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CHAPTER 7.1

On the Nature of Unique Hues

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7.1.1 INTRODUCTION

There exist four colours, the *Urfarben* of Hering, that appear phenomenologically unmixed. The special status of these 'unique hues' remains one of the central mysteries of colour science. In Hering's Opponent Colour Theory, unique red and green are the colours seen when the yellow-blue process is in equilibrium and when the red-green process is polarised in one direction or the other. Similarly unique yellow and blue are seen when the red-green process is in equilibrium and when the yellow-blue process is polarised in one direction or the other. Most observers judge that other hues, such as orange or cyan, partake of the qualities of two of the *Urfarben*. Under normal viewing conditions, however, we never experience mixtures of the two components of an opponent pair, that is, we do not experience reddish greens or yellowish blues (Hering, 1878).

These observations are paradigmatic examples of what Brindley (1960) called Class B observations: the subject is asked to describe the quality of his private sensations. They differ from Class A observations, in which the subject is required only to report the identity or non-identity of the sensations evoked by different stimuli. We may add that they also differ from the performance measures (latency; frequency of error; magnitude of error) that treat the subject as an information-processing system and have been increasingly used in visual science since 1960. Sensory observations of Class A can be interpreted if one allows merely the hypothesis that physiologically indistinguishable signals sent from the sense organs to the brain cause indistinguishable sensations. But to this day we have no secure way of interpreting Class B observations, no way of knowing what weight to place on them. Some might suppose that there exist specific cortical cells (or structures or processes) that give rise to – secrete – sensations of redness and other units that secrete sensations of blueness, and so on; and that mixed hues are seen when two types of cortical cell are concurrently secreting their proper sensations. Psychophysical linking hypotheses of this kind are not often made so unashamedly explicit, but it is a good idea to make them so. For all we really know is that in a given state of adaptation some chromaticities map on to hue sensations that typical observers describe as pure, whereas other chromaticities map on to mixed sensations.

7.1.2 THE CHROMATIC CHANNELS OF THE VISUAL PATHWAY

When chromatically antagonistic signals were first recorded in the retinae of fish (Svaetichin and MacNichol, 1958) and in the lateral geniculate nucleus of macaques (De Valois *et al.*, 1966), it was widely assumed that Hering had been vindicated and that the neural channels of the primate LGN corresponded to the red-green and yellow-blue processes of Opponent Colours Theory. The standard zone model of the 1960s had a receptoral 'Helmholtz' stage and a second 'Hering' stage (Walraven, 1962). Such a view still survives in psychology textbooks and other secondary sources. Today, however, most colour scientists are agreed that the chromatically opponent cells of the early visual system (the 'second stage' of models of colour vision) do not correspond colorimetrically to red-green and yellow-blue processes. Two main types of neural channel have consistently been reported in Old World primates: a phylogenetically recent channel in which the signal of the long-wave cones is opposed to that of the middle-wave cones and a phylogenetically older channel in which the signal of the short-wave cones is opposed to some combination of the signals of the L and M cones (Derrington *et al.*, 1984; Gouras, 1968; Mollon and Jordan, 1988). Figure 7.1.1 (see colour section) shows the chromaticity diagram of MacLeod and Boynton (1979), the axes of which correspond to the two chromatic channels of the early visual system. In such a diagram, a line that runs from unique yellow (c. 572 nm) to unique blue (c. 475 nm) is oblique, and not vertical as it should be if it represented a fixed, equilibrium, ratio of the quantum catches of the M and L cones. Indeed, unique blue is close to the wavelength (460 nm) that maximises the ratio M/L (Mollon and Estévez, 1988).

Recognising this discrepancy, the authors of recent models of colour vision have usually postulated a 'third stage', in which the second-stage signals are re-transformed to give channels that do correspond to those of Hering (De Valois and De Valois, 1993; Guth, 1991). It may be that a third stage of this kind does exist, but electrophysiological recording has not yet revealed it. Lennie *et al.* (1990) recording from neurons in the striate cortex of *Macaca fascicularis*, found that there was a large variation between cells in their preferred direction in colour space, with some bias towards the 'second stage' axes; only a few cells behaved as would be expected of the putative 'red-green' and 'yellow-blue' mechanisms of Hering. In the prestriate region V4, Zeki (1980) reported cells with narrow spectral sensitivities, but the wavelengths of peak sensitivity were distributed through the spectrum, with some avoidance of the yellow region; and extraspectral purples were well represented. Komatsu *et al.* (1992) examined the colour selectivity of neurons in the inferior temporal cortex and found that the population of cells together covered most of the chromaticity diagram. There were, for example, cells that gave their most vigorous response to a desaturated pink.

