The distribution of unique green wavelengths and its relationship to macular pigment density

Lauren E. Welbourne* Department of Psychology, University of York, York, UK

Peter G. Thompson Department of Psychology, University of York, York, UK

Alex R. Wade Department of Psychology, University of York, York, UK

Antony B. Morland* Department of Psychology, University of York, York, UK
Centre for Neuroscience, Hull-York Medical School, York, UK

Monochromatic unique green (UG) is more variable across the population than any other unique hue. Some researchers have reported that this broad distribution of UG settings is bimodal and that the distribution results from the superposition of two or more subpopulations. We have investigated this claim using a Wright colorimeter to measure the unique green wavelength of 58 participants and we have analyzed previous unique green literature by applying a rigorous statistical test to historical datasets. We have also explored the possibility that individual differences in macular pigment density may be responsible for the variation in unique green wavelength. Our results indicate that unique green wavelengths in our population are distributed unimodally and are correlated positively with macular pigment density; individuals with a higher density of macular pigment select longer wavelengths of light as unique green than individuals with a lower density of macular pigment. We model this effect using simulations of monochromatic unique green matching to broadband illuminations and show that matches in the region at approximately 500 nm exhibit particularly high variance both with respect to macular pigment density and also with respect to the precise shape of the broadband reference exemplar spectrum.

Introduction

The "unique hues" of red, green, yellow, and blue have been recognized as having special perceptual properties for well over a century. Subjects are able to set these points reliably using a monochromator and perceive them as being "unique" in that they do not contain a mixture of any other color, for instance, unique green (UG) appears neither yellowish nor bluish (Jordan & Mollon, 1995; Schefrin & Werner, 1990). During the late 19th century and early 20th century, a number of studies were carried out into the spectral locations of the unique hues (Hering, 1890; Maerz & Paul, 1930; Verbeek & Bazen, 1935; Westphal, 1910; von Bezold, 1876—reviewed by Dimmick & Hubbard, 1939). Later studies then began highlighting the distribution of the wavelength settings across the population for each of these unique hues (Dimmick & Hubbard, 1939; Purdy, 1931). While all unique hues show some variability across subjects, the amount of variance is different for different hues and it has been found that unique green settings are the most variable while unique yellow settings are comparatively stable (Kuehni, 2004; Nerger, Volbrecht, & Ayde, 1995; Schefrin & Werner, 1990; Webster et al., 2002; Webster, Miyahara, Malkoc, & Raker, 2000). This observation is highlighted by Kuehni (2004), who compiled data from various studies and found that unique yellow settings vary across a range of approximately 15 nm while the equivalent range for unique green is 54.6 nm.

Despite general agreement that there is more variation in unique green wavelength settings than any other unique hue, it is unclear why this should be. Several studies have argued that the distribution of unique green is bimodal (Cobb, 1975; Richards, 1967; Rubin, 1961; Waaler, 1967), suggesting that the broad distribution observed is actually the superposition of

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two narrower distributions. However, further studies have not supported this claim (Hurvich, Jameson, & Cohen, 1968; Jordan & Mollon, 1995; Metz & Balliet, 1973; Schefrin & Werner, 1990).

Here, we explore the statistical distribution of unique green wavelength settings in our own measurements and in historical datasets using a modern statistical test for unimodality. We also investigate two possible causes for the variation of UG across individuals: variation in macular pigment optical density (MPOD), and slight variations in the spectra of unique green exemplars.

Methods

Participants

Participants were 60 undergraduate and postgraduate students from The University of York (30 female, 30 male) with a mean age of 21.77 years (± 4.27). Two male participants were excluded from the data analysis because their Rayleigh matches indicated inherited color vision deficiency. All other participants were confirmed as color-normal observers using Rayleigh matches. Approval for this study was granted by the departmental Ethics Committee at The University of York.

Apparatus

A Wright Colorimeter (Wright, 1928, 1939), originally built at Imperial College London in the early 1930s, was used for making Rayleigh matches, unique green settings and measurements of Macular Pigment Optical Density (MPOD). A square, bipartite viewing field (1.33° × 1.33°) was viewed monocularly through an eyepiece fitted with a doublet to counteract chromatic aberration of the human eye. The top half of the field contained the "mixing light," which could contain all, or a selection, of primaries blue, green, and red set at 460 nm, 530 nm, and 650nm, respectively. This half could also be occluded completely for performing unique green settings using just the bottom half of the field (resulting in a 0.67° × 1.33° viewing angle), which contained the "test" light. Depending on the measurement taken, the participant could either manipulate the test light in isolation until a particular wavelength value was obtained (i.e., perception of unique green), or alternatively the test light could be used as a reference to which the mixing light was matched by varying the amount of each primary contained in the mixture.

