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Rayleigh Matches and Unique Green

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There are recurrent reports that Rayleigh matches are bimodally distributed in the colour-normal male population. Similar claims have been made for the distribution of the spectral locus of unique green. Moreover, a positive correlation has sometimes been reported between Rayleigh matches and unique green. Using a computer-controlled Maxwellian colorimeter and bias-free psychophysical methods, we measured both variables for 97 colour-normal male observers. We do not find a bimodal distribution either of Rayleigh matches or of settings of unique green. Nor do we find any correlation between the two variables. However, we do observe a very significant relationship between the lightness of the subject's iris and the wavelength that he judges to be unique green.

Colour vision Rayleigh matches Unique green Genetics Bimodality Eye colour Ocular pigmentation

INTRODUCTION

There may be said to be two classes of people in the world: those who constantly divide the people of the world into two classes and those who do not—Benchley

A central issue in colour science is that of the transformations that intervene between the signals at the cone level and the signals that underlie phenomenal experience. Colour matches, such as the Rayleigh match, are thought to be determined at the receptor level, whereas the basis of judgements of unique hues is more mysterious: the unique, or equilibrium, hues do not bear any simple relationship to the chromatically opponent signals recorded electrophysiologically at the early stages of the visual system and it is not known how they are altered by the small spectral shifts of photopigments that are now believed to be present within the colour-normal population.

It has been claimed, and it has been denied, that Rayleigh matches are bimodally distributed within the normal male population. Similar claims and similar denials have been made in the case of unique green. Moreover, it has been held that the two subgroups for Rayleigh matches corresponded to the two subgroups for unique green. In the present study we obtain both measures for a homogeneous group of young male emmetropes.

Rayleigh matches

In a classical Rayleigh match, the observer is asked to adjust the relative amounts of red and green spectral lights in a mixture to match a spectral orange (Lord Rayleigh, 1881). The match is complete when the quantum catches in the M- and L-cones illuminated by the mixture are the same as the quantum catches of the corresponding cones illuminated by the standard. Although molecular genetic studies have shown clear polymorphisms that affect the spectral position of at least the long-wave pigment (Winderickx, Lindsey, Sanocki, Teller, Motulsky & Deeb, 1992), the form of the psychophysical distribution of Rayleigh matches for normal observers remains controversial. Waaler (1967a,b) and Neitz and Jacobs (1986, 1990) independently reported the existence of two distinct groups of men in Caucasian populations. Deegan, Neitz and Jacobs (1989) have reported a similar bimodality for an Asian population; and a strikingly bimodal but asymmetric distribution appears without comment in an earlier study of 2500 Yugoslavs (Sebastian, 1966). Furthermore, Neitz and Jacobs (1989) have re-analysed the colour matches of 33 male observers in the 10-deg colour-matching study of Stiles and Burch (1959) and have reported that Kruskal's test shows a significant bimodality in these data.

However, other studies, while agreeing that normals do vary in their Rayleigh matches, have found distributions that were gaussian or at least were not significantly bimodal (Houston, 1922; Nelson, 1938; Rushton & Baker, 1964; Jordan & Mollon, 1988; Lutze, Cox, Smith & Pokorny, 1990; Winderickx *et al.*, 1992). Also Webster (1992) has re-applied the Kruskal test to the male observers of Stiles and Burch and has shown that there is no statistical evidence for bimodality; a significant result can be achieved only by a form of statistical gerrymandering in which the outliers of the total distribution are suppressed and the Kruskal test is applied only to a selected range of observers lying in the middle of the distribution. The suggestion has been made by Piantanida and Gille (1992) that the form of the

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distribution depends on the psychophysical method: for a sample of 31 male observers, the method of adjustment gave a unimodal distribution while a forced-response method appeared to give a multimodal distribution. However, small samples from normal distributions often look deceptively non-gaussian and Piantanida and Gille offer no statistical test for the multimodality claimed in the forced-choice condition.

Unique green

Unique hues are defined as those hues that are phenomenologically pure or unmixed in quality: thus unique green is that green that appears neither bluish nor yellowish. The four unique hues (blue, yellow, red and green) are central to classical Opponent Process Theory and are held to be those colours for which one of the putative opponent processes, or chromatic response functions, is in balance (Hering, 1878, 1880; Jameson & Hurvich, 1968; Abramov & Gordon, 1994). Thus, unique green represents the wavelength that leaves in neutral equilibrium the blue–yellow chromatic response function.

There have been repeated reports that the distribution of unique green is bimodal for colour-normal observers, with the maxima for the two groups lying near 514 and 526 nm (Rubin, 1961; Richards, 1967; Waaler, 1967a,b; Cobb, 1975). And in a study on the Bezold–Brücke hue shift, Jacobs and Wascher (1967) report two types of observer who exhibit unique green points around 513 and 525 nm at a low luminance level (320 td), but who form a single group at a higher level of luminance (3200 td)—a result which Jacobs and Wascher relate to a shift to short wavelengths that is observed in the spectral crosspoints of "+Y−B" LGN cells as the luminance of the stimulus is increased (De Valois, Abramov & Jacobs, 1966).

