effect increases and simultaneous chromatic contrast decreases.
We have found that at 8 c/deg (where the high-spatial-frequency effect is maximal) illusory colours are restricted to three narrow bands of hue. These are categorised by our observers as yellow, green, blue, and greenish-blue. We will refer to the first three as illusory yellow, green and blue hues. They seem to be close (in terms of the dominant wavelength) to the corresponding unique hues.

It follows that high-spatial-frequency tritanopia is a colour phenomenon which appears different from chromatic induction. Indeed, chromatic induction produces colours which are, at the first approximation, either complementary (simultaneous chromatic contrast) or similar (chromatic assimilation) to the backgrounds colours. Hence, if illusory colours were due to chromatic induction, then in our experiment, there would be a whole variety of illusory hues as we varied the background colour systematically with small steps along the colour gamut border of the monitor. Furthermore, the simultaneous chromatic contrast effect is known to decrease with an increase in spatial frequency (Fach & Sharpe, 1986; Smith et al., 2001) whereas illusory colours were found to increase their saturation with an increase in spatial frequency.

It seems even more unlikely that the illusory colours can be interpreted as a sort of chromatic assimilation. Note that the illusory yellow is produced by the backgrounds appearing green rather than yellow. Moreover, yellow backgrounds produce strong illusory green (not yellow). Likewise, blue backgrounds produce no illusion at all. The strongest illusory blue colours are observed against pink rather than blue backgrounds. All this clearly distinguishes the illusion from chromatic assimilation.

It must be noted that if one uses only two particular backgrounds as, for example, Monnier and Shevell (2003, 2004) and Shevell and Monnier (2005) did, it may look like assimilation takes place. For example, among the variety of greenish backgrounds inducing yellow there is also a yellow-greenish one. If one restricts oneself to only this particular yellow-greenish background, one may superficially interpret this as a chromatic assimilation. Therefore, choosing only particular background colours, one may mistake high-spatial-frequency tritanopia for assimilation. It seems that even the nine chromaticities of the background employed in Smith, Jin, & Pokorny’s study (Smith et al., 2001) were not enough (at least in the context of the present work) to decide whether the colour effect observed at the high spatial frequencies was chromatic assimilation or high-spatial-frequency tritanopia. However, varying systematically the backgrounds’ chromaticities immediately

---

5 There was an important difference in experimental design between our and Monnier and Shevell’s experiments. We used a grid of thin neutral test strips whereas they used a single test strip. Therefore, we studied how the spatial frequency of the test affected the test colour appearance whereas they studied how the spatial frequency of the background affected the colour appearance of the test strip, the spatial frequency content of which was constant in their experiment. Therefore, despite the apparent similarity of the colour illusions, Monnier and Shevell may have studied a different perceptual effect.
reveals the fundamental difference between these two phenomena.6

It should be stressed that our results strongly testify against the receptor account of the illusion (e.g., that based on poor spatial resolution of the S-cone mechanism alone). Indeed, we found that no illusion can be observed when there is a large S-cone contrast between the test grid and background (backgrounds marked with the black circles in Figs. 2–4). On the other hand, the strong illusion can be observed when there is no S-cone contrast between the test grid and background (the data for the ML plane). Thus, S-cone contrast is neither sufficient nor necessary for the illusion to be experienced. It follows that the illusion must be produced at some post-receptor site where the contribution from these mechanisms may be those which produce unique hues. We test this hypothesis in the next experiment.

3. Experiment 2 illusory colours and unique hues

In this experiment, we measured the unique hues for our observers and compared them to the illusory colours obtained in the previous experiment.

3.1. Method

The method of adjustment was used to determine the unique yellow, blue, and green hues for observers DR, TL, and SH who participated in the previous experiment.

3.1.1. Apparatus and stimuli

The same experimental set-up (the Sony colour monitor driven by the VSG 2/5 card) was used. The monitor was viewed by observers sitting at a distance of 4 m. On the monitor, we presented a rectangular homogeneous test stimulus of the same size and in the same place as the matching bar had been in the previous experiment. The test stimulus was surrounded by an equiluminant neutral background (x = 0.314, y = 0.331, lum = 25.0 cd/m²). A keyboard allowed observers to change the hue of the test stimulus.