Lennie *et al.* (1990) speak of the 'red-green and yellow-blue mechanisms whose existence is so firmly established by psychophysics'. Yet what is this psychophysical evidence? The psychophysical experiments most commonly invoked to support a third stage are the chromatic cancellation measurements of Jameson and Hurvich (1955; see also Werner and Wooten, 1979): in these experiments the strength of, say, the green chromatic response was established by finding at each wavelength the amount of a fixed, reddish, wavelength that needed to be added to yield a light that looked neither reddish nor greenish. These measurements are certainly quantitative, but they too are Class B observations and they are in effect only an extension of the basic determination of the unique hues. This is clear when one considers that it is not necessary to perform the measurements as cancellations. It is completely equivalent to ask the subject to identify directly the sets of non-spectral chromaticities that are neither reddish nor greenish or are neither bluish nor

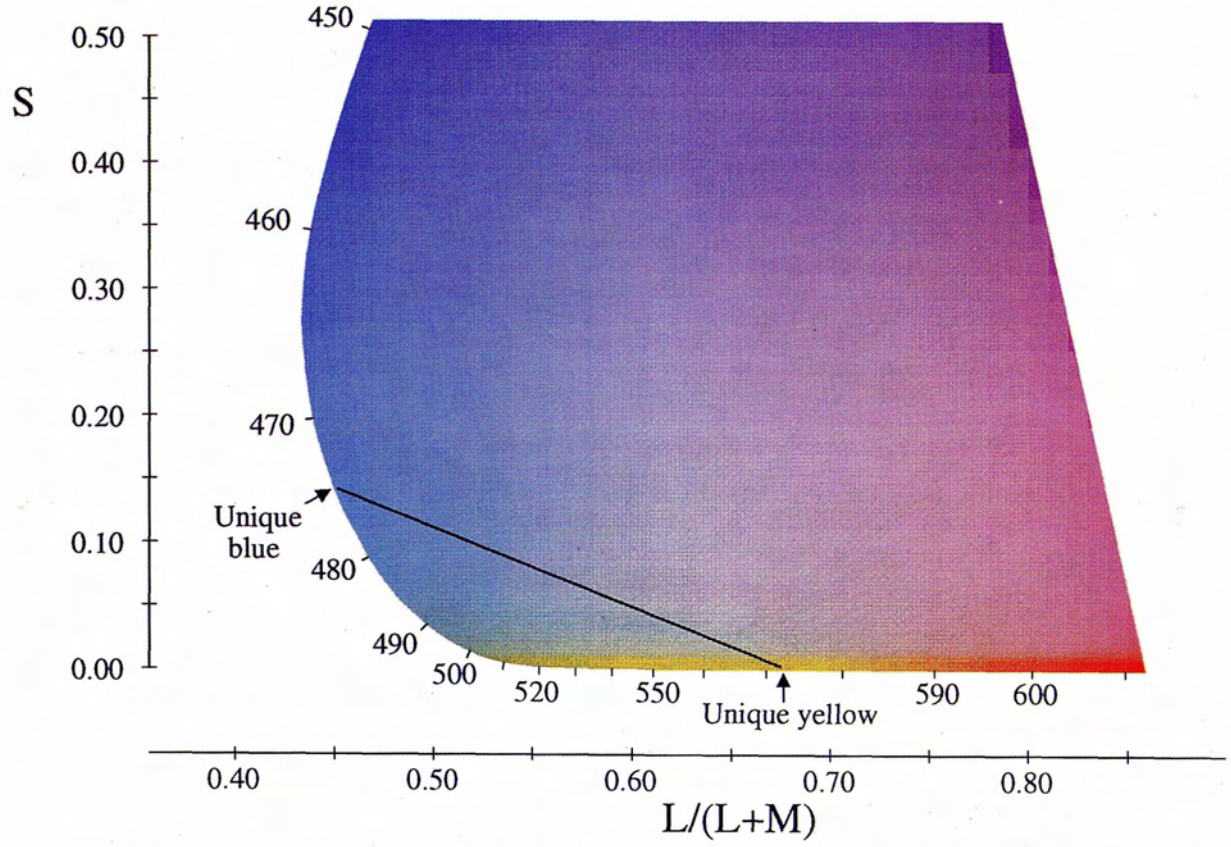

Figure 7.1.1 MacLeod and Boynton chromaticity diagram. The two ordinates of the diagram correspond to the two chromatic channels that have been identified in the early visual system. In this space the line running from unique-yellow to unique-blue is not vertical but oblique. (We are grateful to Ben Regan for preparation of the original colour figure.)

yellowish: in a chromaticity diagram these sets form (often curved) loci that connect the wavelengths of the unique hues to the white point (Burns *et al.*, 1984). Conventional colorimetry will then allow the reconstruction of cancellation curves in the form presented by Jameson and Hurvich.