In contrast to these reports it has been held that the bimodality in the spectral location of unique green is the result of differential chromatic adaptation during the experimental procedure and that the distribution is unimodal when the experimental conditions guarantee a neutral state of adaptation (Hurvich, Jameson & Cohen, 1968). No bimodality is seen in the distribution given by Shefrin and Werner (1990), although it must be said that these authors deliberately included observers of very different ages and were able to show a variation of unique green settings with age, which may have masked an underlying bimodality.

Relationship between Rayleigh matches and settings of unique green

Waaler (1967a,b, 1968) has made the strong claim that the two dichotomies—in Rayleigh matches and in unique green—are genotypically one and the same: he reports that men with a unique green point around 514 make more deutan settings on the anomaloscope (i.e. need more green in the mixture to match the monochromatic yellow) whereas men with unique green points around 525 make more protan settings (i.e. need more red in the mixture to make a match). Equally, however, there are those who report a bimodality of unique green but explicitly deny any relationship with Rayleigh matches (Rubin, 1961). Metz and Balliet (1973) found a correlation of virtually zero between the two measures.

Present experiment

In the experiment reported here, we obtained distributions of Rayleigh matches and settings of unique green for a sample of 97 colour-normal, emmetropic, young male caucasians. In the case of both measures, we were concerned to use modern adaptive psychophysical procedures that could not introduce systematic biases into the subjects' responses: the final estimate of Rayleigh match or of unique green was obtained by a procedure in which four staircases were randomly interleaved. 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, Knoll & Zukofsky, 1982). However, since the method is adaptive, it avoids the 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 (Poulton, 1979).

METHODS

Observers

The observers were 97 emmetropic, male Caucasians in the age range 19–30 yr. All were paid volunteers and were naive as to the aim of the experiment. Subjects were shown to be colour-normal by the Ishihara plates and the Nagel anomaloscope (Model I, Schmidt & Haensch).

Apparatus

Rayleigh matches and unique green points were measured with the aid of a three-channel Maxwellian view colorimeter (Jordan, 1992). The stimulus configuration used for both types of measurement, as well as the primaries used for the Rayleigh matches, were chosen to correspond to those used by Neitz and Jacobs (1986). The stimulus field was circular, subtending 9.6 deg of visual angle, and the central 2.9 deg were occluded. The mixture primaries used for the Rayleigh equation were 546 and 690 nm and were provided by narrow-band interference filters (bandwidths at half-height are 7.6 and 6.3 nm respectively). The comparison wavelength of 600 nm was provided by a Bentham M300 monochromator. This beam alone was used in the estimation of unique green.

The primaries providing the mixture field for the Rayleigh match were orthogonally polarized: the 690 nm beam was transmitted by a sheet-polarizer whereas the 546 nm beam was combined with the red beam by reflection at a glass plate set at Brewster's angle. A rotating polarizer, mounted on a stepper motor, served to control the proportion of red and green in the mixture beam. The 600 nm comparison beam was then introduced by reflection into the mixture beam, by means of a beamsplitting plate so placed as to form a large angle with the mixture beam. Thus, the transmission at the

beamsplitter did not depend on the polarization of the R/G-mixture.

The intensities of the three beams were adjustable by means of neutral-density wedges under computer control. For the Rayleigh match, each beam was set to give 100 td at its maximum. A joystick allowed the observer to adjust the intensity of the standard during the Rayleigh match. In the case of the unique green setting, the computer was programmed to hold the stimulus luminance at 20 td as wavelength was changed during the experiment. Calibrations were taken with a silicon PIN 10 photodiode before each observer was run.

Procedures

Before the measurements began, the subject's pupil was centred on the stimulus beam by means of an adjustable chin-rest. We drew the attention of subjects to the subjective cues of misalignment (asymmetry of the halo of scattered light around the stimulus field; chromatic aberration when mixed fields were presented) and asked them to stop responding and realign their eye if they became aware of misalignment during the measurements.

Unique green. The unique green point was measured before the Rayleigh match to ensure the settings were not influenced by any chromatic adaptation occuring during the Rayleigh matching. An automated adaptive procedure was used to avoid systematic biases. Monochromatic stimuli of 2 sec duration were presented against a dark field and the observer was required to indicate by pushbuttons whether the stimulus looked *too blue* or *too yellow* to be a pure green. A preliminary double alternating staircase procedure was used as a practice run and served to yield starting points for the main experiment. The final estimate was obtained by a program in which four staircases were randomly interleaved, with a final step size of 1 nm. The program ended after six reversals had been obtained on each staircase and the estimate of unique green was based on the last four reversals of each staircase.

