COLOUR-OPPONENT MECHANISMS ARE NOT AFFECTED BY SENSITIVITY CHANGES WITH AGEING

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ABSTRACT

Purpose. The purpose of this study was to assess in a large sample of adult colour-normal observers of a wide age group (n=185; age range: 18-75) whether sensitivity changes due to ageing are associated with corresponding changes in the colour-opponent mechanisms that mediate hue perception. We therefore obtained the following data in the same set of observers: the sensitivity along the protan, deutan and tritan line and setting for the four unique hues from which the characteristics of the colour-opponent mechanisms can be derived. *Results.* We find a significant decrease in chromatic sensitivity with increasing age, in particular along the tritan line. When we predict the relative cone weights (L:S) of the colour-opponent mechanisms from the chromatic (protan, deutan, tritan) thresholds, we find a pronounced dependency on age. The observed relative cone weights (associated with a particular hue), on the other hand, are rather constant throughout the life span. *Conclusion.* The weighting of the cone inputs by the colour-opponent mechanisms (red-green; yellow-blue) appears to change with age. Such an adaptive weighting with is useful to maintain colour constancy throughout the life span in the presence of known changes in the ocular media and retinal sensitivity losses.

Keywords: cone inputs; colour opponency; aging, unique hues, chromatic sensitivity.

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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 sensitivity in the three cone classes are associated with potential hue changes. The effect of age on hue perception [1] and on chromatic sensitivity [2] 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 (n=185) set of colour-normal observers, ranging from 18 to 75 years of age.

METHODS

Two sets of data were collected: (1) chromatic thresholds along the protan, deutan and tritan line (using the Cambridge Colour Test), and (2) unique hue settings (for red, green, yellow and blue) to estimate the cone weightings of the colour-opponent mechanisms (eq 1-4).

Equipment. Stimuli were displayed on CRT monitor (21-inch Sony GDM-F520) which was controlled by a DELL PC with a ViSaGe stimulus generator (Cambridge Research System, Ltd.). The lookup tables were linearised using the ColourCal calibration device (Cambridge Research System, Ltd.) which interfaces with the graphics card. Calibration was checked with a PR650 tele-spectroradiometer (PhotoResearch). The CRT monitor had a correlated colour temperature of about 9300K with a peak luminance of 120 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 one hour before the start of the experiment. The responses of the observers were collected using a button box (CT6, Cambridge Research System, Ltd.). Stimuli were generated using the CRS MatLab toolbox and MatLab 7.4.

Subjects. 185 (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. The experiments were approved by the Ethics committee of the School of Psychology, University of Liverpool.

Chromatic Sensitivity. All observers were tested with the Cambridge Colour Test: thresholds along the protan, the deutan and the tritan line were assessed (Trivector thresholds). Only observers that fell within the normal range were used for the unique hue experiments. Normal range was defined as thresholds lower than 100×10^{-4} *u'v'* units for the protan and deutan lines, and lower than 150×10^{-4} *u'v'* units for the tritan line. 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.

Unique Hue Settings. To obtain settings of the unique hues we used a modified hue selection task [3]. The background was always set to a mid-grey with a luminance of 24 cd/m^2. Each patch had a diameter of 2º of visual angle and was presented at an eccentricity of 4º. Patches of slightly different hues (and same lightness and saturation) were arranged along an annulus at constant eccentricity and the task of the observer was to select a patch that contains neither yellow nor blue (to obtain unique red and green) [4]. Unique yellow (blue) was obtained by asking observers to select a patch that contains neither red nor green. 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 × 9 combinations of different saturation-lightness levels × 10 colour patches per test) were selected.

Estimating the cone inputs to the colour-opponent mechanisms

Colour-opponent mechanisms were first mentioned by Hering [5] 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[6-8] 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:

$$\alpha_Y*L + \beta_Y*M + \gamma_Y*S = RG_Y = 0 \qquad (1)$$

By definition, a yellowish stimulus with these differential L,M,S cone weights (α_Y, β_Y, γ_Y) 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 (α_Y, β_Y, γ_Y) is orthogonal to this plane; this normal vector (α_Y, β_Y, γ_Y) 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:

$$\alpha_B*L + \beta_B*M + \gamma_B*S = RG_B = 0 \qquad (2)$$

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

$$\alpha_R*L + \beta_R*M + \gamma_R*S = YB_R = 0 \quad (3)$$

$$\alpha_G*L + \beta_G*M + \gamma_G*S = YB_G = 0 \quad (4)$$

If unique red and unique green are generated by silencing a single yellow-blue opponent mechanism, then the coefficients in equations 1 and 2 should be identical; similarly, if unique yellow and unique blue silence a single red-green opponent mechanism, then the normal vector in equations 3 and 4 should be the same. In the following we assume that the normal vectors can be different for each unique hue.