So the cancellation experiments amount to the extended determination of unique hues. They show us that the topology of chromaticity space is preserved in our phenomenological colour space, but they remain Class B observations and, as evidence for a third stage, they add nothing to the original observation that some hues are unique and some are phenomenal mixtures.

7.1.3 DOCTRINE OF COINCIDENT CATEGORIES

In the hypothesis that each unique hue represents the activity of a discrete class of cortical cell, we can recognise a modern form of Müller's Doctrine of Specific Nerve Energies. And in judging this hypothesis we should place it in its broader context: one of the chief unsolved questions of brain science is that of whether the elements of perception and thought are represented by the activities of individual cells (Barlow, 1972, 1995).

It may be useful to identify a more general form of the hypothesis, in which we replace 'cell' by a term that can refer to any discrete 'structure' or 'process' or 'neural signal'. Let us speak of 'neural primitives'. It may also be useful to make explicit the distinct question of whether these neural primitives always map exactly on to our phenomenological categories. In the case of colour, then, we can ask: does the existence of unique and non-unique hues tell us that the neural representation of colour is discontinuous, and do the phenomenally unique hues correspond to the discrete primitives of this neural representation whereas mixed hues correspond to more than one kind of neural primitive? We might use the term *Doctrine of Coincident Categories* for the idea that phenomenological categories correspond to neural primitives in the above way.

Suppose that the Doctrine of Coincident Categories were wrong in the following sense. Suppose that colours were represented centrally only by neural primitives that corresponded to the axes of the MacLeod-Boynton space, i.e. primitives that did not correspond to redness, greenness, yellowness and blueness. This would imply that the transformation between the two categorical organisations (the transformation from the second to the third stage in current theories) arose in the relationship between the neural representation and the phenomenological, whatever that relationship might be. But now we are on radical ground. For it is easy for the normal trichromat to base his behaviour, verbal or otherwise, on the categories red, green, yellow and blue – much more easily than he can base his behaviour on the categories of the MacLeod-Boynton space. We should thus be allowing that strictly phenomenological categories can influence behaviour.

It is clear that if we understood the status of unique hues we should probably understand something useful about the general question of neural representation and its relationship to conscious experience. For the present, the nature of the unique hues remains mysterious and we do not know whether they tell us anything about the neural organisation of the visual system. In asking what they are, it may be instructive to adopt a Gibsonian view and to look outside the observer as well as within the fixed wiring of his visual system. Either in phylogeny or in ontogeny, is there some property of the external environment that sets the chromaticities that appear unique?

7.1.4 INDIVIDUAL DIFFERENCES IN UNIQUE YELLOW

One traditional approach to unique hues has been to study the undoubted differences that exist amongst colour-normal observers in the exact wavelength of each equilibrium colour. Let us consider two different hypotheses that have been advanced to explain the variation in unique yellow.

7.1.4.1 Cone ratios

An example of a model that seeks the variation within the fixed wiring of the visual system is that of Cicerone (1990). She proposes that the wavelength of unique yellow depends on the relative proportions of long- and middle-wave cones: the greater the proportion of long-wave cones, the shorter the wavelength of unique yellow. We have carried out two tests of this hypothesis.

A traditional index of L and M cone ratios is offered by the relative flicker-photometric sensitivity at middle and long wavelengths (De Vries, 1947). A measure closely related to flicker photometry is that given by the OSCAR test, in which the subject is asked to minimise apparent flicker by adjusting the relative depths of modulation of a long-wave light and of a middle-wave light, which are modulated in counterphase (Estévez *et al.*, 1983). Negative values on the OSCAR test indicate low sensitivity to long wavelengths. In the course of a recent study in collaboration with Emma-Louise Dormand we had occasion to obtain OSCAR settings and estimates of unique yellow from 50 young men. To measure unique yellow, we used a Maxwellian-view optical system that incorporates a computer-controlled monochromator with integral stepping motor. This system allows us to determine unique hues by a procedure in which four staircases are randomly interleaved (Jordan and Mollon, 1995). Sternberg has estimated that an adaptive method of this kind gives a stimulus sequence that is as random as that of the Method of Constant Stimuli (Sternberg *et al.*, 1982), while it avoids the chief disadvantage of the Method of Constant Stimuli – the tendency of subjects to give equal numbers of responses of the two types and thus to yield a setting in the middle of the fixed range of stimuli. In the present experiment, the background was dark, the stimuli were circular and subtended one degree, and the stimulus duration was one second. Instead of the negative correlation predicted by Cicerone's hypothesis, we found no significant relationship between the OSCAR setting and the wavelength of unique yellow ($r = 0.066$).

