



# Colour-opponent mechanisms are not affected by age-related chromatic sensitivity changes

Sophie Wuerger<sup>1</sup>, Kaida Xiao<sup>1</sup>, Chenyang Fu<sup>1</sup> and Dimosthenis Karatzas<sup>2</sup>

<sup>1</sup>School of Psychology, University of Liverpool, Bedford Street South, Liverpool L69 7ZA, UK, and

<sup>2</sup>Computer Vision Centre, Room 120, Edifici O Universitat Autònoma de Barcelona, Bellaterra Barcelona, Spain

## Abstract

The purpose of this study was to assess whether age-related chromatic sensitivity changes are associated with corresponding changes in hue perception in a large sample of colour-normal observers over a wide age range ( $n = 185$ ; age range: 18–75 years). In these observers we determined both the sensitivity along the protan, deutan and tritan line; and settings for the four unique hues, from which the characteristics of the higher-order colour mechanisms can be derived. We found a significant decrease in chromatic sensitivity due to ageing, in particular along the tritan line. From the unique hue settings we derived the cone weightings associated with the colour mechanisms that are at equilibrium for the four unique hues. We found that the relative cone weightings ( $w_L/w_M$  and  $w_L/w_S$ ) associated with the unique hues were independent of age. Our results are consistent with previous findings that the unique hues are rather constant with age while chromatic sensitivity declines. They also provide evidence in favour of the hypothesis that higher-order colour mechanisms are equipped with flexible cone weightings, as opposed to fixed weights. The mechanism underlying this compensation is still poorly understood.

**Keywords:** ageing, chromatic sensitivity, colour appearance, compensatory mechanisms, unique hues

## Introduction

The purpose of this study was to assess whether hue perception (mediated by colour-opponent mechanisms) changes with age, and the extent to which age-related changes in chromatic sensitivity are correlated with such hue changes. The effect of age on hue perception (Scheffrin and Werner, 1990; Werner, 1996) and on chromatic sensitivity (Knoblauch *et al.*, 2001) has been previously assessed separately using different groups of observers. To understand how age-induced chromatic sensitivity changes relate to hue perception, it is pertinent to obtain both measures in the same set of observers. We therefore measured both sensitivity along

the protan, the deutan and the tritan line as well as the loci of unique hues, in a large set of colour-normal observers, over a wide age range.

## Methods

Here we report two sets of data that were collected as part of a more extensive experiment.

## Subjects

One hundred and eighty-five (82 males and 103 females) naïve subjects participated in the experiment, with a mean age of 34.03 years (range: 18–75 years). Subjects were paid and informed consent was obtained from all subjects prior to the experiment. All subjects had normal, or corrected to normal, visual acuity; subjects with any history of cataracts or any other eye surgery were excluded from the experiment. The experiments were approved by the Ethics Committee of the School of Psychology, University of Liverpool.

Received: 10 September 2009

Revised form: 3 March 2010

Accepted: 7 March 2010

Correspondence and reprint requests to: Sophie Wuerger.  
Tel.: +44 (0) 151 794 2173; Fax.: +44 (0) 151 794 2945.  
E-mail address: s.m.wuerger@liverpool.ac.uk

### Equipment

Stimuli were displayed on CRT monitor (21-inch Sony GDM-F520; Sony Corporation, Tokyo, Japan) which was controlled by a DELL PC with a ViSaGe stimulus generator (Cambridge Research Systems, Rochester, Kent, UK). The lookup tables were linearised using the ColourCal calibration device (Cambridge Research Systems) which interfaces with the graphics card. Calibration was checked with a PR650 tele-spectroradiometer (PhotoResearch Inc, Chatsworth, CA, USA). The CRT monitor had a correlated colour temperature of about 9300 K with a peak luminance of  $120 \text{ cd m}^{-2}$ . The CIE coordinates ( $x$ ,  $y$ , Luminance) of the phosphors at peak output were as follows: red = 0.627, 0.342, 28.12; green = 0.287, 0.608, 80.96; blue = 0.151, 0.074, 14.16, respectively. Since there was some initial monitor drift, the monitor was switched on at least 1 h before the start of the experiment. The responses of the observers were collected using a button box (CT6; Cambridge Research Systems). Stimuli were generated using the CRS MatLab toolbox and MatLab 7.4 (The MathWorks Inc, Natick, MA, USA).