Unique hues were evaluated in the equiluminant plane. Actually, each unique hue was determined on seven circles in the CIE 1931 chromaticity diagram with the centre at the neutral background. All circles had to be within the colour gamut border. The distance between circles had to be such that the same hue on different circles had well distinguished saturations. These two restrictions allowed us to use not more than seven circles. From the literature on unique hues we knew that expected locations of unique hues on these circles would be restricted to rather narrow arcs. Thus, we established an arc on each circle for observers to explore. In a pilot study, observers explored the ends of the arcs to make sure that they were suitably different from unique hues (e.g., the arcs chosen to determine unique green had bluish-greens at one end and yellowish-greens at the other).

3.1.2. Procedure and experimental design

The experiment consisted of three sub-experiments (one for each unique hue). The sub-experiments were completed in random order. In each sub-experiment, unique hues were measured for each of seven circles five times. Circles were chosen in a random order. In all, there were 35 trials in each sub-experiment. These trials were divided into five sessions (seven trials each). Each session lasted approximately 15 min; and two sessions were completed per day.

In a single trial, the observers were presented with a test stimulus having a chromaticity which was chosen at random within the region of the particular unique hue (the corresponding arc). They were asked to adjust the hue of the test stimulus so that it appeared as the unique hue in question (different for different sub-experiments). Observers were given the following definitions of unique hues. Unique green was defined as the hue appearing neither blue nor yellow; unique blue appearing neither green nor red; and unique yellow appearing neither green nor red.

After the observer had made an adjustment and was satisfied the colour of the test stimulus was the unique hue, the experimenter recorded the chromaticity coordinates and the trial was over. There were no timing restrictions. The next trial appeared immediately after the coordinates were recorded. As in the previous experiment, the observer could alternate between the test stimulus and a blank screen by pressing a button.

3.2. Results

The mean settings for unique hues for each observer are plotted in the MacLeod–Boynton chromaticity diagram along with the mean matches to the test grid against the equiluminant backgrounds for 8 c/deg as described in the previous experiment (Fig. 10). As we can see, unique yellow and illusory yellow are in good correspondence for all three observers. It must be said that, in contrast with unique blue and green which produce nearly straight loci, illusory blue and green form clusters.7 For this simple reason, they cannot coincide as they have different shapes. Nevertheless, the unique green stretch for all three observers goes through the middle of the illusory green cluster. Though this is

6 Smith, Jin and Pokorny suggested that chromatic assimilation in their study could be accounted for by scattered light (due to optical aberrations). If this was the case then we studied a different colour phenomena since as, mentioned above, our illusory colours are unlikely to be produced by scattered light.

7 When such a cluster is narrow it is in line with the corresponding unique hue. For example, making a straight stretch, low saturated illusory blue colours coincide with unique blue loci for observer DR (Fig. 10).
not the case for the illusory blue cluster, unique blue is quite close to illusory blue. Hence, in the first approximation, unique hues (especially yellow and green) and illusory hues are in good agreement with each other.

### 3.3. Discussion

Although the notion of unique hues plays an important role in current theories of colour vision, “the special status of these ‘unique hues’ remains one of the central mysteries of colour science” (Mollon & Jordan, 1997, p. 381). Hering (1878) believed that unique hues are produced by two colour-opponent mechanisms: yellow–blue (YB) and red–green (RG). While the idea of colour opponency has been supported by the discovery of opponent visual cells (cone opponency), neither direct psychophysical nor physiological evidence for the existence of mechanisms which produce unique hues—let us call them unique hue mechanisms—has been found. For example, in their review article, van Brakel and Saunders (1997) conclude that “there is no evidence (physiologically or phenomenologically) for specific mechanisms corresponding to Hering’s four unique hues”. More recently, Valberg (2001, 2005) has come to the same conclusion.

The main method to evaluate the spectral characteristics of the hypothetical mechanisms producing unique hues is the hue cancellation technique (Jameson & Hurvich, 1955). However, the axes of the YB and RG equilibrium in the chromaticity diagram as derived from hue cancellation data, do not coincide with the unique hue loci obtained by direct settings (Burns et al., 1984; Webster et al., 2000; Wuerger et al., 2005). For example, RG equilibrium (YB axis) as predicted by Jameson and Hurvich’s model is a vertical line in the MacLeod–Boynton diagram whereas unique yellow and blue loci are not parallel to the vertical axis (as it can be seen in Fig. 10).