A second and particularly interesting test of Cicerone's hypothesis is offered by women who are heterozygous for the common forms of dichromacy. Although such women usually exhibit Rayleigh matches that are within the normal range (Jordan and Mollon, 1993), their retinae almost certainly contain abnormal proportions of L and M cones, owing to the process of X-chromosome inactivation or Lyonisation. Although a woman inherits two X-chromosomes, one from each parent, only one of the two is actually expressed in any individual cell of her body (Gartler and Riggs, 1983; Lyon, 1972). In the retina of a heterozygote, a subset of cones will express the abnormal opsin array that she has inherited from one parent and which will lead to dichromacy if she passes it on to a son. Thus, carriers of protanopia are thought to have reduced numbers of functional long-wave cones, whereas carriers of deuteranopia have reduced numbers of middle-wave cones. It is well established that most carriers of protanopia show a reduced sensitivity to long wavelengths but exhibit a normal Rayleigh match (Schmidt, 1934). This is the behaviour expected if the normal photopigments are present but the long-wave cones are reduced in number (Rushton and Baker, 1964).

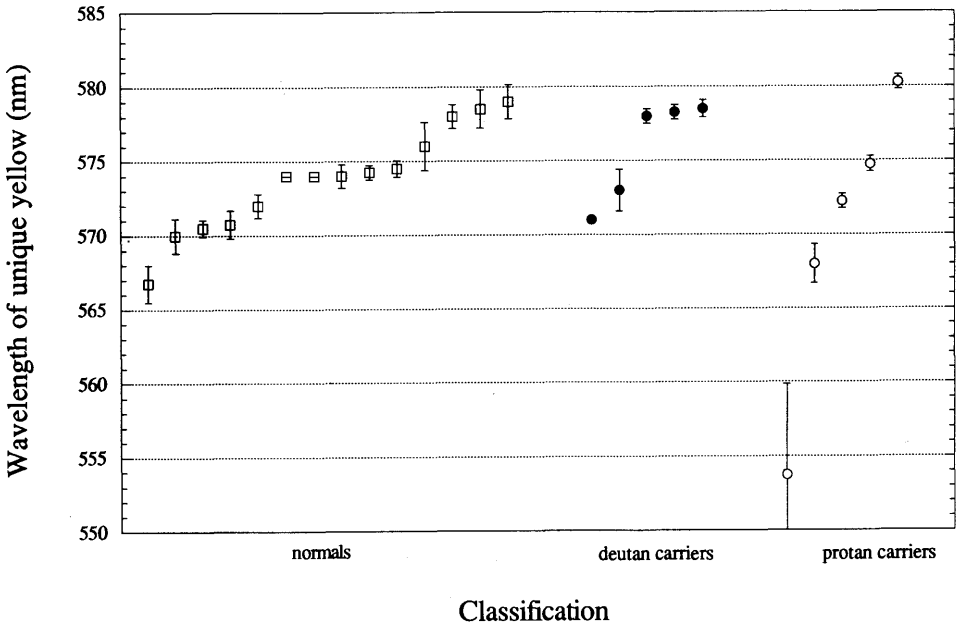

Figure 7.1.2. The wavelength set as unique yellow is plotted for individual normal observers (open squares), carriers of deuteranopia (filled circles) and carriers of protanopia (open circles). There is no significant difference between these groups of observers. Note that one carrier of protanopia exhibits a very short value of unique yellow.

We have collected in Cambridge a panel of obligate heterozygotes whose sons' phenotypes have been established in detail (Jordan and Mollon, 1993). We have determined unique yellow for members of this panel and for normal controls. Results from this experiment are shown in Figure 7.1.2. As groups, neither protanopic nor deuteranopic carriers differ significantly from the normals. One carrier of protanopia sets unique yellow at a very short wavelength (and has a very large standard deviation), but her setting is displaced in the direction opposite to that predicted by Cicerone. In sum, by testing populations who have extreme ratios of L and M cones, we find no evidence for Cicerone's hypothesis.

From the same population of heterozygotes we did concurrently obtain OSCAR settings, as a direct measure of relative sensitivity to middle and long wavelengths. On this test, most individual protan carriers reveal themselves by a clearly depressed sensitivity to long wavelengths, a finding consistent with the hypothesis that they have reduced numbers of long-wave cones. As a population, deutan carriers show a lower relative sensitivity to middle wavelengths than do normals, although in this case the normal and heterozygote distributions overlap substantially. We found that the wavelength of unique yellow showed a non-significant positive correlation with OSCAR setting ($r = 0.32$), a relationship opposite in direction to that expected from Cicerone's hypothesis (Figure 7.1.3).