Rayleigh matches. A temporal substitution method was used, in which the mixture and standard fields were alternated for equal durations of 1.8 sec with an ISI of 100 msec. In using temporal substitution we followed Neitz and Jacobs (1986), but with the refinement that mixture and standard were of equal duration, in order to ensure that the colour match was truly symmetric and unlikely to be influenced by post-receptoral factors. The observer's task was to decide whether the mixture field (indicated by an auditory signal) was *too red* or *not red enough.* As in the case of unique green, a preliminary estimate of the match was obtained with an alternating double staircase procedure. Before this run a brightness match was made to a mixture falling near the middle of the population range, and subsequently a brightness match was made to the preliminary estimate of the observer's match point. Four interleaved and randomized staircases were then used to obtain the final estimate of the Rayleigh match. Eight reversals on each staircase were taken as a criterion for a stable Rayleigh match, and the estimate of the match point was based on the last six reversals of each staircase.

A record was kept of each subject's eye colour. Using natural daylight, the experimenter (GJ) rated the lightness of the subject's iris on a three-point scale and also scored the colour as brown, brown-green, green, green-grey, grey, grey-blue or blue.

RESULTS

Rayleigh matches

Following Neitz and Jacobs (1986), we first converted the raw data into R/(R+G)-values. The actual energy values of the two mixture primaries were multiplied by constants so that the average match-point across all subjects was equal to R/(R+G)=0.5. The power values at this point were 0.188 μW for the 690 nm primary and 0.00108 μW for the 546 nm primary.

The distribution of large-field Rayleigh matches for the 97 observers is plotted in Fig. 1. Normalized to R/(R+G)=0.5, the distribution has a standard deviation of 0.038. The solid line shows a fitted Gaussian with the same mean and standard deviation.The appearance of a plotted distribution can often depend on the bin-size and the choice of bin boundaries; and in Fig. 1 we have deliberately chosen the bin size that most prominently brings out a small dip in the distribution near R/(R+G)=0.475 and so favours the hypothesis that Rayleigh matches are bimodally distributed (Neitz & Jacobs, 1986). However, no significant difference was found between the empirical and theoretical normal distribution by the Kolmogorov–Smirnov and χ^2 tests and no significant departure from normality was found according to Geary's test for non-normality (D'Agostino, 1970). Test statistics are shown in Table 1. Furthermore, Kruskal's measure of "dip intensity", a non-parametric statistic specifically designed to test for bimodality

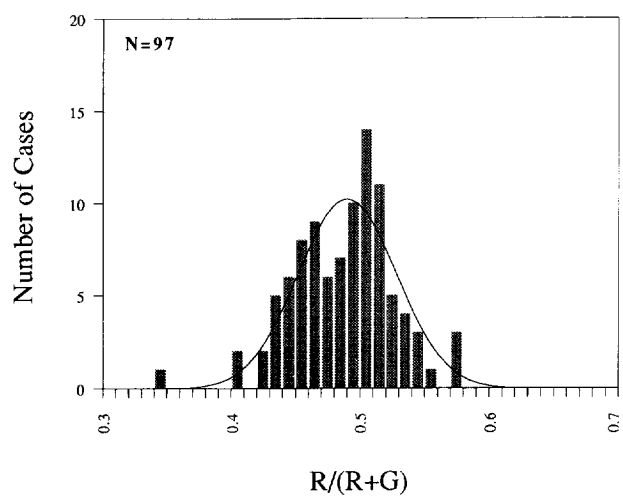

FIGURE 1. Distribution of large-field Rayleigh matches. The number of observers is plotted as a function of the relative proportion of the long-wave primary in the match. A normal distribution with the same mean and standard deviation is shown as a solid line overlaid on the histogram.

TABLE 1. Test statistics for normality (Kolmogorov–Smirnov, χ^2 and Geary) and for bimodality (Kruskal) are shown for the large-field Rayleigh match and unique green distributions

Statistical test		Rayleigh matches	Unique green
Kolmogorov–Smirnov test	D	0.07	0.09
	P	0.22	0.16
χ^2test	χ^2	19.52	7.91
	d.f.	21	14
	P	>0.5	>0.8
Geary's test	a	0.7938	0.7905
	P	>0.1	>0.1
Kruskal's test	Dip intensity	1.263	—
	P	>0.5	—

For $n=100$ and $\alpha=0.05$, the critical value of Kruskal's dip intensity is 2.07.

(Giacomelli, Wiener, Kruskal, Pomeranz & Loud, 1971), was well below the critical value for significance. Note that none of the tests used—except the χ^2 test—depends on assumptions about bin size.

The estimate of each subject's match was based on four randomly interleaved staircases and good agreement was found among the four separate estimates of the match: the average standard deviation of the four staircases was 0.005 when expressed in terms of R/(R+G) units. A one-way analysis of variance gave a highly significant F value of 144 for the ratio of the *between-subjects* and *within-subjects* variance, although it must be understood that the *between-subjects* variance here includes all sources of long-term experimental error.