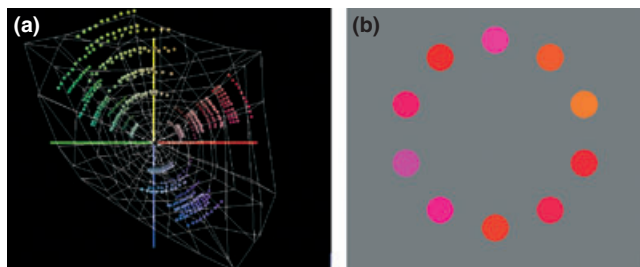
### Experiment 1: chromatic sensitivity

All observers were tested with the Cambridge Colour Test: thresholds along the protan, the deutan and the tritan line were assessed (Regan *et al.*, 1994). The background luminance (field point) was fixed at  $13 \text{ cd m}^{-2}$ . Only observers that fell within the normal range were used for the unique hue experiments. Normal range was defined as thresholds lower than  $100 \times 10^{-4} u'v'$  units for the protan and deutan lines,

and lower than  $150 \times 10^{-4} u'v'$  units for the tritan line; this range is slightly larger than the recently suggested preliminary norms for the CCT (Ventura *et al.*, 2003). Observers with thresholds beyond these limits received a small fee and were excluded from further experiments. All data reported in the results section are therefore from a colour-normal sample.

### Experiment 2: unique hue settings

To obtain settings of the unique hues we used a modified hue selection task (Wuerger *et al.*, 2005). The background was always set to a mid-grey with a luminance of  $24 \text{ cd m}^{-2}$ . Each patch had a diameter of  $2^\circ$  of visual angle and was presented at an eccentricity of  $4^\circ$  (Figure 1b). Patches of slightly different hues (and same lightness and saturation) were arranged along an annulus at constant eccentricity. The task of the observer was to select a patch that contains neither yellow nor blue (to obtain unique red and green). Unique yellow (blue) was obtained by asking observers to select a patch that contains neither red nor green. The step size in hue angle was determined in extensive preliminary experiments; no observer reported that he/she could not find a patch which satisfied the equilibrium criteria. In the current sample, the intra-observer variability for the unique hue settings varied between 1.6 and  $3 \Delta E$  in LUV space (red: 1.6; yellow: 3; blue: 1.8; green: 2.3). Each unique hue was determined at nine combinations of different saturation and lightness levels. Each of these nine settings was repeated three times. In total, 360 test colours ( $4$  unique hues  $\times 9$  combinations of different saturation-lightness levels  $\times 10$  colour patches per test) were selected. The chromaticities of the 10 test colour patches are shown in Figure 1a in a roughly uniform  $u^*v^*$  chromaticity diagram.



**Figure 1.** Unique Hue Selection task. (a) Test stimuli in the roughly uniform  $u^*v^*$  chromaticity diagram. Three hundred and sixty test colours ( $4$  unique hues  $\times 9$  combinations of different chroma-lightness levels  $\times 10$  colour patches per test) were used in this task. The lightness levels ( $L^*$ ) used were as follows: 32, 50, 63 and 76 for red and blue; 32, 50 and 76 for yellow and green. (b) The 2-deg test stimuli were arranged in an annulus at 4-deg eccentricity. On a particular trial, coloured patches had the same lightness  $L^*$  and chroma  $C_{uv}^*$  value. In the example shown here the observer was asked to select the patch that contained neither yellow nor blue to obtain unique red.

### Chromatic specifications

To calculate the cone absorptions in the long-, medium-, and short-wavelength-sensitive cones, we used the 2-deg cone fundamentals derived by Stockman and Sharpe (2000). The cone fundamentals were then scaled in terms of luminance units using the new  $V^*(\lambda)$  (available at <http://www.cvrl.org>) such that luminance equals the sum of the L and M cone absorptions. The S cone signal was scaled such that  $S/\Sigma V^*(\lambda)$  equals 1 for an equal-energy light. The phosphor spectra were measured at peak output, up-sampled to 1 nm spacing and multiplied with the scaled cone fundamentals to obtain the transformation from linearized RGB space to LMS space. To visualise the unique hue settings, we transformed the data from LMS space to DKL space (Derrington *et al.*, 1984). The matrix corresponding to this linear transformation depends on the background