7.1.4.2 Cone sensitivities

The hypothesis of Pokorny and Smith (1977) is one that relates unique yellow to properties of both the observer and the environment. It supposes that unique yellow is that wavelength that produces in the L and M cones the same ratio of quantum catches as does the average

illumination of the observer's environment. A view of this kind was also adopted by Mollon (1982). A neural adjustment with a relatively long time constant would control the channel that differences the L and M cone signals and would ensure that the equilibrium point of the channel corresponded to the average stimulus.[1] Departures from the equilibrium point would be represented by neural signals of opposite sign and (here a psychophysical hypothesis enters) by sensations of opposite quality.

Pokorny and Smith developed their hypothesis to account for the spectral position of unique yellow in protanomaly and in deuteranomaly, and they treated the normal observer as a single phenotype. But it is natural to extend such a hypothesis to account for the variation in unique yellow between normal subjects. We now know that the long- and middle-wavelength photopigments are polymorphic; that is to say, there exist individual variations in the amino-acid sequence of the opsins. Some of these variations produce spectral displacements in the absorbance spectrum of the photopigment: most notably the substitution of alanine for serine at site 180 shifts the peak sensitivity to shorter wavelengths, but there are small, non-additive effects of other sites in the amino acid sequence (Asenjo *et al.*, 1994; Merbs and Nathans, 1992).

These genetic polymorphisms account for a significant part of the variance in Rayleigh matches (Winderickx *et al.*, 1992). Now, in hypotheses of the type advanced by Pokorny and Smith, unique yellow is a kind of a colour match: it is a tritanopic match between a monochromatic yellow and a remembered broad-band white. So we might expect some correlation between a subject's Rayleigh match and his unique yellow, a correlation that reflects underlying variations in the spectral positions of the L and M pigments. In fact, a

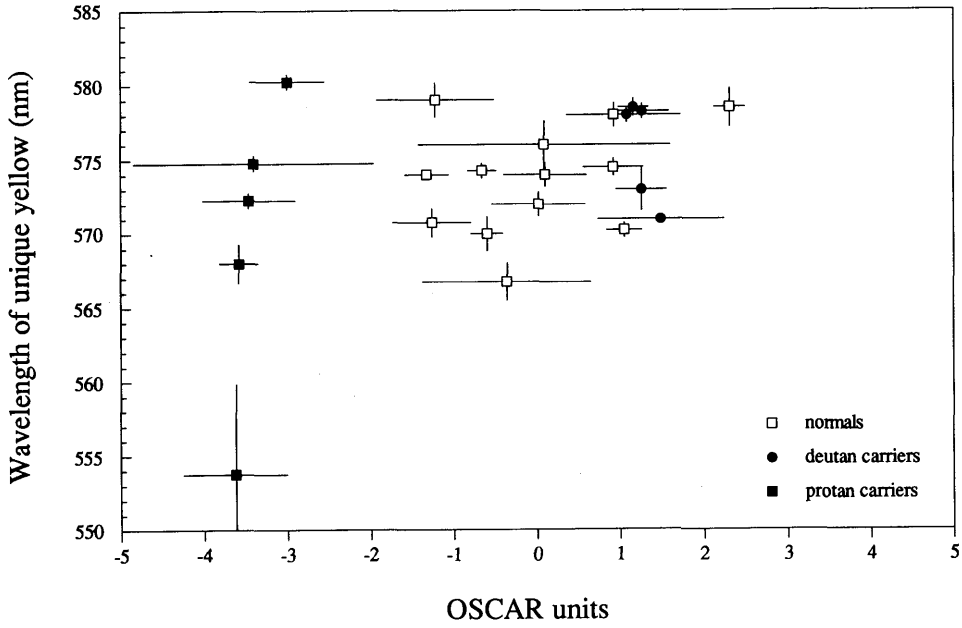

Figure 7.1.3. The wavelength set as unique yellow is plotted as a function of the observer's OSCAR setting for normal observers (open squares), carriers of deuteranopia (filled circles) and carriers of protanopia (filled squares). There is no significant correlation between the two variables. The error bars indicate the standard deviations of five settings on the OSCAR and four estimates of unique yellow (drawn from four interleaved staircases). However, unlike the settings of unique yellow, the OSCAR settings separate well the deutan and protan carriers.

correlation was reported by Donders (1884) for a sample of colour-normal observers: the more red a subject required in the Rayleigh match, the shorter the wavelength of unique yellow. We have plotted in Figure 7.1.4 the data that Donders gives in the tables on pages 536–537 of his paper. However, a study by Hailwood and Roaf (1937) found no correlation at all between Rayleigh matches and unique yellow. This was also the case for our recent sample of 50 young colour-normal males: the value of r was 0.01, giving no hint at all of a relationship. So this test offers no support for the extended Pokorny-Smith hypothesis.

