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Detection of Blue Under Chromatic Adaptation: the Effects of Stimulus Size and Eccentricity

ANTTI IIVANAINEN,* JYRKI ROVAMO†

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We measured thresholds for the perception of blue under chromatic adaptation to white, green, yellow or red at the eccentricities of 0–70 deg in the temporal visual field of four subjects. We used a series of stimulus sizes at each eccentricity, without a prior assumption of any peripheral size-scaling factor. The CIE 1976 UCS (u', v') chromaticity coordinates corresponding to blue perception were subtracted from the chromaticity coordinates of the adaptation field in order to obtain the threshold differences (du', dv') in chromaticity coordinates. Spatial scaling factors for the perception of blue were obtained by non-linear regression. ($E_2 + 5$ deg) refers to the eccentricity at which stimulus diameter had to be doubled in order to maintain performance found at the eccentricity of 2.5 deg. E_2 for the perception of blue tint varied from 1.2 to 36 deg depending on the state of chromatic adaptation and subject. For the perception of blue tint in yellow three subjects and for the perception of blue tint in red one subject had no spatial scaling factor that would make performance independent of eccentricity. Thus, spatial scaling does not always work.

Colour vision Perimetry Chromatic adaptation Spatial scaling Human

INTRODUCTION

Depending on the task, chromatic threshold becomes or does not become independent of eccentricity when stimulus is M-scaled by magnifying its size with increasing eccentricity in inverse proportion to the lowest local sampling density across the human retina (Rovamo & Virsu, 1979). This procedure equalizes the number of bottleneck cells (cones at eccentricities 0–10 deg and ganglion cells above 10 deg, respectively) covered by the stimulus at each eccentricity. For example, chromatic contrast sensitivity for the spatial red–green modulation of a yellow field and blue–yellow modulation of a white field (Noorlander, Koenderink, den Ouden & Edens, 1983) and detection of chromatic deviations from white (Rovamo & Iivanainen, 1991) and yellow (Iivanainen & Rovamo, 1991) become independent of eccentricity when the stimulus is M-scaled (Rovamo & Virsu, 1979). On the other hand, the desaturation threshold of blue but not green or red (Iivanainen & Rovamo, 1992) and the perceived distinctness of a blue–yellow but not red–green, equiluminous, chromatic border can be made independent of visual field location by M-scaling the spatial stimulus parameters (Blatherwick & Hallet, 1992). Also, red–green stimuli with an iso-luminous white surround need a greater increase in stimulus size than blue–yellow stimuli to produce a foveal-like performance at the same eccentricity (Dain & King-Smith, 1989). The above findings imply that the spatial scales of various chromatic mechanisms are different.

There are studies suggesting that the perception of blue or bluish hues are mediated by more than one mechanism. For example, Abramov, Gordon and Chan (1991, 1992) found blue and tritan-blue mechanisms for blue perception, and Mullen and Kulikowski (1990) used a technique of measuring wavelength discrimination at the detection threshold in the fovea and found in the region of short wavelengths one mechanism detecting blue and evidence for another detecting violet. Also Valberg and Seim (1991) suggest that different cones mediate different bluish perceptions: L-cone bluish-red, M-cones bluish-green and S-cones reddish-blue.

Based on the above we studied the perception of blue across the visual field under chromatic adaptation to white, yellow, red or green in order to find out whether there are one or several spatial scales for the perception of blue. Our purpose was not to isolate chromatic mechanisms detecting blue but study the spatial properties of blue perception. We used a method of spatial scaling (Johnston & Wright, 1986; Watson, 1987;

* Institute of Biomedicine, Department of Physiology, PL 9 (Siltavuorenpenger 20 J), 00014 University of Helsinki, Helsinki, Finland.

† To whom all correspondence should be addressed at: Department of Vision Sciences, Aston University, Aston Triangle, Birmingham B4 7ET, England.

Saarinen, Rovamo & Virsu, 1987) where a series of stimulus sizes is tested at each eccentricity without a presumption of any peripheral size-scaling factor (cf. Whitaker, Rovamo, MacVeigh & Mätrelä, 1992).

METHODS

Apparatus

Philips Colour Enlarger PCS 130 and a Philips Tri-one Control Unit PCS 150 combined with an additional control unit were used to produce colour stimuli. Control unit PCS 150 was used as an adaptation unit and the additional unit as a test unit. The light intensities of red, green and blue channels could be independently adjusted by each unit. A manually operated switch was used to choose whether the three-colour mixture presented in the output aperture of the colour enlarger was determined by the adaptation or test unit.

The original blue filter of the colour enlarger was used in all experimental conditions. The original red and green filters of the colour enlarger were used in the experiments with the white adaptation field. They were replaced by Dicrolight (Balzers, Liechtenstein) filters in the experiments with the green and red adaptation fields. Colour filter R65 was used to produce red and G50/55 plus C54 to produce green. For the yellow adaptation field the red filter of the colour enlarger was replaced with a Dicrolight colour filter Y52 to produce yellow. The output aperture was limited to a circular stimulus field of a desired diameter with an adjustable black diaphragm. The test and adaptation fields had always the same diameter. When the perception of blue was studied under green, yellow or red adaptation, a small metal plate with a circular aperture of desired diameter was placed between the halogen lamp and the blue colour filter in order to reduce the luminous output and increase the colour temperature of the light coming from the halogen lamp at each luminance level.

In the foveal experiments the fixation was directed towards the centre of the stimulus field. In the extrafoveal experiments a small spot of green light served as a fixation point. Eccentricity measured along the temporal half of the horizontal visual field meridian refers to the angular distance between the centre of the stimulus field and the point of fixation.

The experiments were monocular. A black eye pad was used to cover the other eye. The only light sources during the trials were the display and the fixation point in the extrafoveal vision, but the room was also lit by an incandescent lamp during the inter-trial period. The head was stabilized with a chin rest. The stimulus field was always perpendicular to the line determined by the centre of the stimulus field and the pupil of the eye used.

Calibration

We calibrated the test and reference units by measuring luminance by means of a Spectra Spot photometer. The CIE 1931 (x, y) chromaticity coordinates were measured using a Minolta Chroma Meter CL-100. In the red corner of the CIE 1931 chromaticity coordinate diagram the meter gives readings that lie outside the experimentally realizable colours. They were corrected as suggested by Rovamo and Raninen (1990). The CIE 1931 (x, y) chromaticity space is nonlinear with respect to perceptual colour changes. Hence, these chromaticity coordinates were further transformed to CIE 1976 UCS (u', v') chromaticity coordinates (MacAdam, 1985) to obtain a more linear representation.

