



Variation of chromatic sensitivity across the life span

Kenneth Knoblauch^{a,b,*}, François Vital-Durand^a, John L. Barbur^c

^a INSERM Unité 371, Cerveau et Vision, 18 avenue du Doyen Lépine, 69675 Bron cedex, France

^b Institut de l'Ingénierie de la Vision, Université Jean Monnet, Saint-Étienne, France

^c Applied Vision Research Centre, City University, London, UK

Received 1 March 1999; received in revised form 9 March 2000

Abstract

Thresholds were measured along three directions in color space for detecting an equiluminant color change of a set of bars embedded in a larger field of spatio-temporal achromatic noise for observers ranging in age from 3 months to 86 years. Pre-verbal observers were assessed with a forced-choice preferential-looking technique while older observers responded orally or manually. Over the life span, thresholds could be described along each color axis tested by a curve with two trends. Thresholds decreased with each doubling of age by nearly a factor of two until adolescence. Thereafter, thresholds increased by a factor of 1.4–2 with each doubling of age. Sensitivity to chromatic differences varied similarly along all three axes tested, suggesting uniformity in the sensitivity of chromatic mechanisms across the life span. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Chromatic sensitivity; Development; Aging

1. Introduction

The immaturity of the newborn human retina (Abramov et al., 1982) and the slow maturation of its anatomical structures (Yuodelis & Hendrickson, 1986; Hendrickson, 1994) have been shown to be important determinants of visual sensitivity (Banks & Bennett, 1988; Brown, 1990, 1993; Banks & Crowell, 1993). It is therefore of interest to ask at what age does human sensitivity to chromatic differences attain its highest value.

Evidence from standard color vision tests on the development of chromatic sensitivity is difficult to interpret for several reasons. First, most tests of color vision are designed primarily to detect or to screen for color defective individuals and do not necessarily give precise indices of chromatic sensitivity. For example, normative data from the Farnsworth-Munsell 100-hue test show decreasing errors with age until between 20 and 30 years of age (Verriest, 1963; Verriest, Laethem, & Uvijls, 1982) and thereafter error scores increase sys-

tematically due to aging rather than developmental factors (Verriest, 1963; Knoblauch et al., 1987). Results from this test, however, pose certain difficulties in interpretation. The test requires the observer perform a large number of very fine chromatic discriminations, rendering its outcome dependent on motivational, attentional and learning factors. An additional observation is that the false positive rate declines with age on many standard color vision tests in a fashion that mimics increases in sensitivity (Hill, Heron, Lloyd & Lowther, 1982). Children do accept normal Rayleigh matches as early as four years (Hill et al., 1982). The relevant parameter, however, is the range of values they accept, and this measure is not available.

It is pertinent to consider the evidence on the development of contrast sensitivity, since many of the same factors that constrain luminance contrast sensitivity also limit chromatic sensitivity (Geisler, 1989; Weale, 1992). Beazley, Illingworth, Jahn, and Greer (1980) reported that luminance contrast sensitivity continues to increase into late adolescence. Bradley and Freeman (1982), on the other hand, found that contrast sensitivity reached adult levels by 8 years of age. They grouped all observers 16 years or older in a single category, however, and did not take into account changes in

* Corresponding author. Tel.: +33-4-72913477; fax: +33-4-72913461.

E-mail address: knoblauch@vision.univ-st-etienne.fr (K. Knoblauch).

contrast sensitivity that might occur during adulthood. They argued, in addition, that younger children's lower contrast sensitivity could be due to attentional factors. In contrast, Abramov et al. (1984) found a sample of normal 6-years-old to be systematically less sensitive to chromatic and luminance differences than adults. They organized the psychophysical tasks so that they were video games. In this way, they were able to guarantee a high level of attention throughout this and a series of other psychophysical tasks.

We have evaluated chromatic sensitivity, using preferential looking in infants ranging in age from 6 to 18 months, by adapting a stimulus developed by Barbur, Birch, and Harlow (1993). Like some classic as well as newer tests (Pokorny, Smith, Verriest, & Pinckers, 1979; Regan, Reffin, & Mollon, 1994), the technique uses random luminance noise to mask possible artefactual luminance signals that could arise from individual differences and/or the small but systematic variations in luminosity with age (Dobson, 1976; Moscowitz-Cook, 1979; Kraft & Werner, 1994; Bieber, Volbrecht, & Werner, 1995). What is unique to Barbur et al.'s approach is that the noise used is modulated temporally as well as spatially. This approach generates more effective masking of luminance contrast signals. Results obtained in normal trichromats show that the presence of dynamic luminance contrast noise does not affect thresholds for detection of chromatic signals (Barbur, Harlow, & Plant, 1994). In the course of our studies, we extended the sample to younger infants and observers older than three years. Older observers responded verbally, however. In this way, we have been able to evaluate sensitivity trends over most of the life span. The data indicate that the development of sensitivity continues into adolescence after which a modest aging trend begins. Throughout the life span, sensitivity in different color directions changes so as to stay in a nearly constant proportion.