The Wright colorimeter was calibrated with a fiber-optic photospectrometer ("Jaz," Ocean Optics, Dumolin, FL) operating at 2 nm resolution. This device was, itself, calibrated against a National Institute of Standards Technology-traceable standard light source.

Color matching and unique green procedures

To assess each participant's color vision, subjects made Rayleigh matches with the colorimeter. For these matches, participants viewed a bipartite field and were required to vary the amount of the red (650 nm) and green (530 nm) primaries in the mixture to match the 590 nm test light. The color match was quantified in terms of log (R/G), where R and G are the relative radiance of the 650 nm and 530 nm matching stimuli.

On-axis macular pigment optical density (MPOD) measurements were obtained using the technique described in Ruddock (1963), in which subjects match a blue-green test light at 490 nm by varying the amount of red (650 nm), green (530 nm), and blue (460 nm) light in the mixture. In each subject we measured the quantity log (B/G), which correlates with MPOD. On-axis color matches made in this region of the spectrum are profoundly affected by MPOD, whereas off-axis matches are not. Therefore the difference between the on- and off-axis matches also yields an estimate of MPOD. However, off-axis matches are challenging for naive subjects and therefore we only had a subset of 12 "expert" observers make off-axis matches. For these color matches, subjects fixated a small, red, dim LED to the right of the bipartite field, placing the center of that field at a visual angle of 6.5° into the left visual field. For the off-axis match, the primaries were all set to the average values obtained from an on-axis match acquired in the same session. The subject then had to fixate the LED and adjust only 460 nm primary until the top and bottom of the stimuli in the participant's peripheral vision appeared to match. While the match was being made, a 4 Hz square wave flicker was applied to the stimulus by spinning a metal disc, which alternated between 90° metal sectors and 90° gaps, to reduce Troxler fading (Simons et al., 2006; Troxler, 1804). The difference between these on- and off-axis measurements was correlated with the expert observers' original on-axis measurements, giving a significant Pearson correlation of 0.78 ($p = 0.003$). Original on-axis values for all participants were then converted by subtracting the intercept value (V)—which was obtained from the regression line equation in the above correlation ($V = -0.50$)—from each participant's original on-axis value, i.e., MPOD = log(B/G)-V. Reassuringly, this correction yielded MPOD values that were in good agreement with previous studies (Davies & Morland, 2004) and no individual registered an anomalous value, i.e., a significant negative or unduly large MPOD.

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Finally, we measured unique green values for each participant. The participant was asked to adjust a single dial, which altered the wavelength of light viewed, until they perceived the viewing field to be pure green, i.e., neither bluish nor yellowish. This measurement was repeated six times—the experimenter manually randomized the starting point by adjusting the dial between each repeat—and the average of these measurements was used throughout the analysis. A broadband filter was inserted into the colorimeter to reduce the luminance variation of the spectral stimuli. The mean luminance was 20 cdm^{-2}. In a preliminary study we compared results when a filter was inserted with results without the filter; no differences occurred.

For the color matching experiments participants were instructed to make an initial match (for color and perceived brightness). For the Rayleigh matches, participants were first instructed to adjust the 530 nm primary in order to match each half based on brightness, before adjusting the 650 nm primary to match each half on color; if necessary the 530 nm primary could be adjusted again in order to get the closest possible match in both color and brightness between each half of the viewing field. Once the best match had been achieved, the values of both the 530 nm and 650 nm primary settings were recorded. The value of the 530 nm primary was then randomly adjusted above or below the "best match value" by the experimenter and the participant was required to reset only the 530 nm primary until the best match was reached again. This process was repeated until a total of four measurements had been recorded (the original value plus three repeats), these measurements were averaged and the 530 nm primary set to this value. The same procedure was then carried out for the 650 nm primary. Once the 650 nm primary had been set to the average value the participant was asked to check the quality of the match—all participants reported that at these mean settings a match was achieved. For the on-axis color match, used to assess macular pigment density, a 460 nm primary was also used, in addition to the 530 nm and 650 nm primaries. An initial best match for the viewing field was produced by the participant, matching for both brightness and color. Subsequently, starting with the 460 nm primary and followed by the 530 nm and then 650 nm primaries, the primary settings were adjusted by the experimenter and then reset to establish a best color match by the participant. This process was repeated three times, and the average of the four measurements was set before moving on to the next primary. In the subset of participants who performed the off-axis color matches, where only the 460 nm primary was adjusted, again a total of four measurements were taken. Participants were not given a time limit to perform any of these measures, and were encouraged to look away from the eyepiece occasionally when making matches and setting the wavelength at which they perceived unique green.