For studying the perception of blue under chromatic adaptation to white, yellow, red, or green, the potentiometers of the green, red and blue channels of the adaptation unit were set to produce a white, yellow, red or green field with photopic luminance of 160, 450, 54 or 120 cd/m^2; scotopic luminance of 360, 490, 8.2, or 440 cd/m^2; and CIE 1976 UCS (u', v') chromaticity coordinates of (0.22, 0.49), (0.31, 0.55), (0.61, 0.51), or (0.09, 0.54), respectively. In addition, the positions of the potentiometers of the test unit that produced the above white, yellow, red, and green fields were recorded. The size of the natural pupil was 6.5–8 mm. Hence, the average photopic and scotopic illuminances were 6600 and 15,000 td for white; 19,000 and 20,000 td for yellow; 2200 and 340 td for red; and 5000 and 18,000 td for green, respectively. The scotopic retinal illuminances indicate that, except for the red adaptation field, rods were saturated (Aguilar & Stiles, 1954).

Then we turned the 10-turn potentiometer of the blue channel of the test unit in small predetermined steps in order to add blue to red, green, white, or yellow described above and the corresponding chromaticity coordinates were recorded. Thus, the test field consisted of blue light added to the adaptation field. The accuracy was ± 0.002 in CIE 1931 (x, y) chromaticity coordinates for two identical settings of the potentiometers.

Procedures

Perception of blue tint in red. The potentiometers of both units were set to the positions that produced the red adaptation field at the beginning of an experimental session.

The session was started by exposing the subject to moderate natural daylight. Thereafter, to produce partial dark adaptation of the cone system, 2 min were spent in total darkness. The retinal location of the eye to be tested was then adapted to the red field for 5 sec measured with an electronic timer. Then the red adaptation field was replaced by the test field for 0.5 sec. Thereafter, an ambient luminance of *ca* 2cd/m^2 on the grey wall of the room, produced by a tungsten bulb (Airam bright, 40 W) with CIE 1976 UCS (u', v') chromaticity coordinates of (0.26, 0.53), was turned on for 5 sec and the subject looked away from the colour enlarger aperture and fixation point. This arrangement prevented peripheral fading and minimized rod intrusion. It also minimized cumulative colour adaptation, because the readings, recorded during an experimental session and used for calculating the threshold, did not tend to decrease or increase indicating that the state of adaptation remained constant. Then the cycle began

again with adaptation to red. The whole cycle was repeated with the same settings if the subject reported that the fixation was not steady or that she/he was not sure about the perception during a trial.

Before the first exposure of the test field the amount of blue light was increased to an extent that made blue colour clearly visible in the test field. Thereafter, the potentiometer of the blue channel was turned to reduce the amount of blue light of the test field in small steps after each exposure until the subject reported that during the 0.5 sec exposure she/he no longer could perceive blue in the test field. The reading of the potentiometer of the blue channel of the test field was recorded. After this, in order to make the test field certainly void of blue, the amount of blue light in the test field was further reduced by a few steps. The amount of blue light in the test field was then increased in small steps until the subject reported perceiving blue in the test field. The reading of the potentiometer of the blue channel of the test unit corresponding to the blue perception was again recorded. The potentiometer of the blue channel was then turned further to increase the amount of blue light in the test field by a few steps so that blue was clearly visible in the test field.

Altogether six readings of the potentiometer of the blue channel of the test unit were recorded by performing the above procedure three times. Each experimental session lasted less than 10 min. The readings were then transformed into CIE 1976 UCS (u', v') chromaticity coordinates and averaged. To obtain the differences du' and dv', the chromaticity coordinates (u', v') corresponding to blue perception were subtracted from the chromaticity coordinates of the adaptation field. The Euclidean distance $dz = (du'^2 + dv'^2)^{1/2}$ between the chromaticity coordinates of the adaptation field and blue perception was then calculated in order to obtain a single measure of the chromaticity difference, because in our data correlation between du' and dv' was found to be 98.9%.

Perception of blue tint in white, green or yellow. The procedure was similar to that used above except that in the beginning the colour of both the adaptation and test fields was white, green or yellow.

Subjects

Four subjects (AA, AI, AR and ML, aged 26–44 yr) participated in the experiments. AI and AR were highly trained in psychophysical experiments whereas AA and ML were naive subjects. AI and AR and ML were emmetropes and AA a corrected myope. Monocular visual acuity of the dominant eye used was at least 1.2. On the basis of Lanthony desaturation panel D-15 and Ishihara (38 plates) tests, the foveal colour vision of the subjects was considered to be normal. All subjects were tested in all four conditions. All procedures followed the principles outlined in the Declaration of Helsinki. Written informed consent was obtained from each subject prior to their participation, except for AI, who was an author of the article and thus fully aware of the experimental procedure.

RESULTS

In our experiments we studied how much blue had to be added to yellow, white, red or green in order to perceive blue. The experiments were performed at the eccentricities of 0–70 deg along the horizontal meridian in the temporal visual field. At each eccentricity a series of stimulus sizes was used. The eccentricities and stimulus sizes were tested in random order. Thresholds were expressed as Euclidean distances in CIE 1976 UCS (u', v') chromaticity coordinates.

In Fig. 1 we studied how much blue light had to be added to white as a function of stimulus size in order to perceive blue tint. Thresholds decreased with increasing stimulus size at all eccentricities. In addition, the thresholds tended to increase with eccentricity at all stimulus sizes. In general the thresholds were lowest for the largest stimulus sizes at the eccentricity of 2.5 deg or at the fovea and highest for the smallest stimulus sizes at the eccentricity of 70 deg.

In the experiments of Fig. 2 we studied how much blue light had to be added to green as a function of stimulus size in order to perceive blue tint. As in Fig. 1, the thresholds decreased with increasing stimulus size at all eccentricities. Also, thresholds at all stimulus sizes tended to increase with eccentricity, except for the fovea in Fig. 2(A, B, D).

In the experiments of Fig. 3 we studied how much blue light had to be added to red as a function of stimulus size in order to perceive blue tint. In Fig. 3(A–C) thresholds decreased with increasing stimulus size at all eccentricities and, except for the fovea, tended to increase with eccentricity at all stimulus sizes. However, in Fig. 3(D) (subject ML) stimulus size had practically no effect on threshold. Also, these thresholds showed a non-monotonical change with increasing eccentricity: the thresholds first increased from 0 to 22.5 deg and then decreased from 22.5 to 70 deg.