2. Methods

2.1. Stimuli

All stimuli were generated by a TIGA graphics card running in a PC with an 80486 CPU. The stimuli were displayed on a 17 in., Eizo RGB monitor and were viewed from a distance of 57 cm. The background luminance was 34 cd m^{-2} and its CIE (x, y)-chromaticity was chosen to correspond to the 'white' reference used by MacAdam (1942), i.e., (0.305, 0.323). The spectral radiance output of each phosphor was measured with a Gamma Scientific Model DR2 telespectroradiometer. The luminance calibration of each monitor gun was carried out automatically and then updated regularly under computer control using a luminance meter (LMT, Model 1003).

The technique we used, involving the presentation of test stimuli on a background of random luminance modulation, was modified from Barbur et al. (1993, 1994) to facilitate the testing of infants. In particular, their four-alternative forced-choice paradigm was reduced to two, the stimuli were made larger, the duration of a trial was lengthened and the number of color directions tested was reduced to three.

On each trial, two fields of spatio-temporal noise of mean luminance equal to that of the uniform background were presented, separated by 7° , edge to edge. The noise stimuli were defined by 7° squares, each composed of small checks of 12 by 24 min angular subtense. The luminance of each check changed randomly every 0.1 s and could take values within a specified range, equally distributed both above and below the luminance of the background value. The random luminance contrast (LC) parameter determined the range of maximum and minimum luminance values possible for each check and was expressed as a percentage of the background field luminance.

A test stimulus was defined on one of the noise fields as a set of three bars subtending a spatial frequency of 0.43 c deg^{-1} which alternated in square wave fashion between vertical and horizontal orientations at a rate of 1 Hz. The test and LC noise patterns were presented for a duration of 5 s in order to allow sufficient time for the youngest infants that took part in the study to be attracted by the display.

In the main experiments, the color of the bars was defined to be a displacement from the background chromaticity at adult equiluminance. Three directions were chosen corresponding to the directions in the 1931 CIE diagram of the protan, deutan and tritan copunctal points (Wyszecki & Stiles, 1982). From the reference color, two directions of modulation are possible along each of these axes. Because of the limited time available to test infants and maintain their attention, we chose arbitrarily the direction toward the line of purples for each axis. Stimulus strength was specified as distance in the xy chromaticity diagram from the background chromaticity along the line between the copunctal point and the background chromaticity. Such a measure should be related to chromatic contrast and colorimetric purity. Two examples of a frame from the presentation of a stimulus pair used in this study are shown in Fig. 1.

In theory, stimuli along the tritan direction modulate the short-wavelength sensitive (S) cones in isolation. For the other two directions, no cone class is modulated in isolation at equiluminance. We will continue to refer to these as protan and deutan axes, however, for the following reason. If an observer is lacking either the middle (M) or long (L) wavelength sensitive cones, then modulation along these 'deutan' or 'protan' axes,

respectively, will appear to be the same color as the background (nominally achromatic). In this case, random luminance noise of sufficient contrast will elevate threshold maximally along this axis relative to other axes.

We chose a LC value of 16% because in pilot studies this value was effective in elevating selectively the thresholds of adult dichromats along the appropriate directions. A lesser effect might be expected for those anomalous trichromatic observers who have poorer discrimination than normal trichromats (Hurvich, 1972; Regan et al., 1994). In an initial set of experiments, the test bars were also modulated only in luminance to produce either a positive or negative decrement. These will be described in more detail below.

2.2. Procedures

Infants were tested using a forced-choice preferential looking procedure (Teller, 1979) after their acuity had been evaluated as described below but before an orthoptic examination. An infant was placed on the lap of one of its parents at a distance of 57 cm from the screen in an otherwise dark room. The experimenter viewed the infant's eyes from behind the display so that the display was not visible to him. When the infant and parent were comfortable, stimulus presentation was initiated by one of the experimenters via a button box.

The presentation of the stimulus was preceded by a short beep. The side of the screen on which the test stimulus was presented was varied randomly across



Fig. 1. Two examples of a frame from a stimulus condition in which the chromaticity difference between the checks that make up the bars and those that make up the background falls along a deutan axis in the xy chromaticity diagram. The image on the top corresponds to a greater chromatic difference (and, thus, a higher chromatic contrast) between the bars and the background than the bottom image.

presentations by the computer with the programmed constraint that the test stimulus could not appear more than three times in a row on the same side. The experimenter judged the location of the test stimulus (left or right side of screen) based on the infant's eye movements. As soon as the experimenter had made a judgment, the response was entered via the button box. If the experimenter's judgment was correct, one of several short melodies randomly chosen was generated by the computer as feedback for the experimenter and as a reinforcement for the infant. If the choice was incorrect, a pair of short dissonant tones was generated. If the infant did not respond or was looking elsewhere during the trial, the trial could be reinitiated without recording a response.