In our study we first estimate the cone weights (α, β, γ) associated with each of the four unique hues (using Eq. 1-4) 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 then scale the cone signals (L,M,S) with the individual thresholds, hence taking into account the individual observer sensitivity. We then estimate again the coefficients (α, β, γ) by solving equations 1-4 based on the scaled cone signals. These coefficients are the *predicted* cone weights. By comparing the observed and predicted cone weights as a function of age, we can ascertain whether changes in chromatic sensitivity across the life-span are associated with changes in the colour-opponent mechanisms. Alternatively, if the colour-opponent mechanisms turn out to be invariant across the life span[1], then compensatory mechanisms must be in place allowing a change in the weightings of the cone signals.

RESULTS AND DISCUSSION

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. Observed changes in hue perception are compared to the predicted changes based on the age-related changes in chromatic sensitivity.

Chromatic Sensitivity

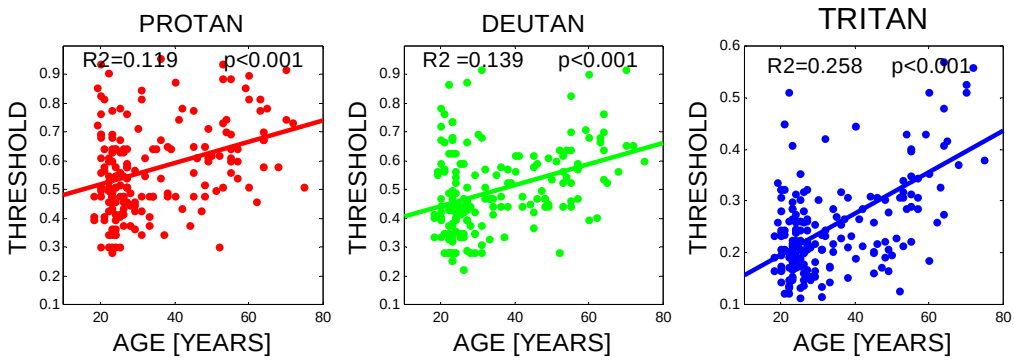

Fig. 1 Thresholds (in units of incremental cone excitations) along the protan, deutan and tritan line.

The Protan, Deutan, and Tritan thresholds (in units of incremental L,M,S cone excitations) for all 185 observers are shown as a function of age in figure 1. 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 0.12, 0.14 and 0.26 for protan, deutan and tritan thresholds, respectively. Knoblauch and colleagues [2]

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 concentrated on very young infants 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 [9] which might increase the variability in contrast thresholds as function of age, hence reducing the R^2. The strongest association between age and chromatic sensitivity occurs for S-cone isolating stimulis (i.e. contrast thresholds along the tritan line) which is consistent with the 'yellowing' of the lens. The slope is almost identical for protan and deutan thresholds; hence any mechanism taking the difference between the L and M cone signals should not be greatly affected by the age-related loss in sensitivity.

Colour-opponent mechanisms

The unique hue settings for all 185 observers and all saturation and lightness levels are shown in figure 2, in a cone-opponent chromaticity diagram [10]. 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. 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 weights of these chromatic mechanisms and how these cone weights change with increasing age, our further analysis was performed in three-dimensional LMS cone space. Figure 2 only serves to visualise the unique hue settings.

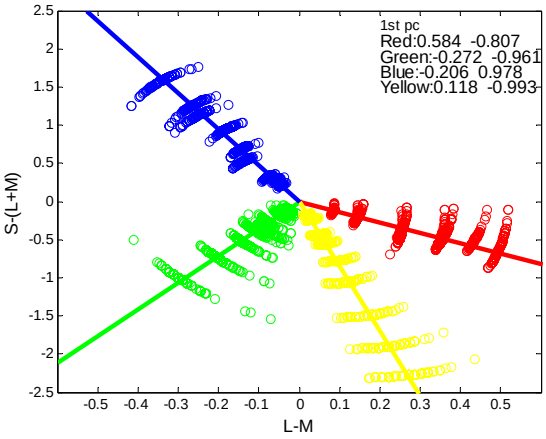

Fig 2. The unique hue settings for all 185 observers in a cone-opponent chromaticity diagram. The grey background is at the origin (0,0) in this diagram. Unique red is close to the L-M axis with a fairly small negative S cone input. All other unique hues are at intermediate directions: unique green requires a substantical negative S cone input and a negative L-M input. Unique yellow and unqiue blue are almost collinear; unique blue is defined by a positive S cone and a negative L-M input; unique yellow is defined by a positive L-M and a negative S cone input.