In the experiments of Fig. 4 we studied how much blue light had to be added to yellow as a function of stimulus size in order to perceive blue tint. The perception of blue tint in yellow means that at threshold the test field had desaturated to achromatic or turned to pink and in addition, contained a marginal blue tint. The perception of pink when blue was added to yellow could have been caused by the short-wave end of red cone sensitivity spectrum (De Monasterio & Gouras, 1977), although yellow adaptation light desensitizes red cones strongly.

Thresholds decreased monotonically with increasing stimulus size and tended to increase with eccentricity only for subject AA [Fig. 4(B)]. For other subjects [Fig. 4(A, C, D)] the effect of the stimulus size on the threshold was at most eccentricities non-monotonical, because threshold reached a minimum at an intermediate stimulus size. Also, the effect of eccentricity on the thresholds was non-monotonical.

The results concerning the perception of blue tint in red for subject ML [Fig. 3(D)] and in yellow for subjects AI [Fig. 4(A)], AR [Fig. 4(C)] and ML [Fig. 4(D)] mean that the threshold vs size functions measured at various

eccentricities cannot be superimposed by horizontal shifts.

On the other hand, the data in Figs 1, 2, 3(A–C) and 4(B) suggest that the threshold vs stimulus size functions from eccentricities of 0 and 8.75–70 deg will collapse onto the 2.5 deg data, when shifted along the horizontal axis, i.e. divided by a scaling factor. The value of the scaling factor, i.e. the amount of size magnification needed at each eccentricity is indicated by the magnitude of the shift. The 2.5 deg eccentricity was chosen to be the reference for the other eccentricities because the thresholds tended to be smallest at the eccentricity of 2.5 deg.

Analysis of a covariance model with log Euclidean difference as the dependent variable, subject as a random factor, eccentricity and stimulus colour as fixed factors and log size as a covariate indicated statistically highly significant third-order interaction ($P < 0.0001$) between subject, stimulus colour and size of the stimulus. This means that scaling factor values as a function of eccentricity had to be calculated separately for each adaptation colour and subject.

In order to find the values of scaling factors as a function of eccentricity for the perception of blue tint in white (Fig. 1), green (Fig. 2), red [Fig. 3(A–C)] and yellow [Fig. 4(B)], a non-linear regression was applied to the data of each subject separately. To make the comparison of scaling factors from the eccentricities of 0 and 8.75–70 deg as simple as possible the scaling factor for the data at the eccentricity of 2.5 deg was chosen to be 1. Our polynomial model was

$$\log \mathrm{d}z'_j(E) = \sum_{i=0}^{2} a_i[\log S_j(E) - \log m(E)]^i, \quad (1)$$

in which E is eccentricity (0, 2.5, 8.75, 22.5, 35 and 70 deg), j is a subscript denoting stimulus size, a_i are the coefficients of the polynomial, $\mathrm{d}z'_j(E)$ is a fit to one of the Euclidean distances in CIE 1976 (u', v') chromaticity coordinates, $S_j(E)$ is the corresponding stimulus size, and $m(E)$ is the scaling factor at each eccentricity. Natural logarithms of dz, stimulus size and scaling factors were used in our polynomial model, because in Figs 1–4 data were plotted in double logarithmic units. The subtraction of the logarithm of the scaling factor from the logarithm of the stimulus size refers to a shift to the left along the logarithmic horizontal size axis in Figs 1–4. This is equivalent to the logarithm of the ratio where stimulus size is divided by scaling factor. The data at the eccentricity of 2.5 deg were not shifted at all, because the natural logarithm of its scaling factor m (2.5) was equal to 0. Thus, the 2.5 deg data have no special role in nonlinear regression, which adjusts all a_i and

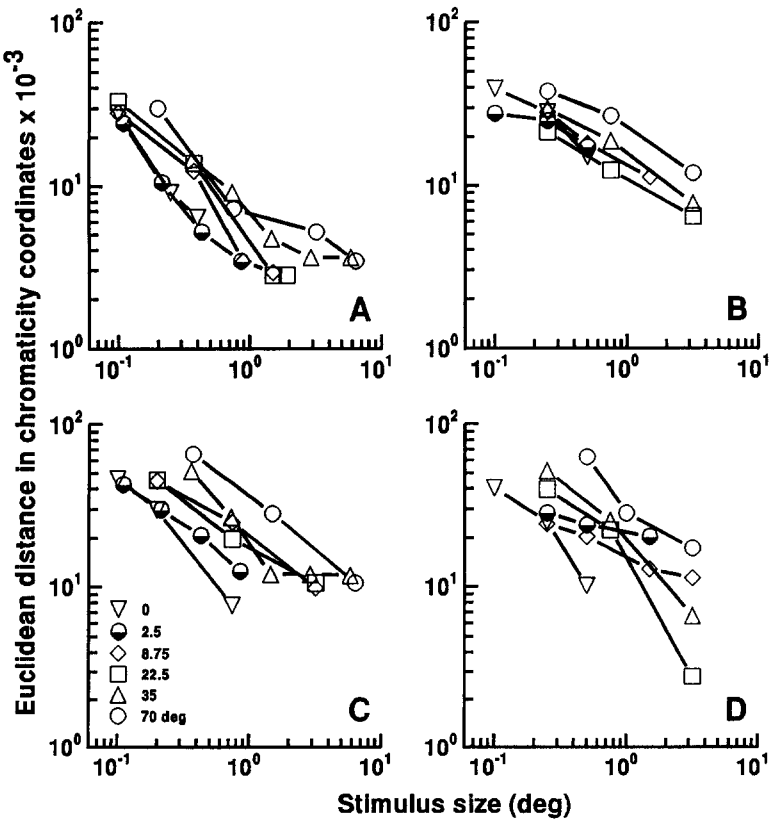

FIGURE 1. Perception of blue tint in white at various eccentricities in the temporal visual field as a function of stimulus size. A series of stimulus sizes was used at each eccentricity, without a presumption of any peripheral size-scaling factor. The Euclidean distance ($\mathrm{d}z = (\mathrm{d}u'^2 + \mathrm{d}v'^2)^{1/2}$ in CIE 1976 UCS (u', v'), chromaticity coordinates between the white adaptation field and the test field, produced by the increment in blue light that just allowed blue tint perception, has been plotted as a function of stimulus size. Viewing distance was 57.3 cm, except for the 6.4 deg stimulus size which required the use of a viewing distance of 28.7 cm because of the limited physical stimulus size. The data from subjects AI, AA, AR, and ML are shown in (A), (B), (C) and (D) respectively.