The three color directions were tested either in the order protan, deutan, tritan or the reverse. The initial offset in the chromaticity diagram was set at a distance of 0.09 units away from the background chromaticity along each of the three color axes tested. Starting chromaticity coordinates for Protan, Deutan and Tritan directions, respectively, were (0.394, 0.309), (0.380, 0.273) and (0.271, 0.240). For each color direction, this value produced a stimulus clearly detected by an adult observer and generated an easily detectable looking response in most infants. After each correct response, the chromatic displacement of the stimulus from the background chromaticity was decreased by half until the first error. At the first error, the chromatic displacement was increased by the last stepsize used. The infant was then judged at this displacement on three additional successive trials. If at least two of the three judgments were correct, then this value was averaged with the previous one at which the infant was judged erroneously to define the threshold. If less than two of these presentations were judged correct, then the chromatic displacement was increased and the procedure repeated. After the threshold criterion was satisfied, the next axis was tested. The total time required to testing the three axes varied between 10 and 20 min.

In a preliminary set of experiments, the selective effect of the noise on the infants' chromatic thresholds was examined. In these experiments, four conditions were tested. First, in the presence of 16% LC noise contrast, the threshold was estimated along one chromatic direction (either protan or deutan) and along one achromatic direction (either negative or positive contrast). Then the noise contrast was set to zero, and the chromatic and achromatic thresholds were remeasured.

Observers older than 3 years of age were tested with the same apparatus and stimulus configuration. In this case, they were seated in front of the display at the same distance of 57 cm. These observers responded verbally or, what was often more reliable, by pointing to the side on which they detected the test stimulus. Fixation was uncontrolled and testing was binocular so

as to be consistent with the fashion in which the infants were tested.

Children were instructed that the test was a video game, the goal of which was to win presentation of the melodies by finding the test stimulus. They were told that each time they succeeded they would move on to a more advanced level of the game for which the test was harder to find. In addition, the children were congratulated verbally each time they correctly detected the test stimulus.

2.3. Subjects

Infant subjects were recruited from parents who had brought them for a routine examination to the Bébé Vision unit at Jules Courmont Hospital of Lyon. The parents were informed that the procedure was experimental and of the risks (none) involved. All infants underwent a series of standard tests that included estimating their grating resolution with preferential looking using either the Teller (1985a) or Bébé Vision Tropicque (Vital-Durand, 1996) acuity cards, evaluation of monocular optokinetic nystagmus, objective refraction and examination by a trained orthoptist. A fundus examination was always performed after the color vision testing. On completion of the color vision testing, each parent was asked whether they were aware of individuals in their families who were color defective and if so, which members.

The infants were primarily between 6 and 12 months of age, as this is the age at which the Bébé Vision unit recommends a first examination. Younger and older infants were recruited from the occasional ones brought into the unit for examination or from the families of friends. Older children and adults were also recruited from the walk-ins to the unit as well, in the case of adults, from the staff of the hospital. The ocular status of all subjects was evaluated ophthalmologically and basic visual functions tested to exclude individuals with abnormal eye conditions from the sample. Fig. 2 shows a histogram of the age distribution of the 172 normal individuals who participated in the main part of the study. Eight infants did not complete testing in all three color directions because they became uncooperative only after having completed two of the three conditions. Their data were included in the initial analyses. An additional 80 infants were tested, but their data were excluded from analysis because they were judged unreliable at the time of measurement due to uncooperativeness or because the infants were diagnosed with an ocular pathology. In addition, those subjects for whom a color deficiency was suspected, were analyzed separately. Note that age is scaled logarithmically on the axis of abscissae, allowing better resolution of the younger than older years. An additional 24 infants participated in an initial study to evaluate the influence

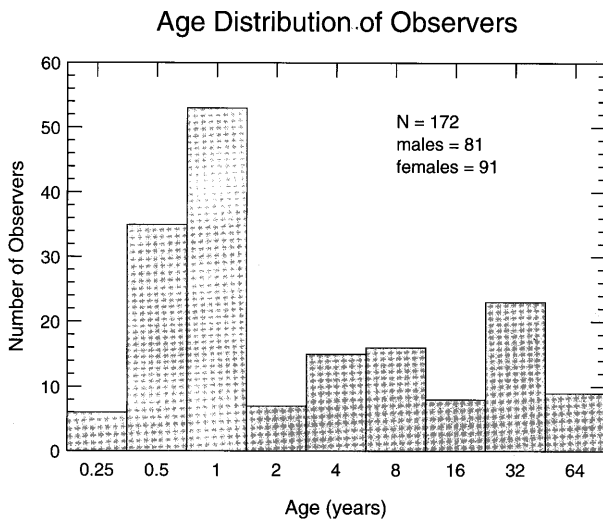


Fig. 2. Histogram of the distribution of subjects by $\log_2(\text{age})$ used in the principal experiment of this study.

of the presence of random luminance noise on their chromatic and achromatic thresholds.

2.4. Statistical analyses

The chromatic thresholds as a function of age were fit with several equations as described in more detail in the results. All of these fits were obtained using the Nelder-Mead Simplex algorithm (Press, Flannery, Teukolsky, & Vetterling, 1988) as implemented in the program MATLAB on a PC computer. In order to obtain confidence limits for the parameters from the fits and to compare them statistically, resampling techniques were employed (Efron & Tibshirani, 1993).