Moreover, the hue cancellation technique essentially rests upon the idea of colour opponency. Without colour opponency the hue cancellation technique loses its validity. The colour opponency assumption built into the hue cancellation technique implies complementarity of unique hues. However, unique hues are not complementary to each other, that is, unique blue is not a complementary colour to unique yellow, and nor is unique green to unique red (Burns et al., 1984; Webster et al., 2000; Wuerger et al., 2005). Therefore, if unique hue mechanisms exist, they should be unipolar (in contrast with bipolar, i.e., opponent) colour mechanisms which do not make an opponent pair. Therefore, the colour-opponent mechanisms on which not only Jameson and Hurvich’s but many other models of colour vision are based (e.g., De Valois & De Valois, 1993; Guth, 1991; Ingling & Tsou, 1977), cannot be those which produce unique hues. On the other hand, while evidence for the existence of unipolar red, green, yellow, and blue colour mechanisms was recently found (Sankeerali & Mullen, 2001), there is no indication that these unipolar colour mechanisms produce unique hues either.

We believe that our data can be interpreted in favour of the existence of unique hue mechanisms. More specifically, the data can be accounted for by assuming that the illusory colours result from “leakage” of the output of the post-receptor mechanisms giving rise to unique (yellow, blue, and green) hues. Indeed, let us assume that the unique blue mechanism has poorer spatial resolution than the unique yellow mechanism, which, in turn, has poorer spatial resolution than the unique green mechanism. This will explain, first, why as well as unique blue, yellow, and green, we also observe green–blue illusory colours at high spatial frequencies. The simultaneous “leakage” of the unique blue and green mechanisms brings about the variety of green–blue illusory colours observed in our experiment. Second, having the better spatial resolution, the unique green mechanisms starts “leaking” only at high spatial frequencies. This explains why the green illusory colours disappear at low spatial frequencies for observers DR and TL (especially in the ML plane) whose data are not contaminated by simultaneous chromatic contrast. Third, our observers never saw a red illusory colour. This can be understood if one assumes that the unique red mechanism has the best spatial resolution amongst the four unique hue mechanisms.

It should be mentioned that, so far, the main evidence in favour of unique hue mechanisms has come from data which are of type B, in terms of Brindley’s classification of observations (Brindley, 1960, pp. 144–145). This was the main reason for Mollon and Jordan (1997), and other authors to question the existence of the unique hue mechanisms. While, we finally compare the illusory colour (as a result of the functioning of some hypothetical post-receptor mechanisms) with the data obtained in this experiment by using colour categorisation (thus of type B), the data on illusory colours themselves were obtained by using asymmetric colour-matching technique (in the previous experiment) which is generally believed to yield type A data. Therefore, we believe that we have got, for the first time, direct psychophysical evidence (of type A) that led to the existence of colour mechanisms which produce unique hues.

The reason why the unique hue mechanisms have not been revealed by numerous studies that use type A measurements so far, might be that a study of type A lends itself easier to a detection/discrimination task rather than a colour appearance task. However, different performances may be based on different colour mechanisms. We believe that different post-receptor colour mechanisms may exist in parallel. For example, colour detection/discrimination performance may be mediated by one set of mechanisms (which are often called “cardinal mechanisms”) whereas colour appearance may be based on the performance of the other mechanisms which we refer to as “unique hue mechanisms” (which may coexist with “cardinal mechanisms” at the same level of the visual system).

If the illusion is induced by the same mechanisms which produce unique hues then by measuring the illusion...
strength one can evaluate the responsivity of these mechanisms. Specifically, evaluating which colours (of the background) bring forth the illusion, and which do not, can shed light on the spectral sensitivity of the unique hue mechanisms. We have undertaken the following experiment to further investigate which backgrounds do not induce the illusion (no-illusion background set).