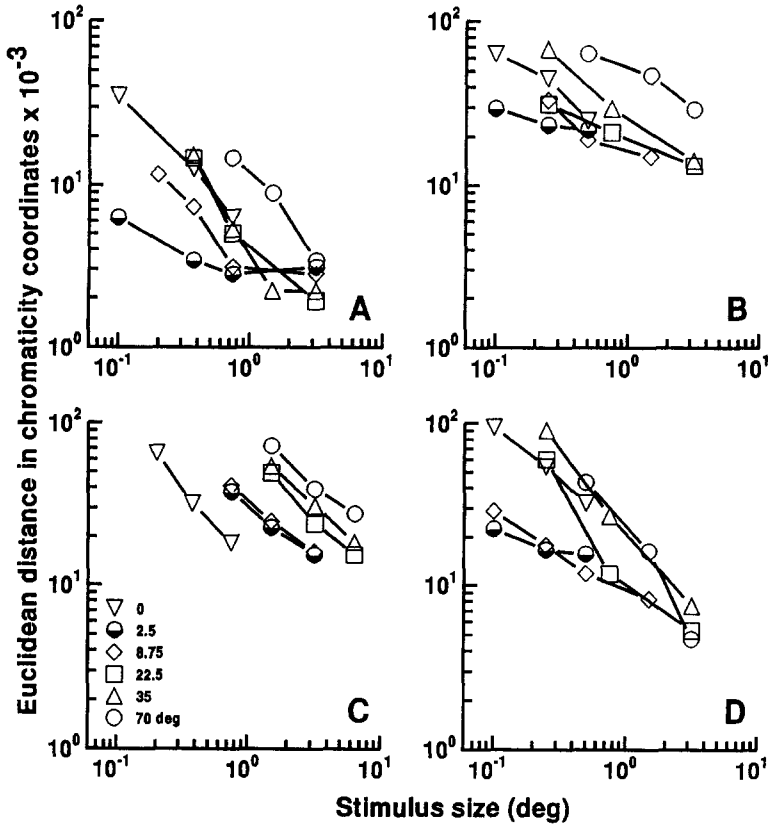

FIGURE 2. Perception of blue tint in green across the temporal visual field. The Euclidean distance dz between the green adaptation field and the test field, produced by the increment in blue light that just allowed blue tint perception, has been plotted as a function of stimulus size. Other details as in Fig. 1.

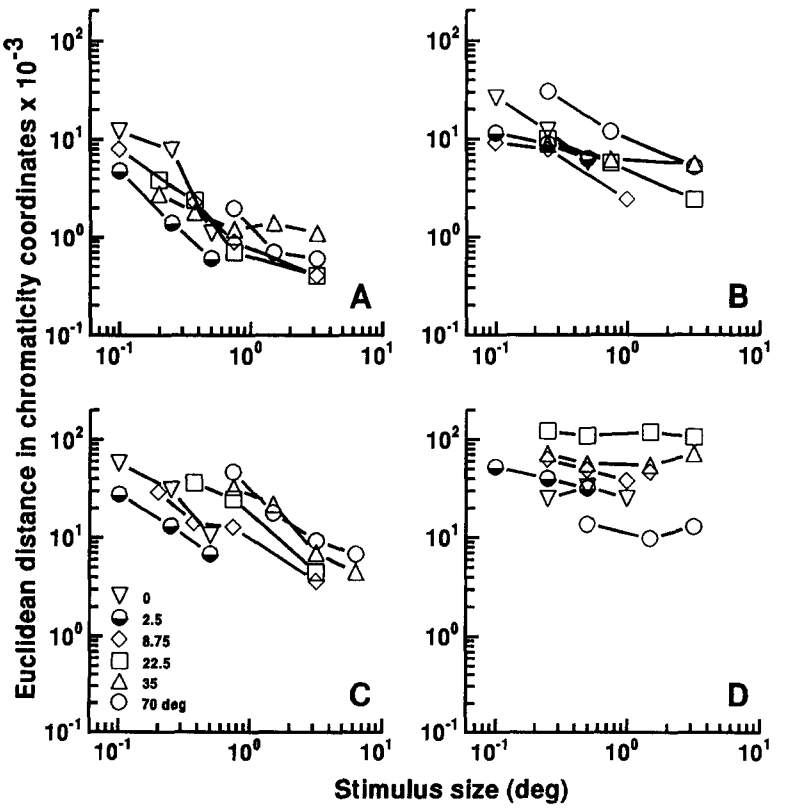

FIGURE 3. Perception of blue tint in red across the temporal visual field. The distance dz between the red adaptation field and the test field, produced by the increment in blue light that just allowed blue tint perception, has been plotted as a function of stimulus size. Other details as in Fig. 1.

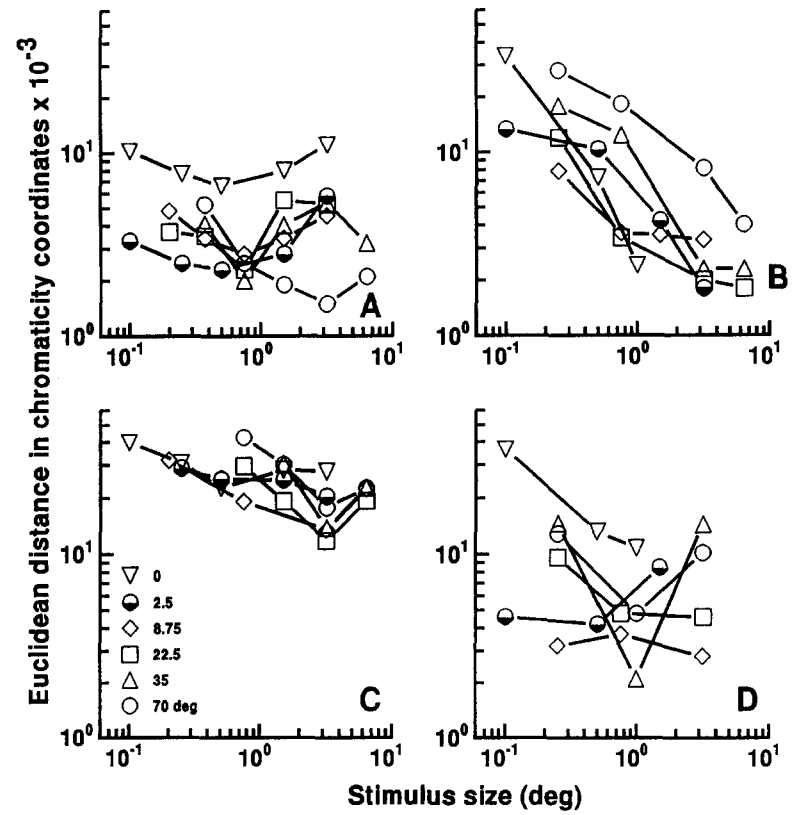

FIGURE 4. Perception of blue tint in yellow across the temporal visual field. The distance dz between the yellow adaptation field and the test field, produced by the increment in blue light that just allowed blue tint perception, has been plotted as a function of stimulus size. Other details as in Fig. 1.