We generated new samples, called bootstrap samples, each one of the same size as the original data set, by sampling from the original data set with replacement. For each of these bootstrap samples, we refit each equation of interest, thus, generating new parameter estimates. As the number of bootstrap samples increases, the standard deviation of the distribution of each parameter estimate approaches that of the standard error of the parameter estimated from the original data set (Efron, 1982).

For our data, we generated 2000 bootstrap samples for the chromatic thresholds from each color direction independently. Each bootstrap sample was fit with the functions described below, and histograms were constructed of the parameters estimated from the fits. Confidence intervals were calculated for each parameter from the histograms, using the BCA technique (Efron & Tibshirani, 1993). To generate confidence intervals around each function, we computed distributions for a set of 90 points at ages equally spaced on either a linear or a $\log_2(\text{Age})$ axis, depending on the function, and interpolated between the estimated errors with a spline

curve. To obtain the estimates for an individual observer, we needed also to add to the bootstrap estimates of variance at each of these 90 points a constant that corresponded to the variance of the data about the function fit to them (Hays, 1973).

To compare statistics of the fits across color directions, an additional 2000 bootstrap samples were generated using only the 164 observers who completed testing along all three color directions. In this case, an individual sample consisted of the triple of thresholds for an observer. A bootstrap sample consisted of a set of 164 such triples sampled with replacement from the original data. The exclusion of these eight individuals produced an insignificant effect on the parameter estimates of each curve, indicating that these data did not constitute an influential set of points. In comparing parameters between curves, the samples for the three color directions should covary with the observers chosen. This covariation induces a correlation in the variances between color directions akin to a within subject analysis rather than one in which the thresholds and the fits are treated as independent across color directions and should in theory yield more sensitive statistical comparisons.

3. Results

The validity of the measures of chromatic sensitivity using the technique that we have described depends critically on the spatio-temporal luminance noise raising the threshold for the detection of luminance contrast selectively and leaving the chromatic sensitivities intact. Barbur et al. (1993) have already demonstrated such an independence in adult observers using a stimulus similar to ours and numerous other investigators have demonstrated selective effects of luminance masking with respect to luminance and chromatic thresholds (e.g. Gegenfurtner & Kiper, 1993; Mullen & Losada, 1994). It has been proposed, however, that intrinsic noise in the newborn's visual system is higher than in adults (Brown, 1993; Skoczenski & Norcia, 1998). In keeping with this hypothesis, Skoczenski, Banks, and Candy (1993) reported that spatio-temporal luminance noise that raised adult thresholds by a factor of two did not raise thresholds of 12-week-old infants.

Fig. 3 shows the threshold elevation produced by luminance noise for luminance (white bars) and chromatic (black bars) patterns for 24 infants ranging in age from 6 to 14 months. The age of each infant is indicated under each pair of bars and the difference of the log threshold between LC noise backgrounds of 16 and 0% LC is indicated on the ordinate. Each infant was tested on either the protan or deutan axis and either with a negative or positive luminance contrast. The luminance noise produced no systematic elevation of