chromaticity and is scaled such that a unit input vector yields a unit response in all three putative mechanisms, i.e. two chromatic mechanisms ( $L - M$ ;  $S - (L + M)$ ) and a luminance mechanism ( $L + M$ ) (for details see Brainard (1996) and Wuerger *et al.* (2002)). Modulations along the tritan line isolate the  $S - (L + M)$  mechanism; isoluminant modulations along the  $L - M$  line isolate the  $L - M$  mechanism; achromatic modulations (same cone contrasts in  $L$ ,  $M$ , and  $S$ ) isolate the luminance ( $L + M$ ) mechanism.

### Analysis: estimating the cone weightings

Colour-opponent mechanisms were first mentioned by Hering (1964) who proposed that any hue can be described in terms of its redness or greenness and its yellowness or blueness. Red and green are opposite hues because they cannot be elicited simultaneously by a single colour stimulus; the same is true for blue and yellow. Hering therefore postulated the existence of two color-opponent channels coding red-green and yellow-blue sensations. Quantitative estimates of these two colour-opponent channels were first obtained by Jameson and Hurvich (Jameson and Hurvich, 1955; Larimer *et al.*, 1974, 1975) using a hue cancellation technique: when a subject adjusts the red and green component of a coloured patch (e.g. a yellowish stimulus) such that it contains neither red nor green, then the red-green opponent channel ( $RG$ ) is at equilibrium; consequently

a red-green opponent mechanism produces a zero response for this yellowish stimulus:

$$w_L * L + w_M * M + w_S * S = RG_Y = 0. \quad (1)$$

By definition, a yellowish stimulus with these differential  $L, M, S$  cone weights ( $w_L, w_M, w_S$ ) is void of any red and green and is therefore referred to as 'unique yellow'. Equation 1 defines a plane in three-dimensional LMS cone space. The vector ( $w_L, w_M, w_S$ ) is orthogonal to this plane; this normal vector ( $w_L, w_M, w_S$ ) characterises the red-green mechanism ( $RG_Y$ ) that is silenced by all the (unique yellow) colours on this plane. The plane is therefore the *null plane for the RG mechanism*. We can derive an analogous equation for unique blue. A bluish stimulus that contains neither red nor green, produces a zero response in a red-green opponent channel:

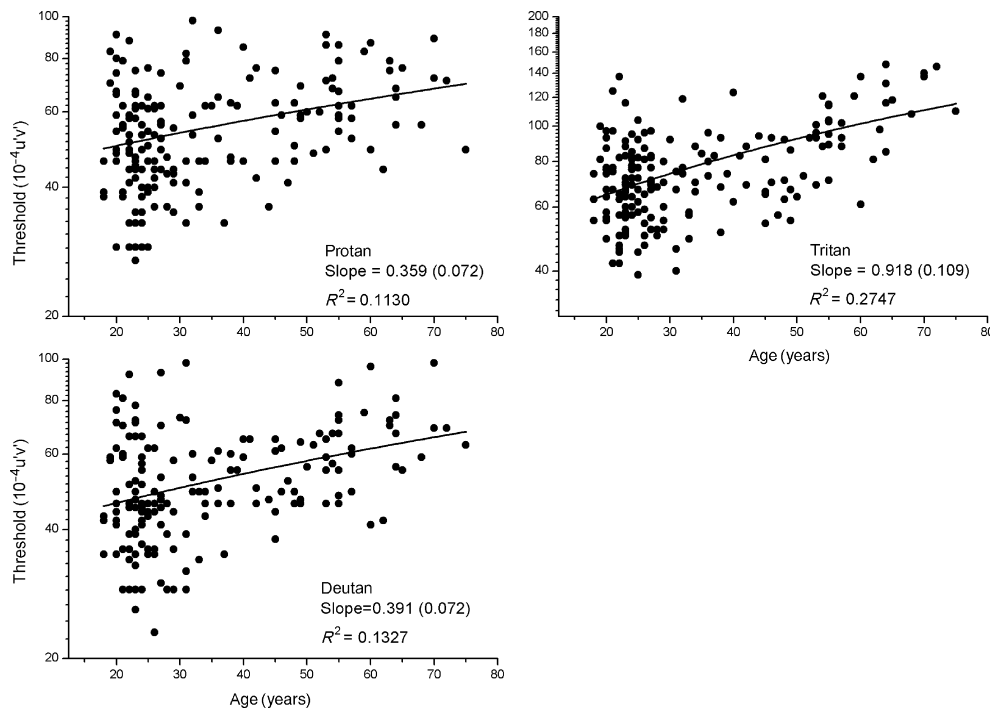
$$w_L * L + w_M * M + w_S * S = RG_B = 0. \quad (2)$$