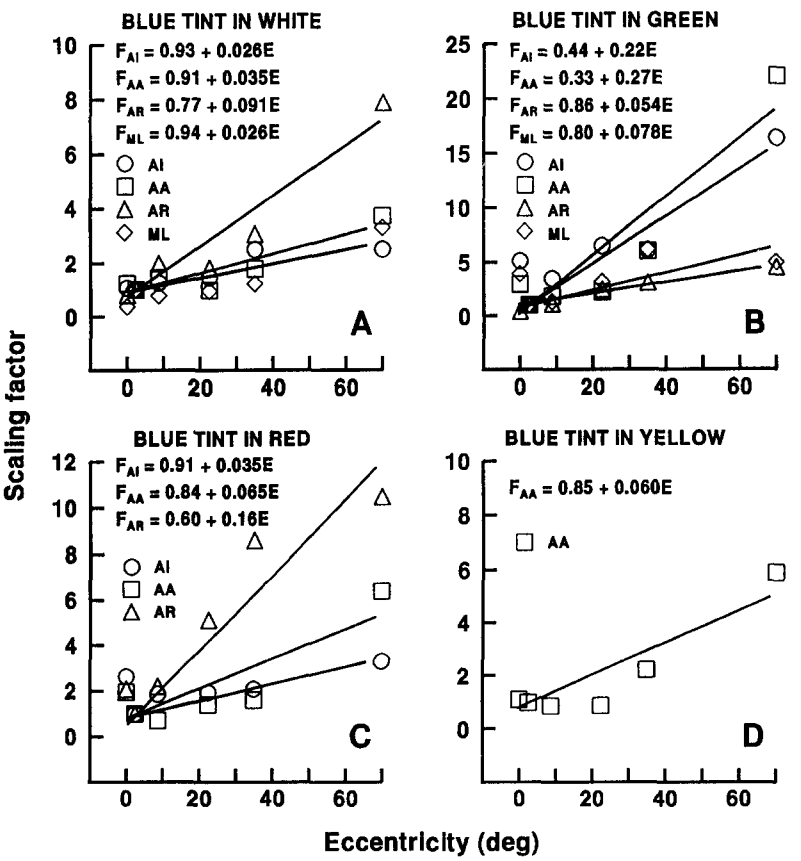

FIGURE 5. Scaling factors (F) for the perception of blue tint in white (A), green (B), red (C), and yellow (D) as a function of eccentricity (E) in the temporal visual field. Least squares lines were fitted to the data of each individual separately.

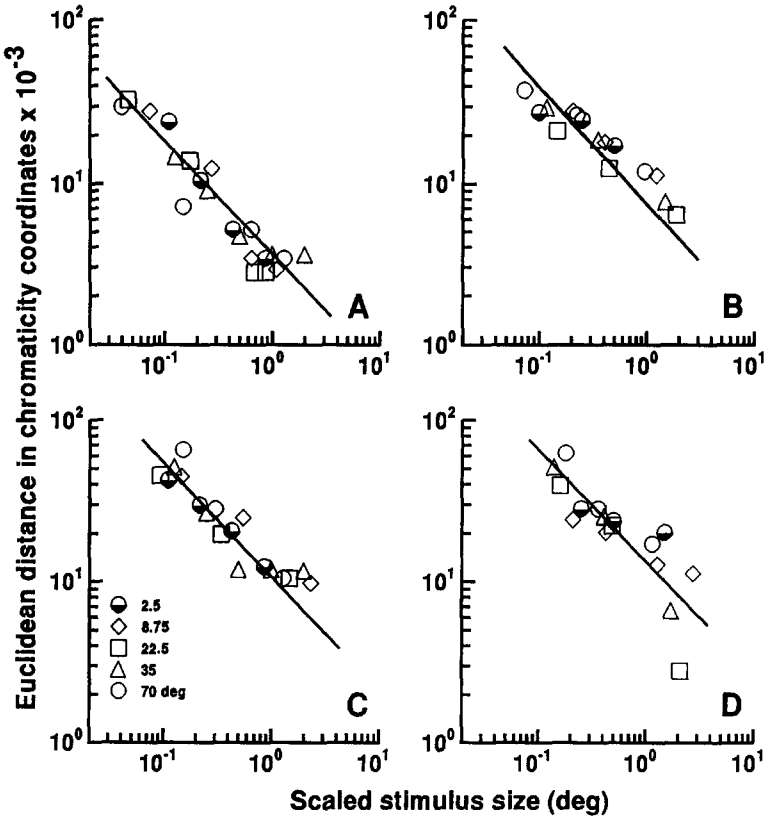

FIGURE 6. The data concerning the perception of blue tint in white from Fig. 1 replotted as a function of scaled stimulus size. Scaling was obtained by dividing stimulus diameters by the scaling factors calculated using the individual least squares lines of Fig. 5. The solid lines have been visually fitted to data so that the slope is similar for all subjects.

$m(E)$ in order to minimize the sum of the squares of the residual deviations

$$\{\log dz_j(E) - \log dz'_j(E)\}$$

of the experimental data $dz_j(E)$ points at all eccentricities and stimulus sizes $S_j(E)$ from the corresponding predictions of the polynomial model defined by equation (1).