There is a second test of the extended Pokorny-Smith hypothesis that we can employ. Suppose we supply a reference white during the experiment. It is plausible that this will supplant the stored white. So, in a chromaticity diagram, the subject's unique yellow ought to lie on the projection of a line that passes through the tritanopic copunctal point and the (supplied) white. For such a line represents a set of chromaticities that produce a constant ratio of quantum catches in the L and M cones, i.e. a set of lights that would be confused by an observer who lacked the short-wave cones.

To test this prediction, we have recently measured the wavelength of unique yellow for one-degree targets presented within a 10-degree steady white annulus. Three different chromaticities, lying close to illuminants A, C and E, were chosen for the annulus. Unique yellow was estimated by means of the four-staircase method described above. The results, shown in Figure 7.1.5, make it clear that unique yellow does not lie on a tritan line passing through the reference white: the hypothesis is not supported. The lines pass much closer to the spectral region of unique blue. There is thus an interesting discrepancy between (1) the wavelength of supra-threshold unique yellow in the presence of a white annulus and (2) the wavelength of Sloan's notch for increment thresholds measured on a white background. In

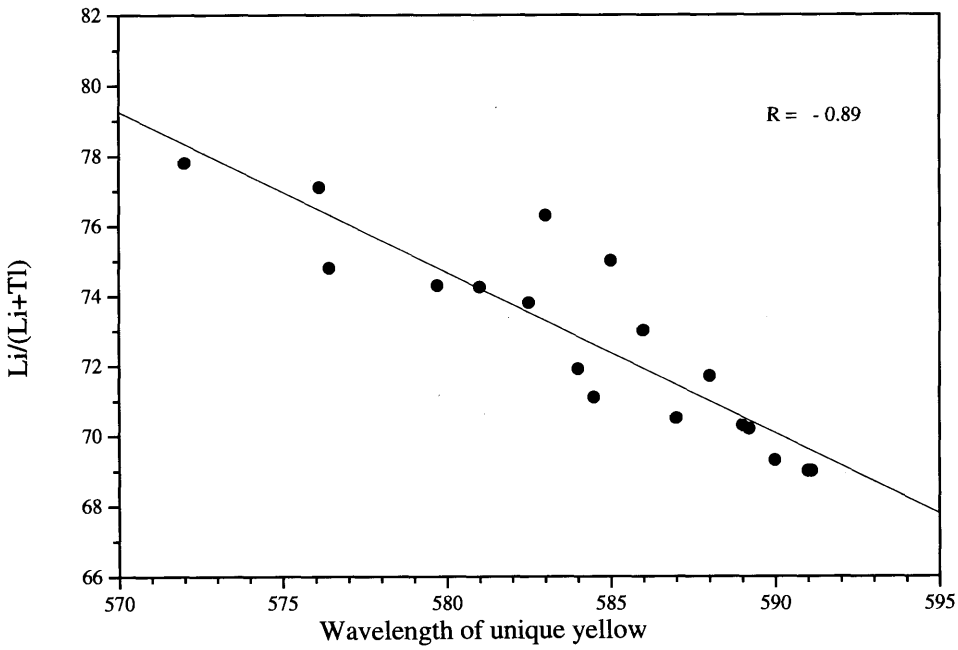

Figure 7.1.4. Rayleigh matches are plotted as a function of the wavelength seen as unique yellow. The data are taken from tables published by Donders in 1884. Li and Tl denote the Fraunhofer lines for spectral red and green. The higher the amount of red in the red-green mixture needed to match the standard yellow (Na), the shorter the wavelength set as unique yellow. This relationship was later termed *Donder's law* by Westphal (1910).

the latter case, the wavelength of minimal sensitivity does lie closely on a tritan line passing through the chromaticity of the background white (Fach and Mollon, 1987).

In summary then, our own investigations have failed to relate unique yellow to either the relative numbers or the spectral sensitivities of the long- and middle-wave cones. Nor does unique yellow prove to be a tritan metamer of a white reference supplied in the experiment. Let us turn to unique green, a case where we have found one correlate of individual differences.