Unique red (Equation 3) and unique green (Equation 4) are defined as colours that produce zero output in a yellow-blue opponent channel:

$$w_L * L + w_M * M + w_S * S = YB_R = 0, \quad (3)$$

$$w_L * L + w_M * M + w_S * S = YB_G = 0. \quad (4)$$

If unique red and unique green are generated by silencing a single yellow-blue opponent mechanism, then



**Figure 2.** Thresholds in  $\log 10^{-4} u'v'$  units along the protan, deutan, and tritan line are plotted as a function of age for all 185 observers. A linear regression analysis revealed that the slope for all three sets of thresholds differs significantly from zero. Protan: slope = 0.359;  $R^2 = 0.113$ ;  $p < 0.001$ ; Deutan: slope = 0.391;  $R^2 = 0.133$ ;  $p < 0.001$ ; Tritan: slope = 0.918;  $R^2 = 0.275$ ;  $p < 0.001$ .

the coefficients in *Equations 3 and 4* should be identical; similarly, if unique yellow and unique blue silence a single red-green opponent mechanism, then the normal vector in *Equations 1 and 2* should be the same. Here we assume that the normal vectors can be different for each unique hue. Using *Equations 1–4* we estimate the cone weights ( $w_L, w_M, w_S$ ) associated with each of the four unique hues assuming that there is no variation in sensitivity among the observers; in particular, no change in sensitivity with age. These are our observed cone weights irrespective of the individual chromatic sensitivity. We can then test whether the cone weightings associated with the four unique hues depend on age.

## Results

Our main aim was to investigate whether changes in chromatic sensitivity with increasing age are associated with changes in the colour-opponent mechanisms that mediate hue perception. We therefore measured sensitivity and hue perception in the same group of observers. We first report the age-related changes in chromatic sensitivity, and then the observed changes in hue perception.