Scaling factors obtained by nonlinear regression for the perception of blue in white, green, red and yellow at 0–70 deg of eccentricity are plotted as a function of eccentricity in Fig. 5. Scaling factors increased with eccentricity, as was expected, and the increase was fairly linear. A line of least squares was fitted to the scaling factors corresponding to each subject and adaptation colour. The scaling factors at each eccentricity were determined relative to the 2.5 deg eccentricity. Hence, the linear regression fit to the data was constrained to go through a value of unity at 2.5 deg of eccentricity. The foveal value of scaling factor was not used in the linear regression fit, because thresholds tended to be higher at the fovea. The data is described well with the lines of least squares, which indicates that the relationship between scaling factor F, and eccentricity, E, is given by the equation (Whitaker *et al.*, 1992)

$$F = 1 + S(E - 2.5) = F(0)(1 + E/E_2), \quad (2)$$

where

$$F(0) = 1 - 2.5S \quad (3)$$

and

$$E_2 = 1/S - 2.5. \quad (4)$$

In these equations S is the slope of the linear increase. The value of $(1/S - 2.5)$ deg represents the eccentricity E_2. The expression $(E_2 + 5$ deg) indicates the eccentricity (E) at which the stimulus diameter of the 2.5 deg eccentricity must be doubled to maintain performance. The value of E_2 was found to be 36, 26, 8.5, and 36 deg for the perception of blue tint in white and 2.0, 1.2, 16, and 10 deg for the perception of blue tint in green for subjects AI, AA, AR, and ML, respectively. For the perception of blue tint in red the value of E_2 was found to be 26, 13, and 3.8 deg for subjects AI, AA, and AR, respectively. For the perception of blue tint in yellow the value of E_2 was found to be 14 deg for subject AA.

A control experiment was performed to test the possible effect of rod intrusion on our results. Neutral density filters (Lee Filters Ltd, Hampshire, England) of 0.3 + 0.6 log units (ND 209 and 210) placed in front of the output aperture of the colour enlarger reduced the scotopic illuminance of the white adaptation field by a factor of 5.6 from 15,000 to 2700 td. The threshold for the perception of blue tint in white was then measured as a function of stimulus size at the eccentricities of 2.5 and 35 deg for subject AI. If the increase of thresholds towards the visual field periphery is caused by rod intrusion, the reduction of luminance should increase the contribution of rods and consequently the thresholds in

the periphery. However, the thresholds at both eccentricities remained practically unchanged, and the scaling factor for 35 deg of eccentricity was found to be 3.4 at 2700 scot td. This does not differ substantially from the scaling factor of 1.9 predicted by the line of least squares at 15,000 scot td.

In Fig 6–8 the extrafoveal threshold data of Figs 1–4 are replotted as a function of scaled stimulus size in those cases where the threshold vs size functions from eccentricities 2.5–70 deg could be superpositioned by spatial scaling. The stimulus diameters at each eccentricity were divided by the corresponding value of the scaling factor determined by equation (2).

As Figs 6–8 show, the data from different eccentricities collapsed together by this scaling operation. Comparison with Figs 1–4 reveals that the inter-eccentricity variation has been reduced considerably and that there is only little systematic variation between the data points from different eccentricities. In Figs 6–8 the decrease of Euclidean distance in CIE 1976 UCS (u', v') chromaticity coordinates as a function of scaled stimulus size was fairly linear in double-logarithmic coordinates. For each adaptation condition the solid lines have been visually fitted to the data so that the slope is similar for all subjects. As Figs 6–8 show, this approach worked quite well.

Figure 9 shows the individual scaling factors for the perception of blue tint in white, green, red and yellow. The scaling factors varied substantially from one task and subject to another. The total range of E_2 values was 30-fold. For example, E_2 was 36 (subject ML) and 1.2 deg (subject AA) for perceiving blue tint in white and green, respectively. The scaling factors also varied substantially from one task to another for each subject. For example for subject AA E_2 was 1.2 and 26 deg for the perception of blue tint in green and white, respectively, and for subject AR E_2 was 3.8 and 16 deg for the perception of blue tint in red and green, respectively. In addition, for subjects AI and AA E_2 value was greater for the perception of blue tint in red and white than for blue tint in green while the reverse was true for subject AR.

DISCUSSION

At all eccentricities the thresholds for the perception of blue tint in white, green, red (three subjects out of four) or yellow (one subject out of four) were found to decrease monotonically with increasing stimulus size. The thresholds tended to be smallest at the eccentricity of 2.5 deg. The threshold vs size functions were similar in shape but shifted horizontally towards larger stimulus sizes with increasing eccentricity. Thus, in order to maintain the performance found at the eccentricity of 2.5 deg, the stimulus size at the other, more peripheral eccentricities had to be magnified with increasing eccentricity. The expression ($E_2 + 5$ deg) indicates the eccentricity at which the stimulus diameter used at the eccentricity of 2.5 deg must be doubled to maintain unchanged performance. The E_2 value was found to be

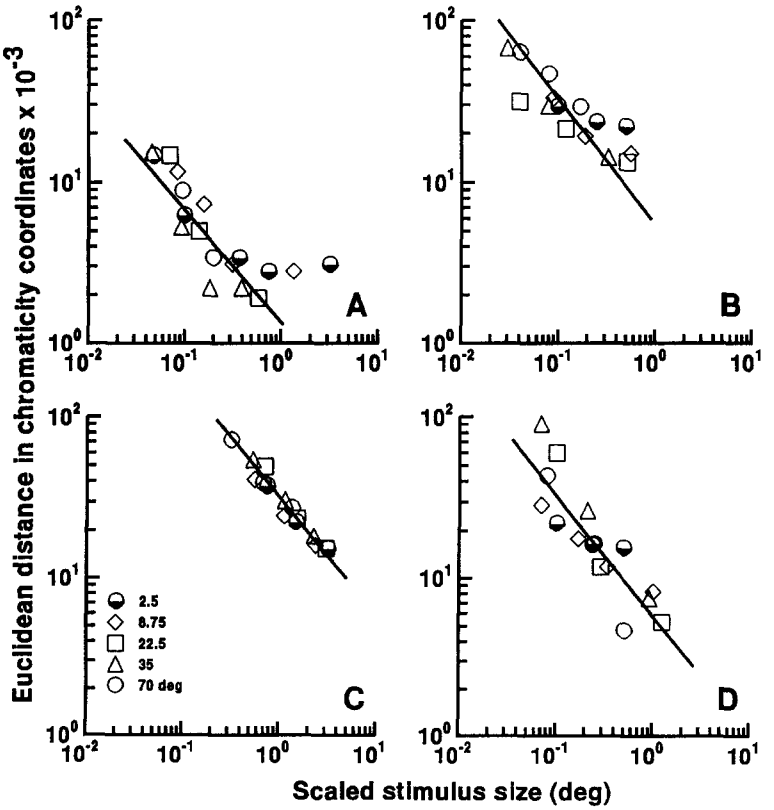

FIGURE 7. The data concerning the perception of blue tint in green from Fig. 2 replotted as a function of scaled stimulus size. Other details as in Fig. 6.