4. Experiment 3 background chromaticities which do not invoke the illusion

The no-illusion background set is indicative of possible colour mechanisms of high-spatial-frequency tritanopia, since any quantitative model of the illusion makes a specific prediction of the no-illusion background set. If high-spatial-frequency tritanopia is because of poor spatial resolution of some linear colour mechanism, then the no-illusion background set should be a plane in the 3D colour space, and a line in a 2D chromaticity plane. In particular, it should be a linear interval in the MacLeod–Boynton chromaticity diagram. However, as mentioned above, a few backgrounds which were tested (represented by the black circles along the colour gamut border in Figs. 2–4), brought about no illusion. While being highly saturated, these background colours do not produce any illusory colours. Furthermore, no illusion was produced for background colours lying on the radii between these backgrounds and the neutral colour. In other words, the no-illusion background set observed in our experiment seems to be a two-dimensional sector in the chromaticity diagram rather than a one-dimensional interval. It contradicts the hypothesis that high-spatial-frequency tritanopia is a result of low spatial resolution of not only the YB-mechanism but any single linear mechanism. Because the two-dimensionality of the no-illusion background set has a serious impact on our understanding of the possible mechanisms of the illusion, we decided to investigate more systematically the no-illusion background set.

4.1. Method

We used the same experimental set-up as that described in the previous experiments. Two females (SH and LS) participated as observers. Both had normal colour vision and wore their corrective eyewear throughout the experiment. In the first part of this experiment, we explore which colours (of the background) in the ML plane bring forth the illusion, and which do not (the S-cone coordinates being equal for the test grid and the background). In the second part of the experiment, the same was done for the equiluminant plane.

The same pattern as in Experiment 1 was presented to observers sitting at a distance of 4 m. The colour of the test grid was kept fixed throughout the experiment \( (x = 0.314, y = 0.331, 25.0 \text{ cd/m}^2) \). The \( S \)-, \( M \)-, and \( L \)-cone coordinates of the grid were 2.428, 3.221 and 3.763, respectively. The spatial frequency of the test grid was 4 and 8 c/deg in the first part of the experiment, and only 8 c/deg in the second part. The background colour was systematically varied, using the same software as in the previous experiments. Specifically, observers used the keyboard which allowed them to vary the colour of the background so that the corresponding point in SML space moved along a particular direction in SML space. Also, it could move circularly around a neutral point.

In the first part of the experiment, observers varied the background colour making a full circle in the ML plane \( (AS = 0) \) with a task to notice when the illusion (i) appeared, reporting what hue it had; (ii) reached its maximum; and (iii) disappeared. While exploring the ML plane, the observer reported what she saw. When the illusion appeared, the observer stopped exploring and the experimenter recorded the position in the ML plane and also the hue. The observer proceeded after the record was made, further exploring, reporting what she saw until the maximum illusion was reached. At this point, the observer stopped exploring and the experimenter recorded the position. When the record was made, the observer continued exploring until the illusion disappeared. This procedure continued until a full circle was made in the ML plane. Six circles of different radii were used to explore the ML plane. For each circle two measurements were done: in clockwise and counter-clockwise directions.

In the second part of the experiment, observers varied the background colour in the equiluminant plane \( (M + L = \text{constant}) \). Specifically, the difference between \( M \)- and \( L \)-coordinates of the background was fixed, and the \( S \)-coordinate was varied to find a border between the areas producing different illusory colours (blue versus yellow or green) and the no-illusion area. Specifically, the observer started from the maximum \( S \)-cone coordinate value (producing maximally saturated illusory blue) gradually decreased it, moving toward the minimum \( S \)-cone coordinate value (producing maximally saturated illusory yellow or green) until she reached the \( S \)-cone coordinate value producing no illusion at all. The observer reported this and the experimenter registered this \( S \)-cone coordinate value. After this value was recorded, the observer continued decreasing the \( S \)-cone coordinate value until she reached the \( S \)-cone coordinate value which produced a yellow (or green) illusion. Then she reported this to the experimenter who registered this \( S \)-cone coordinate value too.

In the next trial, the observer made the same measurements, only moving along the \( S \)-cone coordinate axis in the opposite direction. In other words, the observer started from the minimum \( S \)-cone coordinate value (producing maximally saturated illusory yellow (or green)) and increased the \( S \)-cone coordinate value until she reached the no-illusion point which was then registered. Then the observer continued to increase the \( S \)-cone coordinate value until she reached the blue illusory colour which was then registered.

In all, six measurements were done (three for ascending order and three for descending order).
4.2. Results

After averaging, the measurements are presented for the ML plane in Figs. 16–19 and for the equiluminant plane in Figs. 20 and 21.