7.1.5 INDIVIDUAL VARIATIONS IN UNIQUE GREEN

Unique green has traditionally been found to vary more than does unique yellow or unique blue. There have been recurrent suggestions that the distribution is bimodal (Richards,

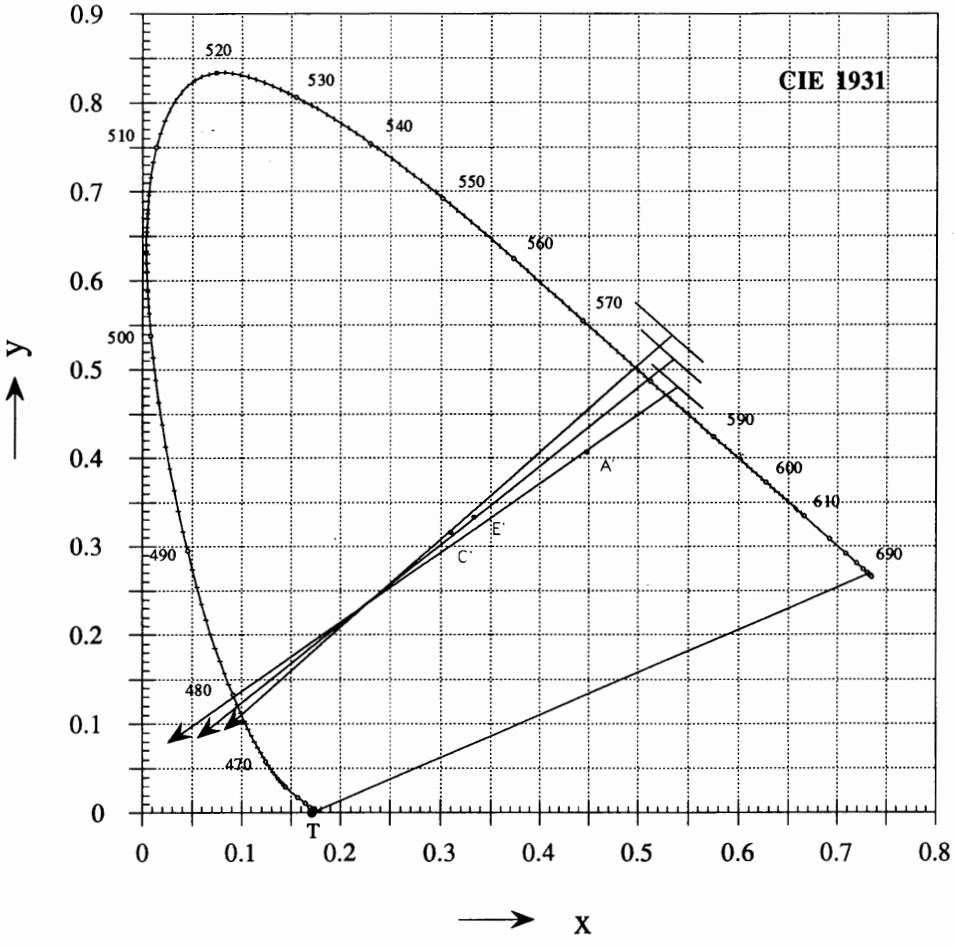

Figure 7.1.5. CIE x, y chromaticity diagram. The mean unique yellow settings for 19 observers are plotted as a function of three different white backgrounds. The short bars parallel to the spectrum locus indicate standard deviations. Lines connect each mean unique yellow with its associated reference white point (A, E, C respectively). Note that these lines do not pass through the tritanopic copunctal point (T).

1967; Rubin, 1961), and indeed some have held that the two phenotypes correspond to two phenotypes revealed by Rayleigh matches (Waaler, 1967). Hurvich *et al.* (1968) suggested that the apparent bimodalities arose from differential chromatic adaptation. Using our randomised staircase procedure to avoid systematic biases in adaptation, we have obtained estimates of unique green from a sample of 97 male observers (Jordan and Mollon, 1995). The background was dark. The distribution (Figure 7.1.6) was not bimodal, although, as others have found, it was skewed to long wavelengths. There was no correlation at all with the observers' Rayleigh matches. We may relate the increased spread of unique green, and the skew, to the way hue discrimination varies in this part of the spectrum: at wavelengths shorter than the modal value of unique green, most colour-normal observers exhibit very fine wavelength discrimination and subjective hue changes quickly, whereas at wavelengths longer than the modal value discrimination is poorer. We may suppose that subjects can more readily tolerate errors towards longer wavelengths than towards shorter.

Our study did, however, reveal one correlate of unique green. The experimenter rated the lightness of each subject's iris on a three-point scale and a Kruskal-Wallis test showed that there was a significant relationship between these ratings and unique green ($H = 13.12$, $p < 0.001$): subjects with light irises have unique green settings that lie at shorter wavelengths than do subjects with medium or dark irises.