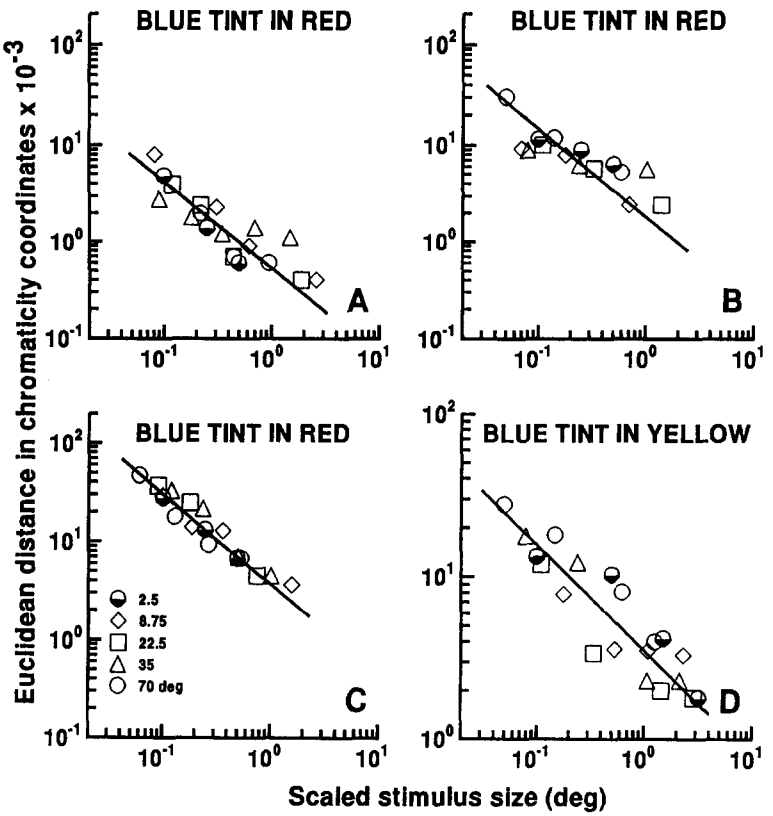

FIGURE 8. The data concerning the perception of blue tint in red and yellow from Figs 3(A–C) and 4(B) replotted as a function of scaled stimulus size. Other details as in Fig. 6.

36, 26, 8.5, and 36 deg for the perception of blue tint in white and 2.0, 1.2, 16 and 10 deg for the perception of blue tint in green for subjects AI, AA, AR, and ML, respectively. For the perception of blue tint in red E_2 value was found to be 26, 13, and 3.8 deg for subjects AI, AA, and AR, respectively. For the perception of blue tint in yellow, the E_2 value was found to be 14 deg for subject AA. The different E_2 values mean that in order to maintain the performance found at the eccentricity of 2.5 deg for the perception of blue tint in white, red, green, or yellow the stimulus size has to be magnified at each eccentricity by different amounts for each adaptation colour and subject.

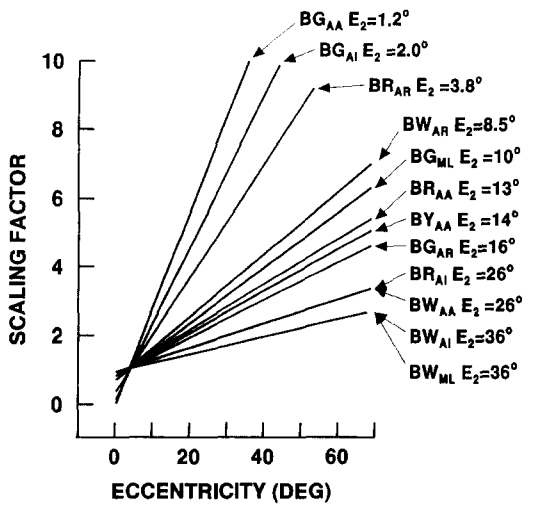

FIGURE 9. Lines of least squares fitted to the scaling factors of Fig. 5 have been replotted together as a function of eccentricity. The corresponding E_2 values are as indicated. BR refers to blue tint in red, BG to blue tint in green, BW to blue tint in white, and BY to blue tint in yellow. Subscripts AI, AA, AR, and ML refer to the subjects.

In addition, our experiments showed that thresholds for perceiving blue tint in yellow (three subjects) and blue tint in red (one subject) varied non-monotonically with increasing stimulus size and eccentricity. Therefore, for these conditions and subjects it was impossible to find a horizontal shift that would superimpose the threshold vs size functions measured at different eccentricities.

The result that size scaling can make the threshold for the perception of blue tint independent of eccentricity does not mean that all perceptual qualities of colour vision can be made independent of eccentricity by size scaling. Abramov *et al.* (1991, 1992), for example, found that although the stimulus size is enlarged, colours cannot be made fully saturated at 40 deg of eccentricity.

The thresholds as a function of stimulus size were higher at fovea than at 2.5 deg eccentricity, except for perceiving blue tint in green for subject AR and blue tint in white for subject ML. Higher foveal thresholds could be explained partly by the absence of blue cones in the centre of the fovea (Williams, MacLeod & Hayhoe, 1981).

Higher absorbance of blue light by macular pigment (Stabell & Stabell, 1980) may also effect our results at 0–2.5 deg of eccentricity. The macular pigment absorbs wavelengths longer than 500 nm only neglibly (Stabell & Stabell, 1980) and thus does not change the adaptative

power of the green, red and yellow adaptation fields as a function of eccentricity. Thus, macular pigment produces an increase in threshold for detecting blue in red, green and yellow. However, the macular pigment reduces the adaptative power of white at short wavelengths, thus tending to make the near foveal region more sensitive to blue. Therefore, the net effect of macular pigmentation on the detection of blue in white is difficult to estimate. Individual differences in the density of macular pigment cannot explain the inter-individual differences found for the perception of blue tint because in order to maintain the performance found at 2.5 deg of eccentricity the stimulus size had to be increased more with increasing eccentricity for the perception of blue tint in green than red for subjects AI and AA, while the reverse was true for subject AR.

The result that the perception of blue at the fovea was possible even with the smallest stimulus size (0.1 deg dia) could be explained by intraocular stray light (Charman, 1983). It is also possible that the perception of blue at fovea is mediated by middle- or long-wavelength sensitive cones (Valberg & Seim, 1991; Drum, 1989).