Estimating the cone weights. (1) First, we determined for each unique hue the best-fitting coefficients (α, β, γ) by using principal component analysis of the LMS coordinates of the unique hues. (eq. 1-4). The last eigenvector (explaining the least variance) is the normal vector; its orientation is defined by the coefficients (α, β, γ) and the coefficients are normalised such that $\alpha^2+\beta^2+\gamma^2 = 1$. An equivalent method for finding the normal vector (with coefficients α, β, γ) is to minimise the Euclidean distances between the individual unique hue co-ordinates (in LMS space) and the plane ('Total Least Squares')[3]. We calculated for each of the 185 observers the normal vectors (that is, the cone weights α, β, γ; cf. eq 1-4) for each of the four unique hues. We refer to these cone weights as *observed* cone weights since the individual sensitivity has not been taken into account. (2) Secondly, we took into account the individual sensitivities along the protan, deutan and tritan line by scaling the cone coordinates (L,M,S) for each observer with the observer's contrast threshold. These scaled cone signals then represent the cone signal available to each of the chromatic mechanisms for this particular observer. We then performed a principal component analysis on the scaled cone signals and derived the cone weights (i.e. normal vectors) for each observer and for each unique hue. We refer to these cone weights that take into account the observers' individual sensitivity, as *predicted* cone weights.