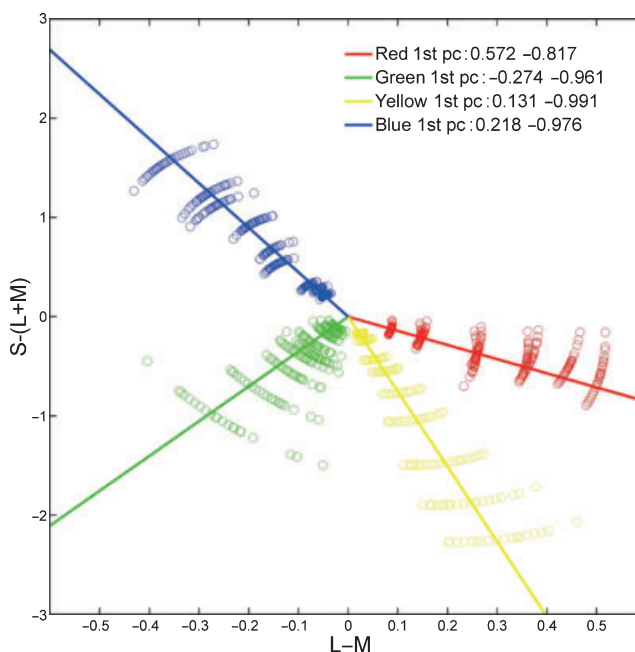
### Chromatic sensitivity

The protan, deutan, and tritan thresholds (in  $10^{-4} u'v'$  units) for all 185 observers are shown as a function of age in *Figure 2*. A linear regression analysis revealed that the slope for all three sets of thresholds differs significantly from zero ( $p < 0.001$ ). The  $R^2$  values are 0.113, 0.133 and 0.275 for protan, deutan and tritan thresholds, respectively. Knoblauch *et al.* (2001) reported much higher  $R^2$  values of about 80%; this discrepancy could be partly due to the different age ranges investigated. Knoblauch *et al.*'s study included a large proportion of very young infants (starting at 3 months of age) whereas our main focus was how sensitivity in adults declines with increasing age; this decline in adult sensitivity is due to numerous optical and neural factors (Werner, 1996) which might increase the variability in contrast thresholds as a function of age, hence reducing the  $R^2$ . The strongest association between age and chromatic sensitivity occurs for the S-cone isolating stimuli (tritan line), which is consistent with the 'yellowing' of the lens and/or with a decline in cone sensitivity (Werner and Steele, 1988). The slope is almost identical for protan and deutan thresholds. While it is in principle possible that the age dependency of chromatic sensitivity is affected by the spatial properties of the test stimulus, the CCT trivector test has been shown to be not greatly affected by visual acuity (Thyagarajan *et al.*, 2007).

### Unique hue settings

The unique hue settings for all 185 observers and all saturation and lightness levels are shown in DKL space (*Figure 3*), in a cone-opponent chromaticity diagram (Krauskopf *et al.*, 1982). The grey background is denoted with (0,0) in this graph. Unique red is close to the L-M axis, whereas unique green clearly requires a significant negative S cone input. Unique yellow and unique blue are not aligned with the  $S - (L + M)$  axis but lie on intermediate directions in this cone-opponent colour space as has been reported previously (Wuerger *et al.*, 2005). Plotting the unique hue settings in this cone-opponent diagram shows that the four unique hues are generated by silencing chromatic mechanisms that receive inputs from all three cone classes (L,M,S). Since the aim of our study was to estimate the cone weightings of these chromatic mechanisms and how these cone weightings change with increasing age, our further analysis was performed in three-dimensional LMS cone space.

For each unique hue we determined the best-fitting coefficients ( $w_L, w_M, w_S$ ) by using principal component analysis of the LMS coordinates of the unique hues. (*Equations 1–4*). The last eigenvector (explaining the least variance) is the normal vector; its orientation is defined by the coefficients ( $w_L, w_M, w_S$ ) and the coefficients are normalised such that  $w_L^2 + w_M^2 + w_S^2 = 1$ . An



**Figure 3.** The unique hue settings for all observers and all saturation and lightness levels are shown in a cone-opponent chromaticity diagram (DKL space). The grey background is denoted with (0,0) in this graph. The luminance values are not shown in this diagram. Solid lines represent the 1st principal components which are here only used to summarise the data.

equivalent method (Wuerger *et al.*, 2005) for finding the normal vector (with coefficients  $w_L, w_M, w_S$ ) is to minimise the Euclidean distances between the individual unique hue co-ordinates (in LMS space) and the plane ('Total Least Squares'). We calculated for each of the 185 observers the normal vectors (that is, the cone weights  $w_L, w_M, w_S$ ; cf. Equations 1–4) for each of the four unique hues.

Figure 4a shows the observed relative cone weightings (i.e. the coefficients  $w_L, w_M, w_S$ ) for unique red and unique green as a function of the age of the observer. On the left column,  $w_L:w_M$  is plotted for red (first row) and green (2nd row); on the right column,  $w_L:w_S$  is plotted. Relative cone weights are indicated by an open circle and the linear regression is indicated by the dashed line.

Figure 4b shows the relative cone weightings for unique yellow and unique blue in the same format. Regression analysis confirms that neither the relative L:M (left column; Figure 4a,b) nor the relative L:S cone weightings (right column; Figure 4a,b) associated with a particular hue depend on age; the  $R^2$  for all four unique hues is close to zero and none of the slopes (s) differs from zero ( $p > 0.09$  in all cases). Note that the scale along the y-axis is the same for red and green (Figure 4a) for easier comparison; clearly, red and green are defined by different L:M and L:S cone ratios, which is also reflected in the lack of co-linearity shown in Figure 3.