Iris lightness

Jordan and Mollon (1995) reported a significant trend for individuals with darker irides to make unique green settings at longer wavelengths. In order to determine whether Jordan and Mollon's trend was also a feature of our data, and to enable correlational analysis with both MPOD and unique green set points, we took photographs of each participant's eye (the same eye that was used to perform the monocular tasks). Photographs were taken using a Canon EOS 50D camera (Canon Inc., Japan) with a Canon EFS 17-85 mm IS F4-5.6 lens, a 67 mm HOYA UV filter (HOYA, Japan), and a Marumi DRF 14C ring flash (Marumi Optical Co. Ltd., Japan). The following camera settings were used: F5.6 aperture; 1/250-s shutter speed; ISO800 sensitivity; and shooting in color profile Adobe RGB. The lens zoom level was kept at 85 mm, and the photograph taken when the iris was centrally focused; this was judged by the appearance of a red indictor light on the camera's viewfinder. Two photographs were taken in quick succession; the flash from the first photograph aided in reducing the size of the pupil before the second photo was taken.

Using MatLab (MathWorks, Natick, MA), Iris lightness values were obtained by taking average RGB values from a manually selected square section of the iris, at the lefthand side of the pupil, and a maximum reflectance value from the camera flash reflection that was visible in the pupil (this was taken to be a constant reference point in each photograph). The ratio of the average iris RGB value to maximum reflectance value was taken as an estimation of iris lightness, therefore, the lightest irises were those with the highest iris lightness value.

In addition, to compare the findings of this study to those of Jordan and Mollon, who categorized their participants into three groups based on iris lightness, this variable was converted to a categorical variable for further data analysis; a K-means cluster analysis was performed using SPSS on the iris lightness data to split the data into three groups (Dark, Medium, and Light). This resulted in 27 participants in each of the Dark and Medium categories, and only four in the Light category. The cluster centers were 0.26, 0.39, and 0.76, respectively.

Analysis of previous unique green literature

A modern, robust test for unimodality, Hartigan's dip test (Hartigan & Hartigan, 1985), was applied to

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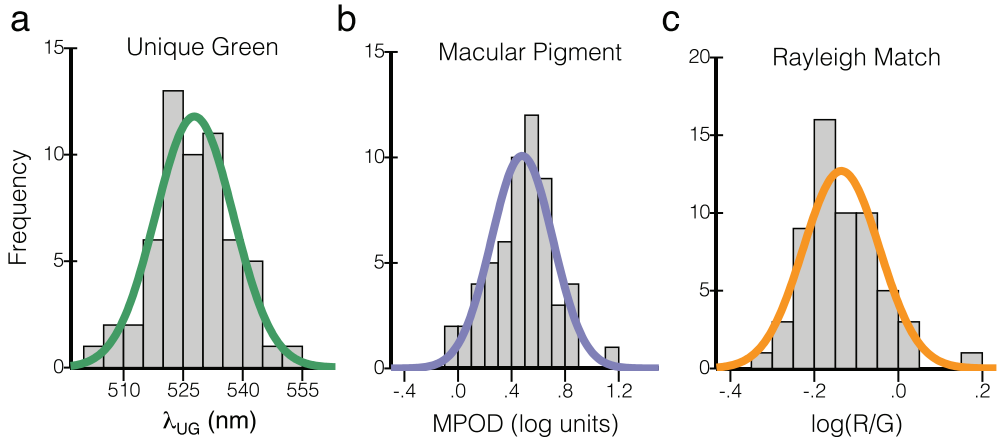

Figure 1. Frequency distribution graphs for a) Unique green wavelength (nm); b) MPOD (log units); and c) Rayleigh Match [log(R/G)].

our data and as many historical unique green datasets as we could obtain. The dip test was implemented by the "*diptest*" package in the statistics program "R." Many of these datasets were digitized from frequency histograms in printed manuscripts that we extracted using DataThief (http://datathief.org/; Tummers, 2006) because the underlying data points used to produce the histograms were not available.

The precise distribution of the data within each bin was generally unknown. One potential way of applying the dip test was to assume a uniform distribution of data within each bin. However, the dip test operates without regard to bin size and the within-bin distributions can affect the final result: Should all the points in two neighboring bins happen to cluster near their common boundary, they would generate more evidence for a peak compared to a distribution where they were distributed evenly across each bin. For this reason, we synthesized 1,000 random data distributions within each bin for each histogram and computed dip tests on each set of synthetic bins. Strong evidence for a bimodal distribution was indicated in those datasets that yielded a significant dip test p value (i.e., <0.05) for more than 50% of the synthesized within-bin data distributions.