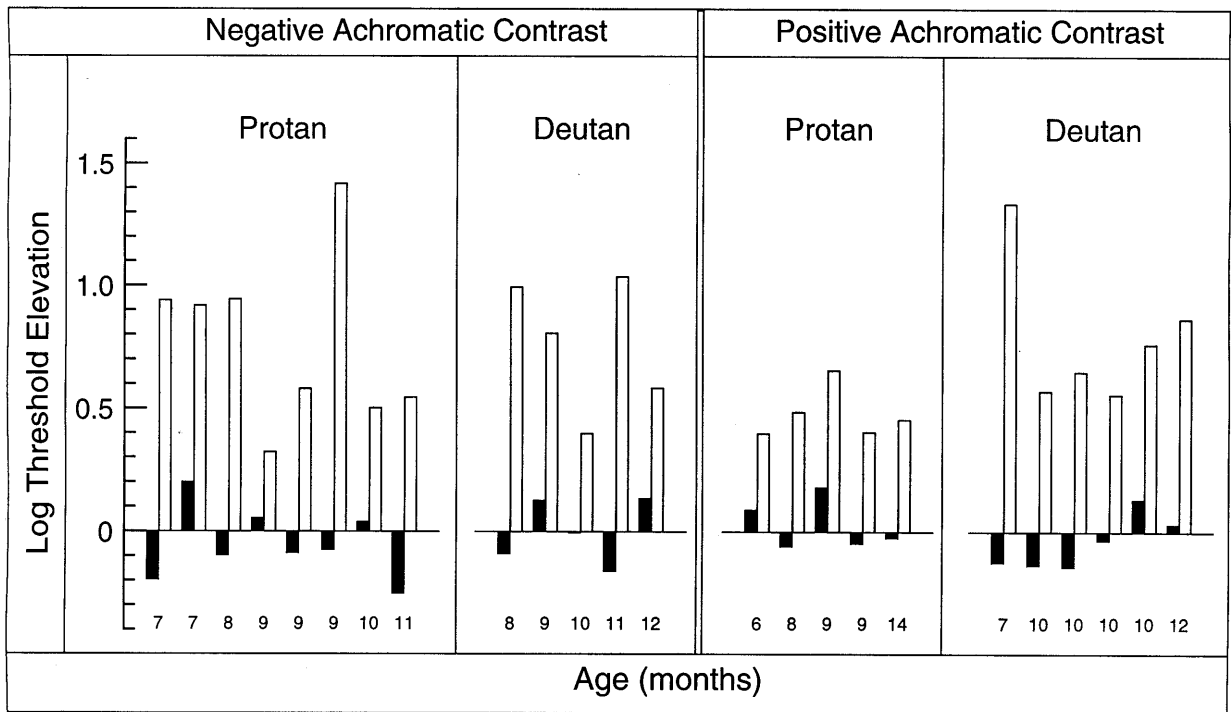


Fig. 3. The log of the ratio of thresholds for detecting the test bars on a background of 16% LC to that of 0% LC contrast. The white bars indicate the threshold elevations for detecting achromatic stimuli. Observers tested with decremental contrasts are indicated on the left and incremental contrasts on the right side of the figure. The dark bars indicate the threshold elevations for detecting chromatic stimuli. The groups are divided according to whether they were presented with a chromatic stimulus that corresponded to a difference along the protan or deutan axes. Age in months of each observer is indicated on the axis of abscissae.

the chromatic thresholds ($t_{23} = 0.91$, $P > 0.05$) but raised the luminance thresholds in every instance ($t_{23} = 11.95$, $P < 0.001$). The effect of luminance noise on test pattern threshold was evaluated with a repeated measure analysis of variance. The only significant effect resulted from whether or not the test pattern was achromatic or not ($F_{1,20} = 112.1$, $P < 0.001$). Neither systematic effect of age is apparent in these data nor significant variation of contrast thresholds between contrast polarities or color directions.

We did attempt to evaluate younger infants in this experiment, but with little success. For example, a 2-month old had similar thresholds for luminance bars with and without the noise, but could not be induced to look selectively at the chromatic stimuli. The failure of the achromatic luminance noise to raise achromatic thresholds may be due to the fact that the check size was below the resolution or the contrast was below the contrast sensitivity for these younger infants. The failure of infants to be attracted differentially to the chromatic stimuli is likely in part due to the limited gamut of contrasts that could be produced at equiluminance on our apparatus.

Figs. 4 and 5 show the logarithm of the chromatic thresholds measured along the protan axis as a function of Age and $\log_2(\text{Age})$, respectively. The two graphs illustrate the same data. The linear abscissa emphasizes

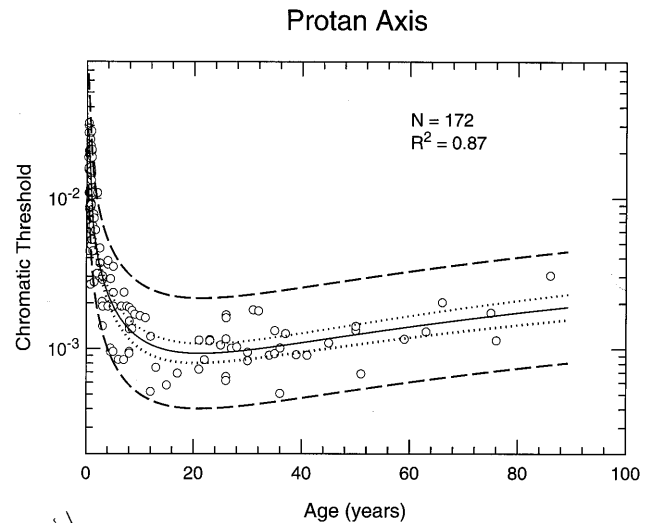


Fig. 4. Log of the chromatic thresholds along the protan axis are plotted as a function of age. The ordinate in this and the succeeding three figures is the logarithm of the distance in the CIE xy diagram between the chromaticities at threshold and the background along the particular axis measured. Each point represents the data from a single observer. The solid curve is the best fit of Eq. (3) to the data. The dotted curve indicates the 95% confidence intervals for the fitted curve. The dashed curve indicates the 95% confidence interval for an individual point.

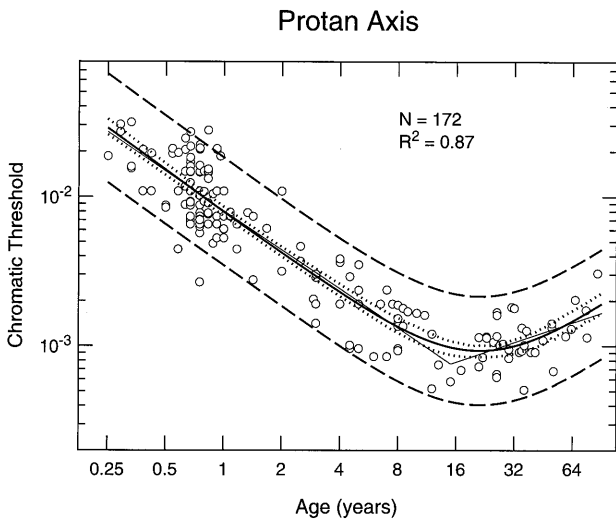


Fig. 5. Log of the chromatic thresholds along the protan axis is plotted as a function of $\log_2(\text{age})$. The data are the same as those from Fig. 4. The thin solid line is the best fit of Eq. (1) to the data. The thin solid curve is the best fit of Eq. (3) to the data. The dotted and dashed curves have the same significance as those from Fig. 4.