To visualise the hue invariance with an increase in age, we compared the hue settings for the younger age group, below 30 years of age, with the older group,

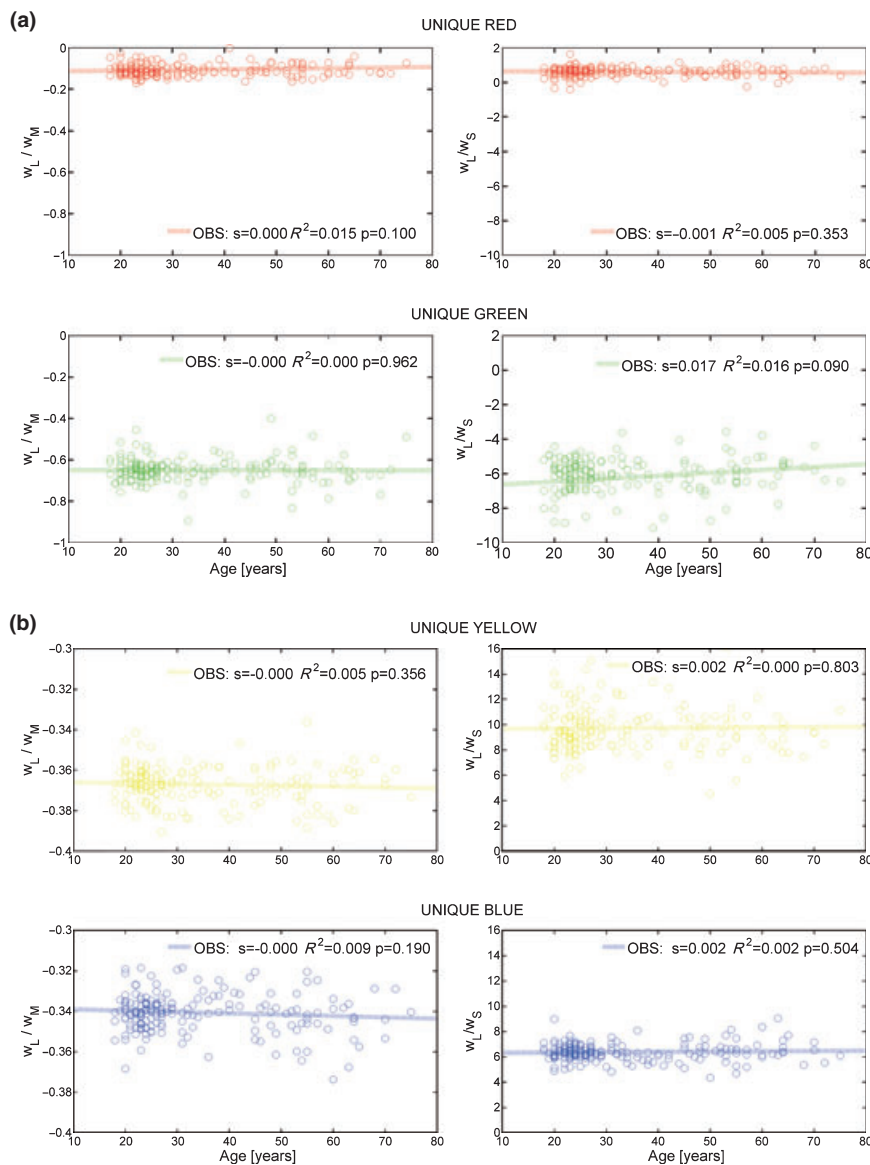
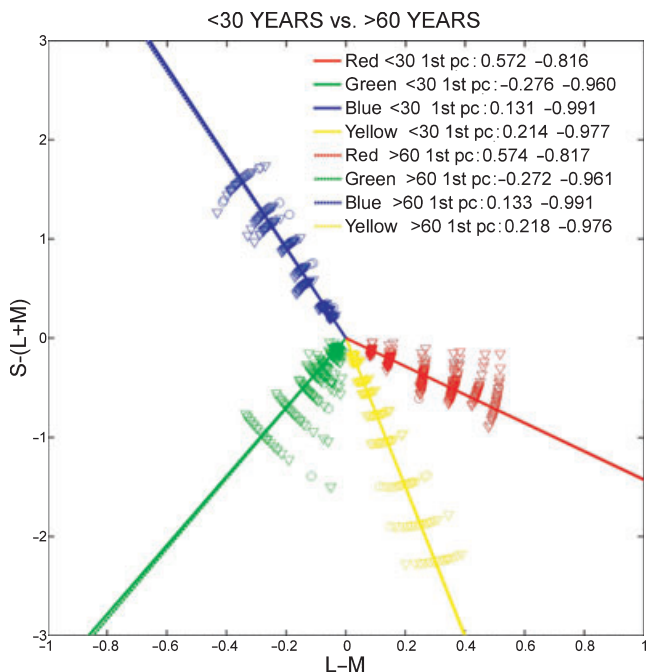