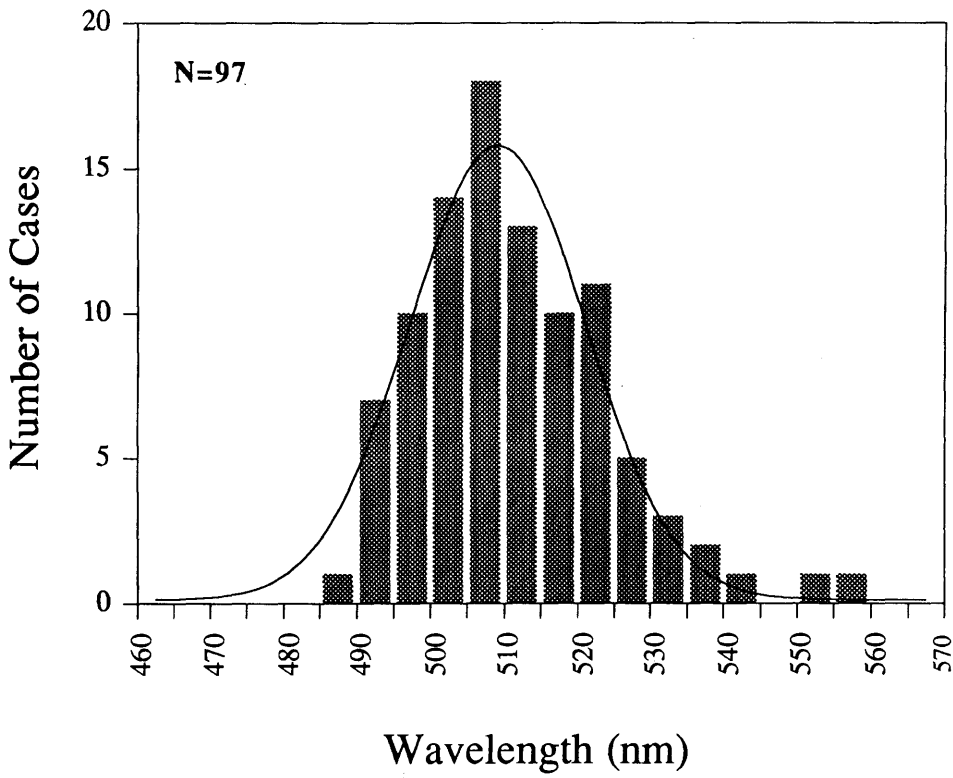

Figure 7.1.6. Distribution of the wavelength set as unique green by 97 normal male observers. The mean value is 511 nm with a standard deviation of 13 nm. The normal distribution with the same mean and standard deviation is shown as a solid line overlaid on the histogram. (The figure is replotted from Jordan and Mollon, *Vision Research*, 1995.)

Is there a clue here as to the nature of unique green? The lightness of the iris is often taken to be an index of the level of pigmentation present in the fundus of the eye, behind and between the photoreceptors. The absorption of light transmitted through the iris and sclera, and of light scattered within the eye, is greatest at short wavelengths, and so will modify the spectral composition of the light actually absorbed in the photoreceptors. However, the stimuli commonly used to establish unique hues are near-monochromatic ones, and ocular pigmentation should not modify the ratios of quantum catches that a given wavelength produces in the different cone types. Yet suppose that the spectral position of unique green does not correspond to a genetically fixed set of cone signals, but instead depends on the observer's interaction with broad-band stimuli in the real world. Consider two observers, one with light pigmentation, one with heavy, but with identical photopigments. Suppose that these observers agree that a certain leaf is neither glaucous nor yellowish. The ratios of quantum catches that the leaf produces in the cones of one observer must differ from the corresponding ratios for the other observer. If these two observers agree on unique green in the real world, then they ought to differ when we bring them into the laboratory and confront them with monochromatic lights. For they will need different monochromatic lights to imitate the cone ratios.

This approach to unique hues makes a clear prediction. The variance between observers should be less when they judge surface colours than when they judge spectral colours. We end by recalling the case of Dr Sulzer, examined by Donders (1884). The Rayleigh match for Dr Sulzer's left eye lay at the protan end of the normal distribution whereas the match for his right eye lay at the deutan end. With his left eye Dr Sulzer chose 577 nm for unique yellow, and with his right eye he chose 587 nm, but there was no difference between his eyes when he was asked to choose the unique yellow in a set of graded papers differing in steps of one j.n.d.

7.1.6 ACKNOWLEDGEMENTS

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7.1.7 NOTES

1. It might seem more accurate to express the hypothesis not in terms of the spectral composition of the average illumination of the observer's world but in terms of the average illumination of the retina. However, the latter stimulus may not correspond to the colour we perceive as neutral, for the average reflectance of surfaces in the observer's world may not correspond to a grey colour but be biased, say to olive green (Brown, 1994). It is the illuminant chromaticity that we judge to be achromatic. This consideration might be taken to suggest that the long-term reference white was neurally incorporated not in the equilibrium points of retinal channels but in a more central process.

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