Results

Distributions

Unique green wavelengths and MPOD were both found to have normal distributions (Figure 1a, b), with no evidence of skew or kurtosis [UG wavelength: mean = 527.85 nm, $Z_{Skewness} = -0.0679$ (NS), $Z_{Kurtosis} = 0.2102$ (NS); MPOD: mean = 0.479, $Z_{Skewness} = -0.1613$ (NS), $Z_{Kurtosis} = 0.6335$ (NS)]. Hartigan's dip test (Hartigan & Hartigan, 1985) was also carried out to confirm that no bimodality was evident in either unique green wavelength ($D = 0.0343$, $p = 0.919$) or MPOD ($D = 0.029$, $p = 0.9904$) distributions. Similarly, the Rayleigh matches (mean = −0.136) did not show a significant skew [$Z_{Skewness} = 1.9951$ (NS)], and there was no evidence of bimodality ($D = 0.0389$, $p = 0.7751$), however a test of kurtosis was found to be significant ($Z_{Kurtosis} = 1.9951$, $p < 0.05$) (Figure 1c).

Analysis of previous unique green literature

In Table 1 we show the 25% and 75% quartiles of the 1,000 p values produced by dip tests on the bootstrapped distributions, as well as the percentage of these p values that were less than 0.05 (indicating that the distribution was not unimodal). As mentioned previously, strong evidence for a bimodal distribution was determined as those datasets that yielded a significant dip test p value for more than 50% of the synthesized within-bin data points.

The dip test was also carried out on the raw data underlying Dimmick and Hubbard's original paper (Dimmick & Hubbard, 1939), and showed no evidence of a bimodal distribution ($D = 0.1202$, $p = 0.1882$). We find that only one out of these 29 unique green distributions (Rubin, 1961) would pass a modern test for bimodality with high statistical probability (87.7% of bootstrapped distributions had p values that were less than 0.05). See Supplementary Material for histograms of all the aforementioned studies that measured UG wavelengths; all histograms are shown with an equally scaled x-axis.

For the present study, where the individual data points are known, the dip test resulted in a p value of 0.919; in other words, we could not reject the null hypothesis of a unimodal distribution. We used this result as a check on our bootstrapping methods. Bootstrapping 1,000 different within-bin distributions

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Study	Condition (measurements taken in λ_{UG} (nm), unless otherwise specified)	Total subjects	25% quartile of *p* values	75% quartile of *p* values	% of *p* values <0.05
Present study	Datasets synthesized from frequencies $0.67^\circ \times 1.33^\circ$	58	0.632	0.945	0.2%
Cobb (1975)	Male	232	0.737	0.970	0.1%
	Female	171	0.749	0.976	0.0%
Volbrecht et al. (1997)	**0.25° stimulus**				
	No B/ground	100	0.860	0.982	0.0%
	62.5 td B/ground	100	0.861	0.981	0.0%
	250 td B/ground	100	0.844	0.976	0.0%
	1,000 td B/ground	100	0.397	0.643	0.0%
	1° stimulus				
	No B/ground	100	0.923	0.991	0.0%
	62.5 td B/ground	100	0.309	0.609	0.1%
	250 td B/ground	100	0.673	0.904	0.0%
	1000 td B/ground	100	0.597	0.833	0.0%
Jordan and Mollon (1995)	9.6° visual angle, central 2.8° occluded	97	0.854	0.990	0.0%
Richards (1967)	3cd/m^2 B/ground, 4° 75 cd/m^2 test field	90	0.864	0.981	0.0%
Hurvich et al. (1968)	(1953) $0.8^\circ \times 1.3^\circ$	26	0.512	0.881	0.6%
	(1967) $0.8^\circ \times 1.3^\circ$	24	0.489	0.870	0.3%
Rubin (1961)	6° visual angle	287	0.019	0.042	87.7%
Schefrin and Werner (1990)	0.95°, luminance 2.2 cd/m^{-2}	50	0.848	0.984	0.0%
Webster et al. (2000)	**Measuring Chromatic Angle**				
	All observers—2°	51	0.803	0.982	0.0%
	Subset of most consistent observers—2°	26	0.648	0.944	0.0%
Webster et al. (2002)	**Measuring Chromatic Angle**				
	School of Optometry, India—indoor	68	0.438	0.653	0.0%
	School of Optometry, India—outdoor	68	0.851	0.988	0.0%
	Silk Merchants, India—indoor	68	0.126	0.362	8.5%
	Rural Tamil Nadu, India—outdoor	25	0.036	0.106	41.8%
	Nevada, Reno—indoor	115	0.882	0.991	0.0%
	Nevada, Reno—outdoor	118	0.824	0.989	0.0%
	Rural Maharashtra, India—Monsoon	32	0.535	0.864	0.0%
	Rural Maharashtra, India—Winter	40	0.708	0.930	0.0%
	School of Optometry, India—desaturated	20	0.222	0.465	1.1%
	Nevada, Reno—desaturated	83	0.906	0.991	0.0%