To summarize, we find considerable inter-individual variation in the Rayleigh matches of 97 observers and the spread is comparable with the spread of data reported by Neitz and Jacobs (1986) and Jordan and Mollon (1988). However, there is no statistical evidence that the distribution is other than normal.

Unique green

Figure 2 shows the frequency distribution of the unique green points of 97 observers. The mean of the distribution is 511 nm with a standard deviation of 13 nm. In the plot shown, the bin size has been chosen to be 5 nm; the use of smaller bin sizes did not lead to significant changes in the appearance of the histogram. The solid line shows a fitted Gaussian with the same mean and standard deviation as the sample distribution. The distribution shows no obvious sign of bimodality, but exhibits some skew to the right.

No significant difference was found between the empirical distribution and the theoretical normal distribution by the Kolmogorov–Smirnov, χ^2 and Geary tests. Test statistics are given in Table 1. However, the skew to long wavelengths is significant ($g_1=0.79$, $t=3.18$, $P<0.01$) and it remains significant when the distribution is expessed in terms of wavenumber rather than wavelength ($g_1=-0.63$, $t=2.53$, $P<0.05$).

The separate estimates of each subject's unique green setting showed good agreement, the average standard deviation of the four estimates being 1.63 nm. An analysis of variance gave a highly significant F value of 191 for the ratio of the *between-subjects* and *within-subjects* variance, although it must again be noted that the *between-subjects* variance includes the long-term experimental error.

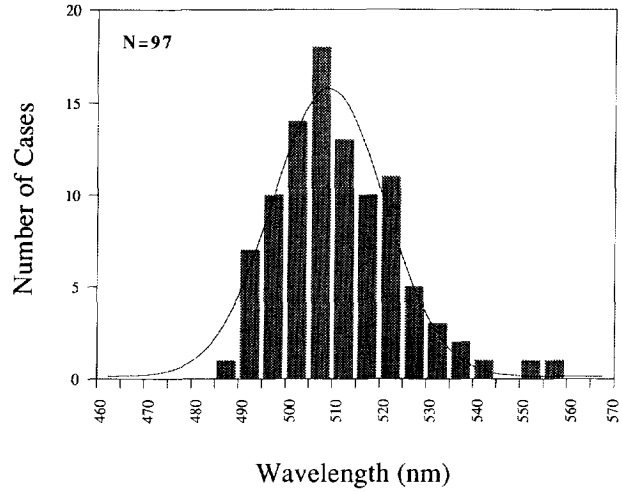

FIGURE 2. Distribution of unique green. The number of observers is plotted as a function of their unique green setting, expressed in units of wavelength. The normal distribution with the same mean and SD is shown as a solid line overlaid on the histogram.

To summarize, there is evidence for a substantial inter-individual variation in the spectral location of unique green and the distribution is skewed to long wavelengths. There is no sign of the bimodality reported by others (Rubin, 1961; Richards, 1967; Waaler, 1967a,b, 1968).

Correlation between Rayleigh matches and unique green

For the sample of 97 observers, we calculated the linear regression of the unique green values on the Rayleigh matches. Figure 3 illustrates the clear absence of a relationship between the two variables: there is effectively no correlation between the Rayleigh matches and settings

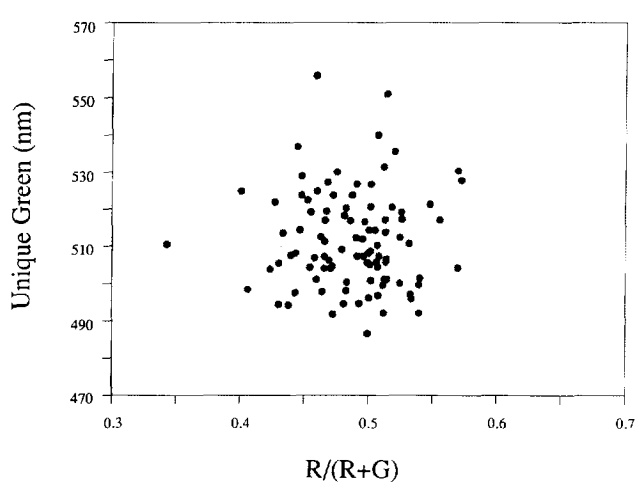

FIGURE 3. Relationship between Rayleigh matches and unique green. For 97 observers the wavelength of unique green is plotted against the proportion of red in the Rayleigh match. There is no correlation between the two variables.