In our earlier studies we showed that threshold for perceiving blue tint in white (Rovamo & Iivanainen, 1991) or green (Iivanainen, Raninen & Rovamo, 1992) can be made independent of eccentricity by M-scaling the stimulus size. M-scaling in the temporal visual field is nominally equivalent to spatial scaling with an E_2 value of 3.4 deg. For the perception of blue tint in green E_2 value was 2.0 and 1.2 deg for subjects AI and AA, respectively. They are not very far from the E_2 value of M-scaling. However, the E_2 values of 10 and 16 deg for the perception of blue tint in green for subjects ML and AR, respectively, and 8.5–36 deg for the perception of blue tint in white for our four subjects, mean that M-scaling magnifies the stimuli in the peripheral vision more than necessary. However, this over-scaling was not found to result in a significant reduction in the threshold with increasing eccentricity because the stimuli used were so large (Rovamo & Iivanainen, 1991; Iivanainen *et al.*, 1992). Also our previous way of plotting the results along the linear threshold axis effectively hides even large relative changes at the vicinity of zero.

Rod intrusion cannot explain the differences in E_2 values for the perception of blue. Firstly, except for the red adaptation field, the scotopic retinal illuminances produced by our stimuli should saturate rods (Aguilar & Stiles, 1954). The room was also illuminated during the inter-trial periods. Secondly, the readings recorded during an experimental trial and used for calculating the threshold did not tend to increase or decrease indicating that the adaptational state remained constant. Because each experiment was started by adaptation to a moderate daylight, one would expect for readings to change during a trial if rods could contribute to the thresholds. Thirdly, our control experiment showed that the peripheral scaling factor for the perception of blue tint in white did not change significantly, although we enhanced the possibility of rod contribution by reducing the scotopic retinal illuminance by a factor of 6.

The E_2 value for parvocellular cells, which are responsible for colour vision processing in the retina, is 1.2 deg (Drasdo, 1991). The E_2 values for the perception of blue ranged from 1.2 to 36 deg and thus necessarily cannot correlate with any single anatomical estimate. It may be possible however, that E_2 values for the density distributions of ganglion cell subpopulations within the parvocellular system could be similar to those found in the current experiments.

One way to explain the different E_2 values found for the blue perception after white, green, red or yellow adaptation is to assume that there are several chromatic mechanisms (Abramow *et al.*, 1991, 1992; Mullen & Kulikowski, 1990; Valberg & Seim, 1991; Krauskopf, Williams, Mandler & Brown, 1986) responsible for the perception of blue. The different E_2 values for each mechanism could result from the different density distributions of sampling units and/or differently growing receptive field sizes as a function of eccentricity. Improvement in performance with increasing stimulus size could result from filling in the receptive fields and/or increase in the number of sampling units activated. The most sensitive chromatic mechanism detecting blue would vary depending on the adaptation colour. The inter-individual differences in blue detection could be explained by assuming that for each adaptation colour the sampling density and/or receptive-field size distributions of the most sensitive chromatic mechanism varies from one individual to another. Also, receptoral and/or prereceptoral interindividual differences can modify the effect of adapting colour on opponent cells.

Two simultaneously active sets of mechanisms, having different size scales and/or sensitivities as a function of eccentricity, could explain the horizontal and vertical shifts combined with the changes in the shape of the threshold vs size functions with increasing eccentricity in the perception of blue after red or yellow adaptation. The threshold vs size functions are in general U-shaped suggesting that these mechanisms have an inhibitory effect on each other at larger stimulus sizes resulting in an increase in threshold.

Another way to explain our E_2 values could be chromatic adaptation, which could influence E_2 value at least in two ways: firstly, if the effect of chromatic adaptation is on the whole threshold vs size curve different at different eccentricities, e.g. because the relative proportions of different classes of opponent cells vary with eccentricity (De Monasterio & Gouras, 1975a, b; Zrenner, 1983), E_2 values are necessarily affected. Secondly, chromatic adaptation changes the spectral location of the neutral point of a colour-opponent cell (Zrenner, 1983; De Monasterio, Gouras & Tolhurst, 1975) and therefore, a colour-opponent cell can react with excitation or inhibition to the same chromatic stimulus under different states of chromatic adaptation. Because the neutral points of red–green colour-opponent ganglion cells are spread across the spectrum (Zrenner, 1983; De Monasterio & Gouras, 1975a, b) the population of ganglion cells responsible for a certain hue perception varies with chromatic

adaptation. So does also the E_2 value, because the relative proportions of different classes of cells vary with eccentricity (De Monasterio & Gouras, 1975a, b; Zrenner, 1983). The above can also apply to blue perception, although the neutral points of blue–yellow colour-opponent ganglion cells are not spread across the spectrum (Zrenner, 1983; De Monasterio *et al.*, 1975) because there are studies that suggest the middle- and long-wavelength sensitive cones may also mediate the perception of blue (Drum, 1989; Valberg & Seim, 1991). Also, interaction between different opponent cell classes is needed in the construction of a neural circuit that corresponds to blue perception (Gouras, 1990). Therefore, chromatic adaptation could explain the widely varying E_2 value of blue perception.

Colour perception for small stimuli deteriorates with increasing eccentricity (e.g. Hedin, 1979; Boynton, Schaffer & Neun, 1964; Moreland & Cruz, 1958). Therefore, colour perimetry, usually performed with relatively small, constant size stimuli, is restricted to eccentricities smaller than 30 deg. However, our results showed that the increase of stimulus size enhanced colour perception in the peripheral visual field, in agreement with Gordon and Abramov (1977), Kuyk (1982), and Krüger (1977). This suggests that enlarging the stimulus size with increasing eccentricity could extend colour perimetry to all eccentricities, thus making it more sensitive for detecting visual pathologies.

Colour perimetry with blue test light may be more sensitive in detecting preglaucomatous changes than luminance perimetry (Friedmann, 1980; Heron, Adams & Husted, 1988; De John, Snepvangers, van den Berg & Langerhorst, 1990; Hart, Silverman, Trick, Nedher & Gordon, 1990; Hugkulstone & Vernon, 1991). Yellow adaptation is often used in blue-colour perimetry to isolate the short-wavelength-cone system. However, our study with different states of chromatic adaptation revealed several chromatic mechanisms with different spatial requirements that are responsible for the detection of blue. They may be differently damaged by a disease process. Therefore, in a colour perimetry using the detection of blue tint, chromatic preadaptation to a colour could prove to be more sensitive in detecting a specific disease than preadaptation to another colour.

On the basis of this study the spatial scale for the detection of blue across the visual field varies widely depending on the adaptation colour and subject. There seems to be no systematic relationship between scaling factor and adaptation colour in all subjects. In addition, only for one subject out of four a scaling factor was found for the perception of blue under all chromatic adaptation conditions studied. Thus, our experiments suggest that understanding the ability of a subject to detect blue tint across the visual field needs testing at least under four adaptation colours (white, green, red, and yellow).

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