Table 1. Previous studies of unique green settings, detailing the conditions, number of participants, and descriptive statistics of the *p* values produced following bootstrapping of 1,000 trials.

of our own data yielded only two distributions (0.2%) that produced dip test *p* values of less than 0.05 (as shown in Table 1).

Predictors of unique green wavelength

Although the distribution of UG values we found was not bimodal, UG was variable across subjects. What factor could explain this variation? Since it is known that macular pigment optical density (MPOD) also varies across subjects, we asked whether this variation could account for some of the variability in unique green settings.

In Figure 2 the UG wavelength is plotted as a function of MPOD. There is a positive relationship between the two variables and the Pearson correlation of 0.31 is significant ($p = 0.016$).

A hierarchical regression of MPOD and iris lightness as predictors of UG wavelength was performed to identify whether either, or both, factors affect an individual's perception of unique green. The model with only MPOD as a predictor significantly predicts UG, $F(1, 56) = 6.123$, $p = 0.016$, as does a model using MPOD and iris lightness, $F(1, 55) = 4.630$, $p = 0.014$. However, Table 2 demonstrates that despite the significance of the two-predictor model, iris lightness did not contribute significantly. Given previous

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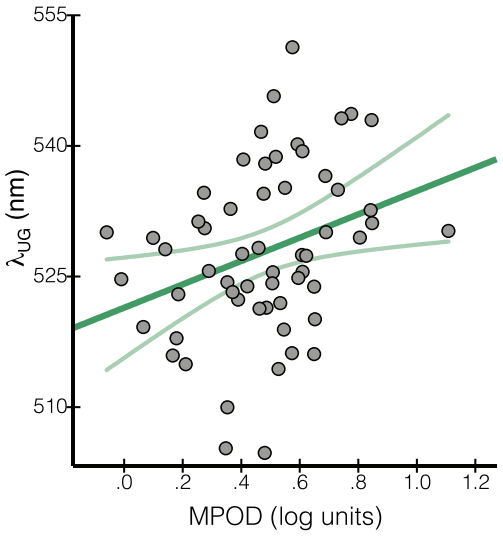

Figure 2. Relationship between unique green wavelength (nm) and macular pigment optical density (log units), with regression line.

research that has indicated a relationship between iris lightness and UG wavelength, we performed a Pearson correlation between the two variables and if a one-tailed test is considered the relationship was close to significance ($r = -0.202$, $p = 0.064$), showing a trend for those with darker irises to have longer UG wavelengths than those with lighter irises. It should also be noted that as there was no colinearity between iris lightness and MPOD (VIF = 1.001), the two variables demonstrate independent effects on UG wavelengths.

One-way ANOVAs performed between the iris lightness categories failed to reach significance levels for either UG wavelength or MPOD.

Given that an on-axis color match performed in the blue-green region of the spectrum (our MPOD measurement) predicts the wavelength of UG we also checked whether variations in the other color match that subjects made in the yellow region of the spectrum (the Rayleigh match) also predicted the wavelength of UG. This allows us to test whether UG is predicted by variations in color matches in general, rather than variations in color matches caused by different MPOD. The correlation between the Rayleigh match settings and UG wavelengths was not significant [$r = -0.075$ (NS)]. Along similar lines, albeit for fewer subjects, we also assessed whether the off-axis color matches made by our expert observers in the blue-green region of the spectrum predicted UG wavelength. This tests the region of the spectrum where *S*-cones are sensitive (the Rayleigh match does not) and therefore allows us to test again whether receptoral properties probed by color matches predict UG. As with the Rayleigh match, the correlation was not significant [$r = 0.314$ (NS)].

	Model	B	*SE* B	β
Step 1	Constant	521.42	2.874	
	MPOD	13.406	5.418	0.314*
Step 2	Constant	526.46	4.083	
	MPOD	13.732	5.330	0.322*
	Iris Lightness	−14.664	8.573	−0.214

Table 2. Hierarchical regression with unique green as the dependent variable. $R^2 = 0.099$ for Step 1; $\Delta R^2 = 0.046$ for Step 2; *$p < 0.05$.