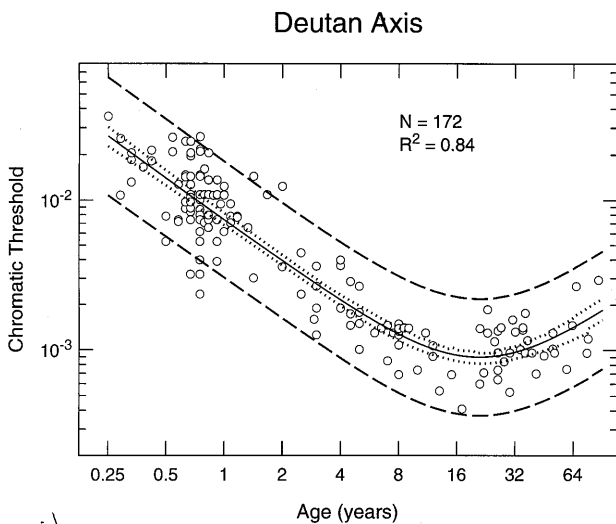


Fig. 6. Log of the chromatic thresholds along the deutan axis are plotted as a function of $\log_2(\text{age})$. The solid curve is the best fit of Eq. (3) to the data. The dotted and dashed curves have the same significance as those from Fig. 4.

the variation in sensitivity later in life; the logarithmic scale allows one to see the variation at the youngest ages in greater detail. At a given age, thresholds vary by about a factor of ten. This variation can be attributed in part to the small number of trials used in estimating each threshold. Theoretically, staircases with small numbers of trials result in threshold estimates with greater variability (McKee, Klein, & Teller, 1985; Teller, 1985b). Nevertheless, the means of these thresholds will be more accurate than any individual threshold and allow us to discern how sensitivity varies with age. Two trends describe the data. Between 3

months and adolescence, thresholds decrease by about a factor of 30. At older ages, thresholds increase at a more modest rate. The trends were similar in the other two color directions (see below Figs. 6 and 7) except that thresholds in the tritan direction were uniformly higher, as is typically found within this color space representation (e.g. MacAdam, 1942).

For descriptive purposes, we found that two different functions fit the data about equally well. In the first instance, a bilinear function in log–log coordinates is shown as the pair of thin solid lines in Fig. 5. This function is described by the equation:

$$\log_{10}(T) = a|\log_2(A) - \log_2(A_x)| + b\log_2(A) + c \quad (1)$$

where T is the threshold chromatic displacement, A the age in years and a , b , c and A_x are fitted parameters. Eq. (1) has certain useful features. The age of intersection of the two linear trends is given by the parameter A_x . Also, the slopes of the two linear segments are given by the values $m_1 = (b - a)$ and $m_2 = (b + a)$. Finally, there is only a single non-linear parameter, A_x , which facilitates the fitting procedure numerically.

Eq. (1) has the disadvantage that the sharp transition between developmental and aging trends is unrealistic. In order to address this concern, a second description of the data was attempted with the sum of two power functions:

$$T = aA^\alpha + bA^\beta \quad (2)$$

where T and A are defined as before and a , b , α and β are parameters. Each of the parameters is associated with one limb of the data, giving the limbs' slopes in log–log coordinates, (α, β) , and their intercepts, (a, b) . In practice as with Eq. (1), the logarithms of the

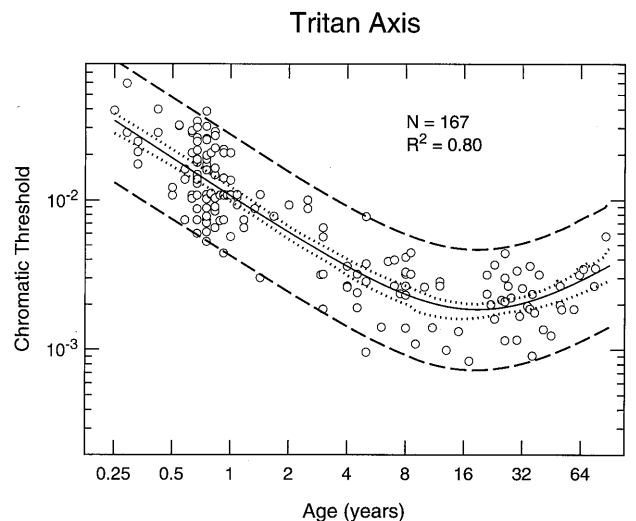


Fig. 7. Log of the chromatic thresholds along the tritan axis are plotted as a function of $\log_2(\text{age})$. The solid curve is the best fit of Eq. (3) to the data. The dotted and dashed curves have the same significance as those from Fig. 4.