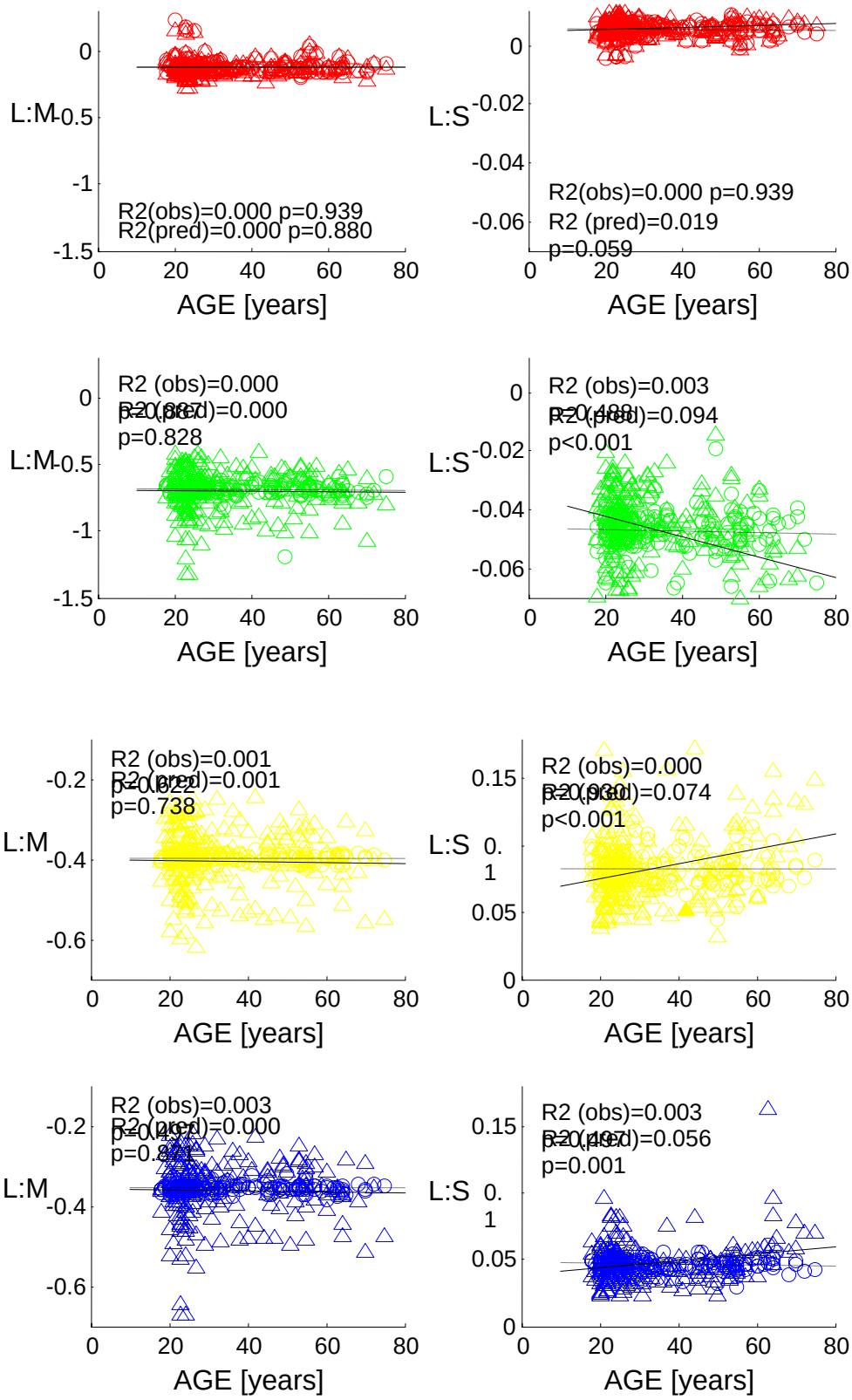

Fig 3. Relative cone weights associated with the four unique hues: red, green, yellow, blue (from top to bottom). The observed (circles and dashed lines) and predicted (diamonds and solid lines) relative cone weights (i.e. the coefficients α, β, γ) are plotted as a function of the age of the observer. Left column: the relative L:M cone weights are plotted as function of age. Right Column: The relative L:S cone weights are plotted as a function of age.

Figure 3 shows the observed and predicted (based on individual observers' contrast thresholds) relative cone weights (i.e. the coefficients α, β, γ) as a function of the age of the observer. On the left column, the relative L:M cone weights are plotted *Observed* relative cone weights are indicated by an open circle and the linear regression is indicated by the dashed line. *Predicted* relative cone weights (L:M) are indicated by diamonds and the best-fitting line is the solid line. Regression analysis confirms that the relative L:M cone weights associated with a particular hue do not change with age; the R^2 for all four unique hues is close to zero and none of the slopes differs from zero. This is the case for both the observed (dashed lines and circles) and the predicted L:M cone weights (solid lines and triangles); this is also expected from close-to-parallel sensitivity changes in the L and M cones. The results are different for the relative L:S cone weights shown on the right side. Whereas the observed relative cone weights show no dependency on age, the predicted relative cone weights show a clear dependency on age for unique green, yellow and blue (regression slopes are different from zero; $p<0.001$; R^2 range from 0.05 to about 0.1). These R^2 values are still rather small, but significant due to our large sample size.

An alternative explanation for our failure to find any age dependency in the observed unique hue settings (i.e. the observed relative cone weights, L:M and L:S, associated with a particular unique hue) 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).

Variable cone weights throughout the life span?

Our main finding is that the chromatic mechanisms that mediate our hue perception are to a large extent invariant across the life span despite a significant age-related decline in sensitivity along the cone-isolating directions (Figure 1). There are two possible explanations for this hue invariance across the life space. The first possibility is that the decline in sensitivity in the L,M, and S cones is parallel as a function of age and therefore any chromatic mechanism taking the difference between the cone signals (e.g. L-M) will not exhibit any age dependency. To test this possibility, we have estimated the differential cone inputs to the chromatic mechanisms that mediate hue perception and calculated the relative cone weights (L:M and L:S; Figure 3). We find that the predicted relative cone weights (L:S) – based on the individual observers' sensitivity - are age-dependent, whereas the observed cone weights (L:M and L:S) do not depend on age. We can therefore exclude the first explanation. Instead, comparing the relative (L:S) cone weights (observed vs predicted) suggests that human observers change the weighting of the individual cone inputs when the effective cone signal (due to neural loss or changes in the lens) deteriorates which is known to be the case for S-cone signals. If the relative effectiveness of a cone signal declines with age, then the relative weighting for this particular cone class seems to be increased to achieve approximate hue invariance throughout the life span. Therefore this compensation mechanism must arise at a post-receptoral site, such as a colour-opponent site[11, 12]. Neitz and colleagues[12]. showed that shifts in unique yellow induced by long-term changes in the chromatic environment are not due to receptoral changes, but must be of cortical origin, probably after chromatic information from both eyes as been integrated. The question remains how the human visual system receives feedback on the strength of their 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 the average daylight [13]. Our results provide further evidence that the brain uses information about the statistical properties of our chromatic environment to adjust the weighting of the receptor signals to achieve hue constancy.

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