Modeling

How can we explain the dependence of UG wavelength on MPOD? Macular pigment (MP) contains two yellowish carotenoids (lutein and zeaxanthin), which absorbs light strongly between 400 and 500 nm (Broekmans et al., 2002; Davies & Morland, 2004; Trieschmann et al., 2008). It has been found that the density of macular pigment (MPOD) can vary over 1 log unit between individuals (Dain, Cassimaty, & Psarakis, 2004; Davies & Morland, 2004; Trieschmann et al., 2008; Werner, Donnelly, & Kliegl, 1987)—a range that we also observe in the current dataset.

Following Jordan and Mollon (1995), we assume that individual subjects learn to associate a unique green with a set of natural broadband spectra that generate a specific ratio of cone excitations. These spectra might originate, for example, from natural daylight illuminants reflecting from foliage. We call these broadband spectral distributions "exemplars."

The actual cone absorption ratio generated by an exemplar spectrum will vary across individuals depending on MPOD. In particular, subjects with high MPOD will have proportionately less activity in their *S*-cones than subjects with little MPOD. Yet we assume that all subjects will agree on the qualitative color of the broadband exemplar spectrum.

The monochromatic light sources used to test unique hues are artificial. Being narrow-band they are unrepresentative of any illuminant that the subject normally encounters. Nevertheless, they can be matched to an internal representation of a unique hue exemplar simply by adjusting their wavelengths until they generate the equivalent cone absorption ratios.

A subject with little macular pigment will have a significant level of *S*-cone activation when stimulated by a "green" broadband light source centered on, say, 520 nm. This subject will, therefore, choose a relatively short wavelength of monochromatic light (say, 500 nm) to generate the same cone ratios. In comparison, a subject with a high MPOD experiences less *S*-cone activity for the same broadband "green" illuminant and will therefore choose a monochromatic light source with a longer wavelength (say, 530 nm) in

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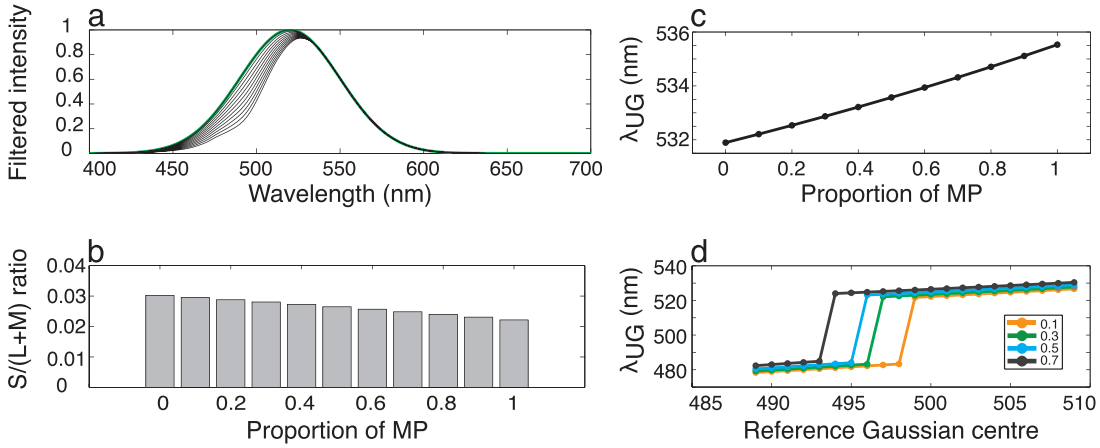

Figure 3. Simulation of the effect of increasing macular pigment on monochromatic Unique Green. a) A broadband (Gaussian) spectrum centered at 520 nm (green line) and the effect of prereceptoral filtering by increasing amounts of macular pigment (black lines). b) Ratio of *S* to L+M cone responses to the broadband stimulus with increasing MPOD. As the amount of macular pigment increases, *S* cone responses ratios decrease significantly. c) Wavelengths of monochromatic light sources that match the cone ratios in b). As the macular pigment density increases, the wavelength of the monochromatic light source also increases. d) Unique hues around 495 nm may be relatively variable across subjects. Broadband Gaussian spectra in this region are matched by monochromatic light sources that may change rapidly over tens of nm. This step occurs at different peak wavelengths depending on the macular pigment level (colored lines indicate level of MP). There are no other similar regions of high variability in other parts of the spectrum.

order to make the match. This effect is demonstrated in Figure 3.

In Figure 3a we show the effect of increasing MPOD levels on spectral distribution of a broadband "green" light source. Increasing MPOD filters the short wavelength side of the distribution and therefore reduces *S*-cone excitation. This asymmetric filtering effect is a result of the fact that the reference Gaussian overlaps the edge of the MP absorption spectrum at around 500 nm—Gaussian distributions centered at other wavelengths do not experience such an asymmetric change due to MPOD.