Table 1
Summary of parameter fits for Eq. (1)

Axis	m_1	m_2	A_x (years)	R^2
Protan	-0.262 [-0.288, -0.244]	0.131 [0.066, 0.199]	15.0 [13.2, 18.9]	0.86
Deutan	-0.261 [-0.276, -0.246]	0.127 [0.029, 0.225]	14.5 [10.0, 17.0]	0.85
Tritan	-0.231 [-0.258, -0.204]	0.083 [-0.022, 0.179]	11.7 [5.0, 15.7]	0.78

thresholds were fit, a procedure which equalized the variance across ages. Without the log transformation, neither Eq. (1) nor Eq. (2) could be made to fit correctly the data of adult observers, whose linear thresholds in absolute terms are much lower than those of the infants. Preliminary estimates of the parameters of Eq. (2) for the data indicated that to a first approximation $\alpha = -\beta$. With this constraint the equation is rewritten as.

$$T = aA^{-\alpha} + bA^{\alpha} \quad (3)$$

We refit the data with this additional constraint and found that the fits were not significantly worse in that the proportion of variance accounted for changed by less than 1%. So, while Eq. (3) represents a less tractable function analytically than Eq. (1), it allows the data to be described with only three parameters.

The fit using Eq. (3) is shown in Figs. 4 and 5 as the thick solid curve. The dotted curves in these two figures (and other figures depicting fitted curves) indicate the 95% confidence limits calculated for the fit. The dashed curves indicate the 95% confidence limits for an individual observation. To illustrate the similarity of Eqs. (1) and (3), the data and curve fits for Eq. (3) for the other two color directions tested are replotted in double logarithmic coordinates in Figs. 6 and 7.

The values of the slopes and the ages of minimal threshold are given in Tables 1 and 2 for the fits using Eqs. (1) and (3), respectively. Beneath each value, its 95% confidence interval is given in brackets. The values of R^2 indicate the proportion of variance in the data

Table 2
Summary of parameter fits to Eq. (3)

Axis	$a \cdot 10^3$	$b \cdot 10^5$	α	A_{\min} (years)	R^2
Protan	7.902 [7.439, 8.489]	2.740 [2.135, 3.265]	0.928 [0.88, 1.01]	21.2 [18.5, 24.7]	0.87
Deutan	7.372 [6.759, 8.099]	2.749 [2.190, 3.459]	0.920 [0.869, 0.980]	21.1 [18.1, 25.3]	0.84
Tritan	10.592 [9.846, 11.703]	8.089 [6.408, 10.280]	0.831 [0.767, 0.910]	18.8 [15.9, 22.9]	0.78

accounted for by the fitted curves and can be considered as measures of goodness of fit. Note the similarity of these measures for the two equations when fitted to the same data. A linear trend seems to describe adequately the development of chromatic sensitivity. Chromatic thresholds were found to decrease by nearly a factor of two with each doubling of age up to the minimal value of about 20 years. A linear trend of positive slope describes well the thresholds for older observers. The slopes for each limb are similar across each color direction except that thresholds along the tritan axis seem to develop at a slightly slower pace than along the protan/deutan axes and age slightly less rapidly, as well. None of the parameters differed significantly between protan and deutan directions, so in subsequent analyses, protan and deutan values were averaged. For Eq. (1), the differences of the tritan from the mean of protan and deutan slopes were not significant as the 95% confidence intervals for this difference included zero (m_1 , [-0.052, 0.006]; m_2 , [-0.057, 0.192]). Using Eq. (3), however, the confidence interval for the difference of tritan from the mean of protan and deutan slopes did exclude zero, (α , [0.019, 0.156]) indicating significance at $P < 0.05$.

The minimum of Eq. (3) can be estimated by taking its derivative, setting it equal to zero and solving for A_{\min} .

$$A_{\min} = \left(\frac{a}{b}\right)^{1/2\alpha}$$

These values are also given in Table 2. The calculated minima all lie at slightly older ages than for Eq. (1), falling in the range 18–22 rather than 11–16 years. The tritan fit yields a slightly younger age of minimal threshold for both equations tested. These differences are not significant, however, as the 95% confidence intervals for the difference of minimum ages between tritan and mean protan and deutan directions includes zero for both equations (Eq. (1), [-2.25, 9.79]; Eq. (3), [-0.61, 4.96]).