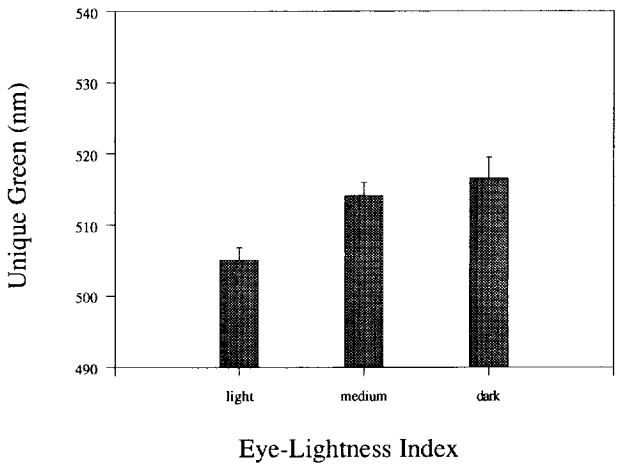

FIGURE 4. Eye lightness and unique green. Average settings of unique green when observers were categorized according to the lightness of their iris. The error bars represent 1 SEM. Observers with light irises make unique green settings at shorter wavelengths.

of unique green ($r = -0.02$). Our result is concordant with those of Westphal (1910) and of Metz and Balliet (1973), but contradicts the claim of Waaler that there are two genotypes consistently distinguished by their Rayleigh matches and by their settings of unique green.

Eye colour and lightness

The Kruskal–Wallis test showed no relation between Rayleigh match and either the colour or the lightness of the iris. Nor was there a significant relationship between unique green and colour of the subject's iris. However, a highly significant relationship was found between unique green and the lightness of the iris ($H = 13.12$, $P < 0.001$): subjects with light irises have unique green settings that lie at shorter wavelengths than do subjects with medium or dark irises. This finding is illustrated in Fig. 4.

DISCUSSION

Distribution of Rayleigh matches

Our distribution of large-field Rayleigh matches for 97 colour-normal males cannot be described as significantly bimodal and it cannot be statistically distinguished from a Gaussian distribution. Nevertheless, we confirm that there is a large variation in Rayleigh matches among normal observers and our results are consistent with underlying polymorphisms of the genes that code for the long- and middle-wave photopigments. Such polymorphisms are now securely established, but what is still at issue is whether phenotypically there are two main groups of male observer and a correspondingly bimodal distribution of Rayleigh matches.

Neitz and Jacobs (1986) originally postulated that a polymorphism of the L pigment accounted for the distinct bimodal distribution in Rayleigh matches and they subsequently suggested that the polymorphism consisted in a single substitution of alanine for serine at site 180 in the amino-acid sequence of the opsin molecule (Neitz, Neitz & Jacobs, 1991b): the presence of alanine at this site displaces the peak sensitivity of the photopigment to shorter wavelengths, thus giving a lower sensitivity to long-wave light and higher settings of Rayleigh match-points. In a study by Winderickx *et al.* (1992), the phenotypes of a population of 50 normal trichromats were related to their underlying opsin genes. The authors report that a common polymorphism does occur at amino acid residue 180 of the long-wave opsin. However, Winderickx *et al.* also report additional, less frequent, amino-acid polymorphisms in the L pigment of colour normals ($230^{ile/thr}$, $233^{ala/ser}$), which may affect the phenotype, while Merbs and Nathans (1992) and Asenjo, Rim and Oprian (1994) have expressed opsins *in vitro* and have shown that the spectral sensitivity of the molecule can indeed be affected by substitutions of positions other than site 180 and the two sites (277, 285) that primarily determine whether the pigment is long-wave or middle-wave. Although the polymorphism found at site 180 clearly accounts for much of the phenotypic variance, the distribution shown by Winderickx *et al.*, does not appear to be statistically bimodal.

Curiously, Neitz *et al.*, who originally reported a firm bimodality of Rayleigh matches and postulated a single polymorphism of the long-wave pigment, have more recently reported molecular results that are hardly compatible with a phenotypic bimodality. Thus, Neitz and Neitz (1992a) report that not only the long-wave, but also the middle-wave opsin is characterized by a polymorphism at site 180. Moreover, they also suggest (Neitz, Neitz & Jacobs, 1991a, 1993; Neitz & Neitz, 1992b, 1993) that males may carry, and express, more than one copy of both the long-wave and the middle-wave opsin gene. If both pigments are polymorphic, if men may express more than one allele of each gene, and if polymorphisms are also present at other sites, then it is very odd that there were two such discrete groups of men in the psychophysical study of Neitz and Jacobs (1986) and that the distribution for women was so different from that for men.

Other sources of variance in Rayleigh matches. Factors other than the peak sensitivities of the long- and middle-wave photopigments may contribute considerably to the phenotypic variation of normal observers (e.g. Webster & MacLeod, 1988). Among such factors are: wavelength-selective absorption by the optic media; macular pigment [which may absorb at wavelengths used in the Rayleigh equation (Ruddock, 1963; Pease, Adams & Nuccio, 1987)]; optical density of the photopigments; and intrusion from rods and short-wave cones. In using a homogeneous population of young men, we have probably minimized the variance due to variations in the lens and other optic media. We have followed Neitz and Jacobs (1986) in using an annular field with the centre blocked off and so have probably minimized the influence of variations in macular pigment and in the optical density of the foveal photopigments. Our 10-deg stimulus field is well into the photopic range (100 td) but it falls on a retinal area containing many rods and we cannot rule out the possibility that rod intrusion may account for some

of the variance in our observers. However, we have also failed to find a bimodality of Rayleigh matches when using 1000-td fields (Jordan & Mollon, 1988). The shortest primary used in the Rayleigh equation was 546 nm and thus we expect the influence of short-wave cones to be minimal.