The reduction of *S*-cone responses with increasing MPOD is shown in Figure 3b. In our simulations, the ratio of L+M to S cone activity changes by approximately 50% between the low and high MPOD conditions.

When asked to adjust a monochromatic light source to generate a "unique green," subjects must match the cone ratios generated by the broadband illuminant. In general, the peak wavelength of light required to achieve this will not correspond to the peak of the broadband illuminant. In Figure 3c we show the monochromatic wavelength required to match the Gaussian distribution centered on 520 nm (shown in Figure 3a) as a function of MPOD. At low MPOD, the monochromatic UG is around 532 nm. Increasing MPOD require matches to cone ratios with decreasing amounts of *S*-cone excitation and this, in turn, requires a longer wavelength. At the highest MPOD, the wavelength of the match point has increased by 4 nm to around 536 m. This increase could drive the observed correlation between MPOD and monochromatic unique green wavelength.

Unique green appears to be particularly sensitive to the peak wavelength value of the reference Gaussian. Figure 3d shows monochromatic match values as a function of the central wavelength of the broadband illumination spectrum. Over much of the range, these match values change smoothly as a function of reference wavelength but a step in the function exists at around 495 nm. The exact position of this discontinuity depends on the amount of macular pigment present (as well as details of the modeling procedure and the spectral distribution of the exemplar) but it represents a difference in monochromatic match values of at least 40 nm. It is possible that the existence of this step is responsible for the relatively large range of UG values reported in the literature.

Discussion

Impact of MPOD on unique green

Our primary finding is that there is a significant correlation between MPOD and unique green with higher MP densities predicting longer monochromatic UG wavelengths. We explain this finding by showing that MP affects the spectral distribution of broadband exemplars stimulating the three cone classes and therefore changes the cone ratios that must be matched using monochromatic lights.

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Iris lightness

To the degree that other factors such as iris color or melanin are correlated with prereceptoral filter density, it is possible that these too may have an effect on unique green settings. We found a trend, similar to that described by Jordan and Mollon (1995), for subjects with darker irises to select longer wavelengths for their UG settings, but this relationship was not significant. As there was no colinearity between MPOD and iris lightness, we can assume that these factors are not related. We note that Schefrin and Werner (1990) report a small decrease in unique green wavelength with age. Our models suggest that lens density should be positively correlated with UG wavelength but the size of the effect is much smaller—changing by only a nanometer or so over a reasonable range of lens densities. It is possible, therefore, that other factors are responsible for the effects seen by this group.

Distributions

In agreement with recent findings by Jordan and Mollon (1995) and Schefrin and Werner (1990), our distribution of UG wavelengths was normal: We detected no statistically significant evidence of skew or kurtosis, and no evidence of bimodality using Hartigan's dip test (Hartigan & Hartigan, 1985). The same tests also found a normal distribution of MPOD across subjects.

In addition, we found no significant evidence of bimodality or skew in the Rayleigh match data, and there was no statistically significant correlation between UG wavelengths and Rayleigh matches, which confirms previous findings by Jordan and Mollon (1995).

Some researchers have reported bimodal distributions of unique green wavelengths (Cobb, 1975; Richards, 1967; Rubin, 1961; Waaler, 1967). These findings motivated a significant amount of research on the subject (including our own) and the original explanation for a bimodal distribution was the presence of two different *M*-cone opsin genes ("alleles") in the human population.

The absence of a bimodal distribution in our own data, and in recent data from other laboratories (Jordan & Mollon, 1995; Schefrin & Werner, 1990), prompted us to look for an explanation for these earlier findings. One possibility is that, historically, statistical tests of bimodality were not sufficiently rigorous. Dips in frequency distribution can occur by chance, and when large numbers of datasets are collected the chance of identifying a "significant" dip by chance also increases. We performed Hartigan's dip test on as many unique green data sets we could obtain (most were reported in wavelength, some were reported in chromatic angle), in order to establish whether using a robust, modern statistical test would produce the same findings as those that had been reported (see Table 1).

What is most striking from our analysis is that although the original dataset on which the hypothesis of bimodality was based—Rubin (1961)—does show a strongly bimodal distribution (87.7% of bootstrapped distributions had p values <0.05), there is little or no evidence of this distribution in any subsequent measurement of unique green wavelengths.