Figs. 16 and 17 show the results obtained for the test grid of 4 c/deg in the ML plane for observers SH and LS, respectively. In these figures the horizontal axis is the difference, $\Delta M$, between the $M$-cone coordinates of the background, $M_{\text{background}}$, and the neutral colour of the test grid, $M_{\text{neutral}}$

$$\Delta M = M_{\text{background}} - M_{\text{neutral}}. \quad (1)$$

Likewise, a corresponding difference for the $L$-cone coordinates is plotted along the vertical axis

$$\Delta L = L_{\text{background}} - L_{\text{neutral}}. \quad (2)$$

As mentioned in the method section, $M_{\text{neutral}} = 3.221$ and $L_{\text{neutral}} = 3.763$. The polar angle $\alpha = \arctan(\Delta L/\Delta M)$ for various directions in the ML plane are shown on the circumference of the circle. Each blue filled circle represents the average of two measurements. All the blue filled circles constitute a border between two regions in the ML plane. One (where approximately $\Delta L > \Delta M$) represents the backgrounds which produce the illusory blue–green and the other (where approximately $\Delta M > \Delta L$) which produce no illusion at all (marked as "neutral" in Figs. 16–19). Therefore, for the test grid whose spatial frequency was 4 c/deg, there were no yellow illusory colours observed. This is in line with our previous experiments where it was shown that the yellow illusory colour requires a higher spatial frequency to be seen than the blue illusory colour.

For the test grid of spatial frequency 8 c/deg, two borders were found (Figs. 18 and 19). They divide the ML plane into three areas: an area (mainly $\Delta L > \Delta M$) which represents the backgrounds which produce the illusory blue–green, an area (mainly $\Delta M > \Delta L$) which produce the illusory yellow and an area (around the line $\Delta M = \Delta L$) which produce no illusory colours.

It should be mentioned that within the blue–green (or yellow) area, the various backgrounds were not equally...
Author's personal copy

More specifically, when moving from one border radius to another through the blue–green (or yellow) area, the illusory colours monotonically increased in saturation (but kept the same hue), reaching the maximum in the middle of this area and then gradually decreased. Unfilled circles in Figs. 18 and 19 show the location of the background colours producing the maximum strength of illusions. As one can see, the blue–green illusory colour was found to be most pronounced for the 130°–150° directions for observer SH and 150°–170° for observer LS. The most saturated yellow illusory colour was observed for the 320°–340° directions for SH and 340°–360° for LS.

The results for the second part of the experiment where observers varied the background colour in the equiluminant plane are shown in Figs. 20 and 21. In the semi-plane $\Delta M < \Delta L$, the no-illusion set was a curvilinear line separating an area of blue (above the line) and green (below the line) illusory colours. In the semi-plane $\Delta M > \Delta L$, an area was found that produced no illusion (marked as neutral in Figs. 20 and 21). In this semi-plane, the area above the no-illusion set produced blue illusory colours and the area below it gave rise to yellow illusory colours.

4.3. Discussion

If high-spatial-frequency tritanopia emerges because of lower spatial resolution of the YB-mechanism, then the no-illusion background set will be the set of colours which produce zero response from this mechanism. However, different models of colour vision suggest different YB-mechanisms, thus predicting different no-illusion background sets. Specifically, the no response set (thus no-illusion background set) for Hurvich and Jameson’s model (1957) is a plane in the $SML$ cone excitation space described by the following equation:

$$S = (M + L) = 0.$$  \hspace{1cm} (3)

If the $S$, $M$, and $L$ coordinates are scaled appropriately so that the response of the Hurvich and Jameson YB-mechanism to the neutral colour equals zero, then Eq. (3) defines in the $SML$ space, a plane through the neutral point. In the MacLeod–Boynton chromaticity diagram Eq. (3) defines a line through the neutral point parallel to the $S$-axis.