To minimize the effects of optical density and of pre-receptoral screening pigments, He and Shevell (1994) have used dual Rayleigh matches in which the green and yellow primaries are fixed but the remaining primary is either 620 or 670 nm. When the ratio of the two matches was considered, 16 male subjects fell into two non-overlapping groups according to whether their long-wave opsin gene coded for alanine or for serine at site 180 (Sanocki, Shevell & Winderickx, 1994). If this clear separation were to hold for a larger sample and if the primers used for the PCR analysis do isolate the long-wave gene, then there can be little variance attributed to (a) polymorphism of site 180 in the middle-wave gene or (b) polymorphisms at other sites in either gene, particularly if alternative versions of either the middle- or the long-wave gene can be expressed within one retina.

Distribution of unique green

Hurvich *et al.* (1968) have emphasized that settings of unique green may be influenced by the subject's state of adaptation. Our psychophysical procedure, employing four randomally interleaved staircases, avoids any systematic bias in the order in which stimuli are presented to the observer; and it also avoids the range effects that are likely to be introduced by the Method of Constants. The luminance of the target was automatically held constant as wavelength was varied. No stimuli were present except the 9.6-deg annular target. Using this method we do not find the two distinct types of observer reported by others (Rubin, 1961; Richards, 1967; Waaler, 1967a,b, 1968; Cobb, 1975): our distribution of unique green points is unimodal, although it resembles those of Rubin, Richards and Cobb in so far as it is positively skewed towards long-wavelengths. Our mean value of 511 nm is close to the value of 515 nm reported by Dimmick and Hubbard (1939), to the value of 510 nm reported for 3200-td stimuli by Jacobs and Wascher (1967), and to the value of 513–515nm typically reported for the shorter-wave mode by those who have obtained two groups of observers (Rubin, 1961; Richards, 1967; Jacobs & Wascher, 1967; Waaler, 1967a,b, 1968). To explain the skew often seen in distributions of unique green, we might most simply suppose that observers are more sensitive to short-wave departures from unique green than to long-wave departures, owing to the asymmetry of the hue-discrimination curve in this region of the spectrum (Wright & Pitt, 1934).

Our finding that settings of unique green are not correlated with Rayleigh matches is consistent with the early report of Westphal (1910), who noted that outliers in unique green settings (>520 nm) did not differ on the anomaloscope from observers who fell centrally in the distribution for unique green. No correlation was seen in a later study of 26 male observers by Metz and Balliet (1973) nor in a study of 91 female observers by Cobb (1975). It is generally held that colour matches, such as the Rayleigh match, depend only on the quantum catches in the photoreceptors and not on subsequent neural processing (Rushton & Baker, 1964), whereas the determinants of unique green are not yet understood. As we discussed above, the main source of variance in Rayleigh matches is likely to be variation in the spectral position of the long-wave and middle-wave photopigments. If there were a fixed and direct relationship between first-stage and second-stage processing (Jameson & Hurvich, 1968), then we might expect the polymorphism of the photopigments to account for much of the individual differences observed in settings of unique green. The fact that we find absolutely no relationship between our subjects' Rayleigh matches and their settings of unique green suggests that very little of the variance in settings of unique green is due to variation in the spectral positions of long- and middle-wave photopigments.

We did, however, find one correlate of unique green, and that was the lightness of the observer's iris. This relationship, between a psychophysical variable and an externally observed property of the subject, was highly significant and it shows that a substantial part of the variance in unique green settings cannot be instrumental in origin. But why should there be a relationship between these two variables? And does our finding offer a clue towards a theory 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. Yet the stimuli used to establish unique hues are near-monochromatic and so the level of pigmentation would not affect the ratios of absorptions produced in the cones by a given stimulus. We might suppose, however, that the spectral position of unique green does not correspond to a set of (transformed) cone signals that is genetically fixed. Rather it may depend on the observer's experience with broad-band stimuli in the real world. Consider a green-painted wall that is judged in daylight to be neither yellowish nor bluish by two observers, one with heavy pigmentation, the other with light pigmentation. Although these observers agree in the outside world, they ought to differ when judging monochromatic lights in the laboratory. In the real world, there will be a difference in the ratios of quantum catches that the green paint produces in the three cones, owing to the differential absorption of short wavelengths in the eye with heavier pigmentation. If now the two observers are asked in the laboratory to find the wavelength that produces the same ratios of quantum catches as does the pure green wall, then they ought to differ: the observer with the heavier pigmentation should choose a longer wavelength; and that is the result that we find.