The fact remains that there is strong evidence of bimodality in one of the original papers in the field. One clue to this discrepancy might lie in the discontinuity of the unique green match point seen in Figure 3d. Here, we show that as the peak of the exemplar stimulus shifts through a region around 495 nm, a step change in the optimal monochromatic matching wavelength occurs. In a large population with a range of unique green exemplars, this results in a bimodal unique green even if only a single allele of each cone photopigment gene is present in the population. We note that Rubin's (1961) dataset was one of the largest reported in the literature, it covered a large age range (16–64 years), and may have been collected over a relatively large period of time. It is possible, therefore, that it included subpopulations whose unique green exemplars differed—either as a result of their occupation or due to seasonal differences in the environment.

The effect of this is illustrated in Figure 4. Here, we assumed that the peak of the unique green exemplar was distributed normally across a range centered on 480 nm ($\sigma = 20$ nm) for a population of 10,000 otherwise identical individuals with 1% independent noise in each of their cone photoreceptor absorption rates. We then computed the monochromatic unique green values that these individuals would use to match their exemplar. These data are plotted in a histogram in Figure 4a, data from Rubin (1961) are shown in Figure 4b for comparison. Although the range of our monochromatic match points is broader than those in Rubin and shifted to shorter wavelengths, even our simple model is clearly able to capture a previously unsuspected aspect of the UG settings: a bimodal distribution arising from the match discontinuity at 495 nm.

The precise location of the dip and the width of this distribution depend on the distribution of the broadband spectrum used as an exemplar. In our models we chose a relatively narrowband Gaussian for simplicity but it would be interesting to examine the effect of using broader, naturally-occurring distribution such as leaves or grass illuminated by a range of natural daylight spectra.

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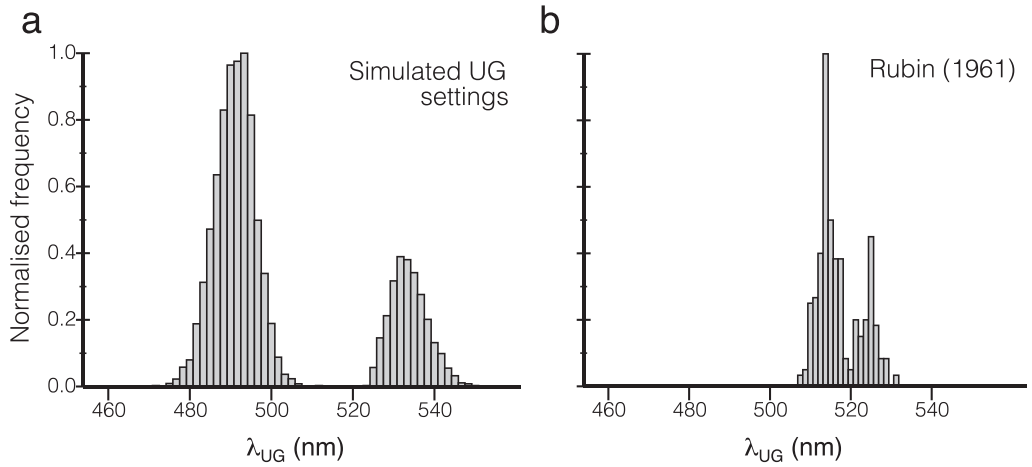

Figure 4. a) Histogram of simulated monochromatic unique green settings in a population with a normally distributed range of broadband unique green exemplars. b) Histogram of unique green settings from Rubin (1961) shown for comparison. A discontinuity in optimal LMS matching values at 495 nm can result in a bimodal distribution of UG values in large, heterogeneous populations.

Conclusion

We find that UG wavelengths have a unimodal normal distribution across our measurement group and this is consistent with almost all previously published UG datasets. The single exception is the dataset of Rubin (1961), which passes this robust test for bimodality.

Our results also demonstrate for the first time, that a subject's MPOD predicts their UG wavelength. When we model this using a simulation of cone receptor absorptions and prereceptoral filtering, we find that the relationship between MPOD and UG is consistent with subjects attempting to match the learned cone ratios generated by a broadband source using a monochromatic light. The increase in UG wavelength with higher MPOD is well explained by the prereceptoral filtering due to MP, which primarily affects the relative *S*-cone excitation values.

An additional finding from our modeling procedure is that monochromatic matches for broadband stimuli may be particularly variable in the region around 490 nm, and MPOD levels determine the region of highest variability. We believe that this inherent variability may explain the broad distribution and rare observations of bimodality of UG settings found in the literature.

Keywords: unique green, macular pigment, unimodal, bimodal, unique hue, modeling

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Corresponding authors: Antony B. Morland; Lauren E. Welbourne.
Email: antony.morland@york.ac.uk; lew507@york.ac.uk.
Address: Department of Psychology, University of York, Heslington, York, UK.

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