The no-illusion background set as predicted by Guth’s (1991) model is a plane defined by the following equation:

$$S + (0.1M - 0.8L) = 0.$$  \hspace{1cm} (4)
and by De Valois and De Valois’ (1993) model, the following plane:

\[ S + (2.7M - 3.7L) = 0 \]  

Eq. (5)

Fig. 22 presents the predictions for the no-illusion sets derived from Hurvich and Jameson’s (1957), Guth’s (1991) and De Valois and De Valois’ (1993) models of colour vision. As one can see, the worst prediction that is made is from Hurvich and Jameson’s model since the no-illusion line predicted by this model nearly coincides with the direction in the ML plane where the maximal illusion was observed. The no-illusion line predicted by Guth’s model also passes through the area where the illusion is rather pronounced. While the no-illusion line derived from De Valois and De Valois’ model coincides with the no-illusion set found in our experiment, this model erroneously predicts the illusory hues. Indeed, De Valois and De Valois’ model predicts that when \( 2.7\Delta M > 3.7\Delta L \), blue should be seen and when \( 2.7\Delta M < 3.7\Delta L \), yellow should be seen. However, we found the reverse. In fact, when \( 2.7\Delta M > 3.7\Delta L \), either yellow or neutral were seen and when \( 2.7\Delta M < 3.7\Delta L \), either blue or neutral were seen.

Furthermore, as mentioned above, all these theories predict a one-dimensional no-illusion set (a straight line) in the ML plane. Contrary to this, we found the no-illusion set to be a two-dimensional curvilinear sector (Figs. 18 and 19). One might argue that one should not expect a defined border between the areas producing yellow and blue illusions using the threshold measurement technique. Indeed, in psychophysical experiments, a threshold is always ‘fuzzy’, that is, there is always a threshold zone with an interval of uncertainty (Guilford, 1954). Therefore, the two-dimensionality of the no-illusion zone in Figs. 18 and 19 may be a result of the probabilistic uncertainty of threshold measurements. However, this is unlikely to be the case.

As one can see in Figs. 20 and 21, the border between the illusory colours in the equiluminant plane is one-dimensional when \( \Delta M < \Delta L \). Probabilistic uncertainty of threshold measurements manifests itself in these graphs in the roughness of the border between blue and green illusory colours (especially for observer LS) rather than in the two-dimensionality of the no-illusion area (as in the right-hand side of these graphs). Likewise, it seems plausible that it is the roughness of the borders rather than the two-dimensionality of the no-illusion area in Figs. 18 and 19 that is a result of probabilistic uncertainty of threshold measurements.

The two-dimensionality of the no-illusion area in the ML plane can be accounted for if there are two separate unipolar—yellow (Y) and blue (B)—mechanisms with non-overlapping spectral characteristics such that they do not cover the whole SML space, that is, there is a three-dimensional area (i.e., no-illusion set) where both mechanisms are silent.

As mentioned above, a decomposition of one opponent (bipolar) mechanism into two unipolar mechanisms was suggested to take place for post-receptor colour mechanisms by other authors (De Valois & De Valois, 1993; Sankeralli & Mullen, 2001). But it was assumed that these unipolar mechanisms are linear and symmetrical, whereas the unipolar mechanisms as revealed in the present study are obviously neither linear, nor symmetrical. Indeed, as follows from the shape of the boundary curves in Figs. 20 and 21, the S-cone signal contributes non-linearly to the Y- and B-mechanisms. Also, strong evidence for non-linearity of the YB-mechanism was found by many other researchers (Cicerone, Krantz, & Larimer, 1975; Ejima & Takahashi, 1985; Larimer, Krantz, & Cicerone, 1975). While a few non-linear models of the YB-mechanism were put forward (Elzinga & De Weert, 1984; Larimer et al., 1975; Pugh & Mollon, 1979; Werner & Wooten, 1979), there is no consensus on this issue yet. For instance, recent findings on yellow–blue equilibrium (i.e., neither yellow, nor blue stimuli) are in apparent contradiction with all these models (Chichilnisky & Wandell, 1999).

It also follows from Figs. 20 and 21 that the S-cone signal contributes differently (non-symmetrically) to the Y- and B-mechanisms. This is in line with asymmetry in opposed colour signals found by some other researchers (Mausfeld & Niederee, 1993; McLellan & Eskew, 2000; Shinomori, Spillmann, & Werner, 1998; Smith & Pokorny, 1996).