This account places the ultimate determinant of unique green in the external world rather than within our psychophysical apparatus. But it does not say why a certain set of stimuli should come—phylogenetically or ontogenetically—to appear unique green. We may suppose that such stimuli correspond to a state of equilibrium in the phylogenetically older of the two sub-systems of human colour vision, i.e. the sub-system that draws inputs of opposite sign from the short-wave cones, on the one hand, and some combination of the signals of the long- and middle-wave cones, on the other (Mollon & Jordan, 1988). This would be analogous to the hypothesis that unique yellow corresponds to the ratio of quantum catches that is produced in the younger colour sub-system by the average stimulation of our world (Pokorny & Smith, 1977; Mollon, 1982). In the case of unique green, it remains to be determined whether the equilibrium set of quantum catches corresponds to that produced by the average illumination experienced by the observer or, say, to that produced by vegetation.

REFERENCES

Abramov, I. & Gordon, J. (1994). Color appearance: On seeing red—or yellow, or green, or blue. *Annual Review of Psychology, 45*, 451–485.

Asenjo, A. B., Rim, J. & Oprian, D. D. (1994). Molecular determinants of human red/green color discrimination. *Neuron, 12*, 1131–1138.

Cobb, S. R. (1975). The unique green phenomenon and colour vision. *Clinical Genetics, 7*, 274–279.

D'Agostino, R. B. (1970). Simple compact portable test of normality: Geary's test revisited. *Psychological Bulletin, 74*, 138–140.

Deegan, J. F., Neitz, J. & Jacobs, G. H. (1989). Variations in color matching among asian males. *Investigative Ophthalmology and Visual Science (Suppl.), 30*, 127.

De Valois, R. L., Abramov, I. & Jacobs, G. H. (1966). Analysis of response patterns of LGN cells. *Journal of the Optical Society of America, 56*, 966–977.

Dimmick, F. L. & Hubbard, M. R. (1939). The spectral location of psychophysically unique yellow, green, and blue. *American Journal of Psychology, 52*, 242–254.

Giacomelli, F., Wiener, J., Kruskal, J. B., Pomeranz, J. V. & Loud, A. V. (1971). Subpopulations of blood lymphocytes demonstrated by quantitative cytochemistry. *Journal of Histochemistry and Cytochemistry, 19*, 426–433.

He, J. C. & Shevell, S. K. (1994). Individual differences in cone photopigments of normal trichromats measured by dual Rayleigh-type color matches. *Vision Research, 34*, 367–376.

Hering, E. (1878). *Zur Lehre vom Lichtsinne. Sechs Mittheilungen an die Kaiserliche Akademie der Wissenschaften in Wien*. Wien: Carl Gerlold's Sohn.

Hering, E. (1880). *Zur Erklärung der Farbenblindheit aus der Theorie der Gegenfarben*. Sonderabdruck aus dem Jahrbuch für Naturwissenschaft 'Lotos'. Neue Folge. 1. Band. Prag: Von F. Tempsky.

Houston, R. A. (1922). An investigation of the colour vision of 527 students by the Rayleigh test. *Proceedings of the Royal Society of London A, 102*, 353–360.

Hurvich, L. M., Jameson, D. & Cohen, J. D. (1968). The experimental determination of unique green in the spectrum. *Perception & Psychophysics, 4*, 65–68.

Jacobs, G. H. & Wascher, T. C. (1967). Bezold–Brücke hue shift: Further measurements. *Journal of the Optical Society of America, 57*, 1155–1156.

Jameson, D. & Hurvich, L. M.(1968). Opponent-response functions related to measured cone photopigments. *Journal of the Optical Society of America, 58*, 429–430.

Jordan, G. (1992). Polymorphism of normal colour vision in humans. Ph.D. dissertation, Cambridge University, Cambridge.

Jordan, G. & Mollon, J. D. (1988). Two kinds of men? *Investigative Ophthalmology and Visual Science (Suppl.), 29*, 164.

Lord Rayleigh (1881). Experiments on colour. *Nature, 25*, 64–66.

Lutze, M., Cox, N. J., Smith, V. C. & Pokorny, J. (1990). Genetic studies of variation in Rayleigh and photometric matches in normal trichromats. *Vision Research, 30*, 149–162.

Merbs, S. L. & Nathans, J. (1992). Absorption spectra of the hybrid pigments responsible for anomalous color vision. *Science, 258*, 464–466.

Metz, J. W. & Balliet, R. F. (1973). Two genetic types of normal colour vision. *Nature New Biology, 242*, 190.

Mollon, J. D. (1982). Color vision. *Annual Review of Psychology, 33*, 41–85.

Mollon, J. D. & Jordan, G. (1988). Eine evolutionäre Interpretation des menschlichen Farbensehens. *Die Farbe, 35*, 139–170.

Neitz, J. & Jacobs, G. H. (1986). Polymorphism of the long-wavelength cone in normal human colour vision. *Nature, 323*, 623–625.

Neitz, J. & Jacobs, G. H. (1989). Polymorphism of cone pigments among color normals: Evidence from color matching. In Drum, B. & Verriest, G. (Eds), *Colour vision deficiencies IX* (pp. 27–34). Dordrecht: Kluwer.