Figure 4. Relative cone weightings associated with the four unique hues: (a) red and green, (b) yellow and blue. The relative cone weightings are plotted as a function of the age of the observer. Left columns:  $w_L/w_M$  cone weightings. Right Columns:  $w_L/w_S$  cone weightings.



**Figure 5.** The unique hue settings for all observers below 30 years of age ( $n = 107$ ; triangles) and for all observers above 60 years of age ( $n = 16$ ; circles) are plotted in the DKL chromaticity diagram. Solid and dashed lines represent the 1st principal component for the younger and the older age groups, respectively.

above 60 years of age, in the DKL diagram (Figure 5). The lines denoting the 1st principal component for the younger and the older age group are almost co-incident, hence confirming that the unique hue settings do not change significantly with age (cf. Figure 4a,b).

## Discussion

When we get older, the hue of objects does not change (Werner, 1996). This is surprising given that the lens becomes yellowish with ageing, and neural losses occur in the retina (Werner and Steele, 1988) and maybe even at cortical sites, suggesting that the signal that is available to higher-order colour mechanisms that mediate hue perception is deteriorating with age. Here we studied colour appearance (unique hue settings) and chromatic sensitivity in a large sample of colour-normal observers ranging from 18 to 75 years of age. While we find significant age-related decreases in chromatic sensitivity, in particular along the tritan line (Figure 2), we find no evidence for any age-related colour appearance changes (cf. Figure 5).

Two explanations for this hue constancy have been proposed (Werner, 1996). The first possibility is that the decline in cone sensitivity is parallel in the different cone classes; hence a mechanism that takes the difference between these cone signals will not be greatly affected by a decline in sensitivity. The second possibility is that the

human visual system can adjust its cone weightings over the lifespan, and thereby compensate for a decline in peripheral signals. These two possibilities are not mutually exclusive. Our results provide supporting evidence for the second possibility. The relative cone weightings associated with the unique hue mechanisms, in particular the L:S cone weightings (Figure 4a,b right panel), remain constant with an increase in age. At the same time there is a significant decrease in sensitivity for S-cone isolating stimuli (tritan line; Figure 2). Assuming that thresholds along the tritan line reflect the strength of the S cone signal available for further analysis by higher-order colour mechanisms, one would expect changes in the perceived hue in particular for yellow and blue colours since these hues receive a large S cone input (positive for blue; negative for yellow; Figures 3 and 5). However, this is not the case; yellow and blue remain constant in the age range we studied in this experiment (18–75 years of age; Figure 4a,b) suggesting the gain for the S cone signal is increased before it feeds into higher-order colour mechanisms that mediate hue perception.

An alternative explanation for our failure to find any age dependency in the observed unique hue settings is that our hue selection method was not sensitive enough to reveal these changes. We consider this explanation unlikely, since observers never reported that the steps between the hues were too large to identify a patch which was neither red nor green (or neither yellow nor blue). Hence we believe that our observed hue invariance in conjunction with the age-related decline in sensitivity along the protan, deutan and tritan line, provides further evidence for compensatory colour mechanisms. These compensation mechanisms are likely to arise at a post-receptoral site, such as a colour-opponent site (Neitz *et al.*, 2002; Delahunt *et al.*, 2004). Several research groups (Neitz *et al.*, 2002; Delahunt *et al.*, 2004) have shown that shifts in unique yellow induced by long-term changes in the chromatic environment are not due to receptor changes, but must be of cortical origin, probably after chromatic information from both eyes has been integrated. The question remains how the human visual system receives feedback on the strength of its cone inputs. Neitz *et al.*'s unique yellow data are consistent with the hypothesis that the gains of the L and M cones are adjusted such that the red-green opponent mechanism is at equilibrium for average daylight (Mollon, 1982).

## Acknowledgements

The work has been supported by the Wellcome Trust (GR/080205) and a Spanish research project TIN2008-04998. We would like to thank Galina Paramei for helpful comments.