The spatial characteristics of the Y- and B-mechanisms are also different. It follows from that for 4 c/deg only the blue illusory colour can be observed. Hence, the Y-mechanism has better spatial resolution than the B-mechanism. Likewise, the fact that the green illusory colour is always less saturated than the yellow and blue ones, and that it requires higher spatial frequency to appear than the illusory yellow and blue, leads to a suggestion that the green unipolar mechanism has better spatial resolution than the Y- and B-mechanisms.
At this point we run into a problem. As mentioned above, a pattern clearly looking blue may produce no illusion at all (Fig. 23). Why does the blue mechanism resolve contrast between the grid and the background in Fig. 23, but not in Fig. 1? This paradox can be resolved if there are at least two B-mechanisms, with different spectral and spatial characteristics, which contribute into the blue component (Logvinenko & Hutchinson, 2005). Indeed, let us assume that there are two B-mechanisms: one (fine B-mechanism) with spatial resolution high enough to resolve the contrast of the 8 c/deg grid (Fig. 23) as perfectly as the mechanisms driven only by M- and L-cones, and the second one with lower spatial resolution (coarse B-mechanism). Also, let us assume that the spectral sensitivity of the fine B-mechanism is such that it is virtually insensitive to the background’s colour in Fig. 1. Therefore, the blue component of the background in Fig. 1 is produced by the coarse B-mechanism. Since the coarse B-mechanism has low spatial frequency resolution, the blue component of the background starts ‘leaking’ into the test strips at high spatial frequencies. It explains why we see a strong blue illusory colour in Fig. 1. As the fine B-mechanism is involved in producing the blue component of the background in Fig. 23, its high spatial frequency resolution prevents the blue component leaking from the background into the strips, thus there is no illusion in Fig. 23.

It should be mentioned that Humanski and Wilson (1993) came to a similar conclusion. Specifically, they argued that there were three S-cone mechanisms with different spatial frequency characteristics. Two of the mechanisms are band-pass with peak sensitivities at 0.7 and 1.4 c/deg; the third mechanism is low-pass with a high-frequency cut-off at approximately 2.0 c/deg. They interpreted their results to be in line with the idea that multiple spatial frequency chromatic mechanisms exist (e.g., De Valois & De Valois, 1990, pp. 233–235).

Finally, note that while colour mechanisms are, traditionally, considered as purely chromatic processors, they must have spatial (and temporal) characteristics, if they really exist in the visual system as neural mechanisms. The important implication of this is that the output of these mechanisms (i.e., colour signals) has to be determined by not only their spectral characteristics but also by their spatial (and temporal) characteristics. Hence, any colour theory should include spatial (and temporal) as well as chromatic dimensions. In other words, colour mechanisms should be considered as spatio-temporal-chromatic processors from the very beginning. To be more exact, they should be characterised by their sensitivity function of four variables—wavelength, two spatial variables and time. Likewise, the input into such a mechanism should be light intensity considered as a function of the same four variables as well.

5. Conclusions

The high-spatial-frequency tritanopia found here differs from both simultaneous chromatic contrast and chromatic assimilation since the illusory hues were restricted to unique blue, yellow and green (and sometimes a mixture of green and blue). Contrary to small-field tritanopia, high-spatial-frequency tritanopia cannot be accounted for by the sparsity of the S-cone mosaic as such. One possible interpretation is that high-spatial-frequency tritanopia is a result of a difference in spatial resolution of the unique hues mechanisms (i.e., the post-receptor colour mechanisms producing unique hues).

We found that the spectral characteristics of the unique hues mechanisms differ from linear colour-opponent mechanisms involved in classical colour vision models (De Valois & De Valois, 1993; Guth, 1991; Hurvich & Jameson, 1957). We deduce from our results that the unique hues mechanisms are unipolar, non-linear, and asymmetrical, with non-overlapping spectral characteristics. These mechanisms also have different spatial characteristics. Specifically, the unique blue mechanism was found to have worse spatial resolution than the unique yellow mechanism. Furthermore, our data indicate that there should be at least two unique blue mechanisms—one with higher and the other with lower spatial resolution. This finding is in line with the existence of multiple colour spatial frequency mechanisms.

Acknowledgments

This study was supported by a research grant from The Wellcome Trust (GR068672MA) to A. Logvinenko. We thank Martin Sawey for writing the code to run the experiment. We also thank Deborah Ross, Lisa Scott, and Tieying Lu for participating as observers.

References