Neitz, J. & Jacobs, G. H. (1990). Polymorphism in normal color vision and its mechanism. *Vision Research, 30*, 621–636.

Neitz, J. & Neitz, M. (1992a). Do people with anomalous color vision have anomalous pigments? *Investigative Ophthalmology and Visual Science (Suppl.), 33*, 754.

Neitz, M. & Neitz, J. (1992b). Males usually have more than one L pigment gene. *Investigative Ophthalmology and Visual Science (Suppl.), 33*, 754.

Neitz, M. & Neitz, J. (1993). Individual males can express five different cone pigment genes. *Investigative Ophthalmology and Visual Science (Suppl.), 34*, 911.

Neitz, J., Neitz, M. & Jacobs, G. H. (1991a). Matches from normal trichromatic males suggest some eyes contain more than three cone types. *Investigative Ophthalmology and Visual Science (Suppl.), 32*, 1092.

Neitz, M., Neitz, J. & Jacobs, G. H. (1991b). Spectral tuning of pigments underlying red–green color vision. *Science, 252*, 971–974.

Neitz, J., Neitz, M. & Jacobs, G. H. (1993). More than three different cone pigments among people with normal color vision. *Vision Research, 33*, 117–122.

Nelson, J. H. (1938). Anomalous trichromatism and its relation to normal trichromatism. *Proceedings of the Physical Society, 50*, 661–690.

Pease, P. L, Adams, A. J. & Nuccio, E. (1987). Optical density of human macular pigment. *Vision Research, 27*, 705–710.

Piantanida, T. P. & Gille, J. (1992). Methodology-specific Rayleigh-match distributions. *Vision Research, 32*, 2375–2377.

Pokorny, J. & Smith, V. C. (1977). Evaluation of single-pigment shift model of anomalous trichromacy. *Journal of the Optical Society of America, 67*, 1196–1209.

Poulton, E. C. (1979). Models for biases in judging sensory magnitude. *Psychological Bulletin, 86*, 777–803.

Richards, W. (1967). Differences among colour normals: Classes I and II. *Journal of the Optical Society of America, 57*, 1047–1055.

Rubin, M. L. (1961). Spectral hue loci of normal and anomalous trichromats. *American Journal of Ophthalmology, 52*, 166–172.

Ruddock, K. H. (1963). Evidence for macular pigmentation from colour matching data. *Vision Research, 3*, 417–429.

Rushton, W. A. H. & Baker, H. D. (1964). Red–green sensitivity in normal vision. *Vision Research, 4*, 75–85..

Sanocki, E., Shevell, S. K. & Winderickx, J. (1994). Serine/alanine amino acid polymorphism of the L-cone photopigment assessed by dual Rayleigh-type color matches. *Vision Research, 34*, 377–382.

Sebastian, M. (1966). Oligochromasia. Bericht über den internationalen Kongreß für Ophthalmologie in München. *Exerpta medica, 146*, 996–999.

Shefrin, B. E. & Werner, J. S. (1990). Loci of spectral unique hues throughout the life span. *Journal of the Optical Society of America A, 7*, 305–311.

Sternberg, S., Knoll, R. L. & Zukofsky, P. (1982). Timing by skilled musicians: Perception, production, and imitation of time ratios. In Deutsch, D. (Ed.), *The psychology of music* (pp. 181–239). New York: Academic Press.

Stiles, W. S. & Burch, J. M. (1959). NPL colour-matching investigation: Final report. *Optica Acta 6*, 1–26.

Waaler, G. H. M. (1967a). Heredity of two types of normal colour vision. *Nature*, *215*, 406.

Waaler, G. H. M. (1967b). The heredity of normal and defective colour vision. *Archiv Det Norske Videnskaps-Akademi*, *1*, 1–25.

Waaler, G. H. M. (1968). Heredity of two types of normal colour vision. *Nature*, *218*, 688–689.

Webster, M. A. (1992). Reanalysis of λ_{max} variations in the Stiles–Burch 10-deg color-matching functions. *Journal of the Optical Society of America A*, *9*, 1419–1421.

Webster, M. A. & MacLeod, D. I. A. (1988). Factors underlying individual differences in the color matches of normal observers. *Journal of the Optical Society of America A*, *5*, 1722–1735.

Westphal, H. (1910). Unmittelbare Bestimmungen der Urfarben. Eine Untersuchung zur Psychologie und Psychophysik. *Zeitschrift für Sinnesphysiologie*, *44*, 182–230.

Winderickx, J., Lindsey, D. T., Sanocki, E., Teller, D. Y., Motulsky, A. G. & Deeb, S. S. (1992). Polymorphism in red photopigment underlies variation in colour matching. *Nature*, *356*, 431–433.

Wright, W. D. & Pitt, F. H. G. (1934). Hue-discrimination in normal colour vision. *Proceedings of the Physical Society*, *46*, 459–473.

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