## References

- Brainard, D. (1996) Cone Contrast and Opponent Modulation Color Spaces. In: *Human Color Vision* (eds P. K. Kaiser and R. M. Boynton), Optical Society of America, Washington, DC, pp. 563–579.
- Delahunt, P. B., Webster, M. A., Ma, L. and Werner, J. S. (2004) Long-term renormalization of chromatic mechanisms following cataract surgery *Vis. Neurosci.* **21**, 301–307.
- Derrington, A. M., Krauskopf, J. and Lennie, P. (1984) Chromatic mechanisms in lateral geniculate nucleus of macaque. *J. Physiol.* **357**, 241–265.
- Hering, E. (1964) *Outlines of a theory of the light sense*. Harvard University Press, Cambridge, Massachusetts.
- Jameson, D. and Hurvich, L. (1955) Some quantitative aspects of an opponent-colors theory I. Chromatic responses and spectral saturation. *J. Opt. Soc. Am.* **45**, 546–552.
- Knoblauch, K., Vital-Durand, F. and Barbur, J. L. (2001) Variation of chromatic sensitivity across the life span. *Vision Res.* **41**, 23–36.
- Krauskopf, J., Williams, D. R. and Heeley, D. W. (1982) Cardinal directions of colour space. *Vision Res.* **22**, 1123–1131.
- Larimer, J., Krantz, D. and Cicerone, C. (1974) Opponent-process additivity I: red/green equilibria. *Vision Res.* **14**, 1127–1140.
- Larimer, J., Krantz, D. and Cicerone, C. (1975) Opponent-process additivity II: yellow/blue equilibria and nonlinear models. *Vision Res.* **15**, 723–731.
- Mollon, J. D. (1982) Color vision. *Annu. Rev. Psychol.* **33**, 41–85.
- Neitz, J., Carroll, J., Yamauchi, Y., Neitz, M. and Williams, D. R. (2002) Color perception is mediated by a plastic neural mechanism that is adjustable in adults. *Neuron* **35**, 783–792.
- Regan, B. C., Reffin, J. P. and Mollon, J. D. (1994) Luminance noise and the rapid determination of discrimination ellipses in colour deficiency *Vision Res.* **34**, 1279–1299.
- Schefrin, B. E. and Werner, J. S. (1990) Loci of spectral unique hues throughout the life span. *J. Opt. Soc. Am. A* **7**, 305–311.
- Stockman, A. and Sharpe, L. T. (2000) Spectral sensitivities of the middle- and long-wavelength sensitive cones derived from measurements in observers of known genotype. *Vision Res.* **40**, 1711–1737.
- Thyagarajan, S., Moradi, P., Membray, L. and Laidlaw, D. A. H. (2007) Technical note: the effect of refractive blur on colour vision evaluated using the Cambridge Colour Test, the Ishihara Pseudoisochromatic Plates and the Farnsworth Munsell 100 Hue Test. *Ophthalmic. Physiol. Opt.* **27**, 315–319.
- Ventura, D., Silveira, L., Rodrigues, A., De Souza, J., Gualtieri, M., Bonci, D. and Costa, M. 2003 Preliminary norms for the Cambridge Colour Test. In: *Normal & Defective Colour Vision* (eds J. Pokorny; J. D. Mollon and K. Knoblauch), Oxford University Press, Oxford, pp. 331–339.
- Werner, J. S. (1996) Visual problems of the retina during ageing: compensation mechanisms and colour constancy across the life span. *Prog. Retin. Eye Res.* **15**, 621–645.
- Werner, J. S. and Steele, V. G. (1988) Sensitivity of human foveal color mechanisms throughout the life span. *J. Opt. Soc. Am. A* **5**, 2122–2130.
- Wuerger, S. M., Watson, A. B. and Ahumada, A. 2002 Towards a spatio-chromatic standard observer for detection. In: *Human Vision and Electronic Imaging VII* (ed. B. E. Rogowitz and T. N. Pappas), Proceedings of SPIE, San Jose, CA, 4662, pp. 159–172.
- Wuerger, S. M., Atkinson, P. and Cropper, S. (2005) The cone inputs to the unique-hue mechanisms. *Vision Res.* **45**, 3210–3223.