Given that equal slopes in Eq. (3) fit the data well, we reconsidered a three parameter version of Eq. (1) constrained to have equal slopes on both linear segments.

$$\log_{10}(T) = m|\log_2(A) - \log_2(A_x)| + b \quad (4)$$

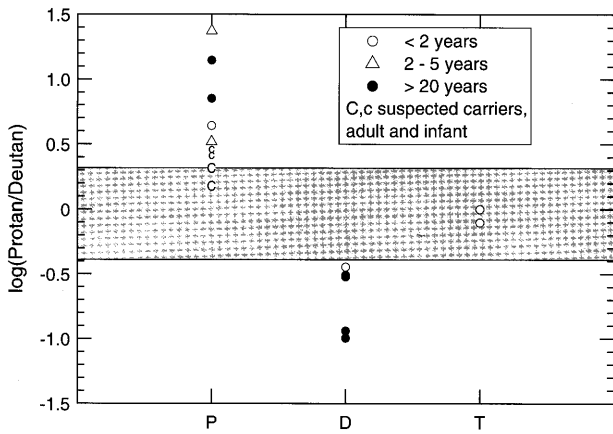


Fig. 8. The ratio of thresholds along the protan to deutan axes are plotted for a selected set of observers known (solid symbols) or candidates (open circles and triangles) to be color defective or carriers of a color defective gene ('C' and 'c' symbols).

Along all directions, the variance accounted for diminished by over 20%, and the minimum age, A_x , increased. The fitted curves tended to be higher than most of the points between 2 and 16 years, indicating that the three-parameter equation deviated systematically from the data and, more generally, did not as accurately characterize them as Eqs. (1) and (3).

Tritan thresholds were on average slightly over one and half times higher than those along protan and deutan directions. Barbur et al. (1993, 1994) previously reported adult chromatic thresholds measured against a background of the same chromaticity that were two and a half times larger on the tritan axis with respect to the protan and deutan axes, in agreement with previous adult discrimination data in this part of color space (MacAdam, 1942). Pilot data that we collected suggest that the somewhat smaller difference observed here is due to both the larger stimulus size and longer duration that we used.

The large variation in threshold with age poses a problem for using a test of chromatic sensitivity to screen for individuals with defective color vision. A high threshold could be due to the age of the observer or a loss of sensitivity selective for that color direction. The similar variation with age along all three axes suggests that the ratio of thresholds across age might be approximately constant as a function of age. Consistent with this hypothesis, the best fit line of the ratio of thresholds along the Protan and Deutan axis as a function of age does not differ significantly from zero (slope = -0.002 , $r^2 = 0.016$, $t_{162} = 1.062$, $P > 0.05$). In contrast, the slope of the ratio of Tritan to mean Protan and Deutan thresholds changes significantly across age (slope = 0.014 , $r^2 = 0.086$, $t_{162} = 3.928$, $P < 0.01$). Nevertheless, this variation is small and constitutes less than a factor of two across the entire life span. Thus, a ratio-of-thresholds rule should permit the

detection of protan and deutan defects independent of age. A ratio rule should permit detection of S-cone related deficits, too, except that the small variation of the ratio as a function of age will have the effect of enforcing a more conservative criterion for being outside the norms, i.e. the variation of the ratio with age will increase the confidence limits about the average age.

Fig. 8 shows the log of the ratio of thresholds along protan and deutan axes. For normal observers, this ratio is usually near 1 (or 0 on a log scale). The gray region indicates plus and minus 1 standard deviation around the normal ratio based on the data in Figs. 5 and 6. Protan observers, plotted at the abscissa value labeled *P*, would be expected to have their thresholds raised along the protan axis relative to those measured along the deutan axis, while deutans, plotted at the value labeled *D*, would be expected to show the reverse. The filled symbols represent adult observers diagnosed as protan or deutan by standard plate or arrangement tests. The unfilled symbols plotted at the *P* and *D* ticks indicate infants ranging in age from 7 to 23 months (unfilled circles) and 2–5 years (unfilled triangles) and whose mothers reported knowledge of an appropriate family member being color defective. These children can be considered to be suspects for color deficiency. The capital *C*'s indicate mothers who are suspected to be carriers (reported color deficient father) and the little *c*'s indicate the daughters of one of these mothers (tested at 9 months and 2 years). The elevated thresholds in three of these four suspected carriers might be a manifestation of Schmidt's sign (Schmidt, 1955), a luminosity loss in the long-wavelength region shown by some protan heterozygotes. While the LC noise patterns were intended to mask small individual differences from the standard luminosity function, the altered luminosity functions of some protan heterozygotes might be sufficiently different from the normal that these observers detect contrasts along the protan axis, equiluminant for a normal observer, by luminance differences, like a protanope. Were this the case, the LC noise would raise thresholds along this axis.

Similarly, by examining the ratio between thresholds along the tritan axis and the average of those along the protan and deutan axes, we should be able to distinguish individuals with sensitivity losses restricted to S cone pathways. The gray region of Fig. 9 indicates plus and minus one standard deviation of this ratio for the normal observers of Figs. 5–7. The ratios of some protan and deutan observers indicated in the figure are significantly lower than those of normal observers, perhaps indicating that they were overly sensitive along the tritan direction or more likely, slightly less sensitive along the deutan and protan directions, respectively. Two infant observers, indicated at *T*, show elevated

threshold ratios. These individuals were a 7- and 16-months-old. The 7-months-old had been hospitalized with retinal hemorrhages. The 16 months old presented an extreme myopia (10 Diopters). He was retested at 23 months with similar results. For both of these observers, the ratio between thresholds along the protan and deutan axes was in the normal range (Fig. 8). For both infants, the individual thresholds were within the normal ranges for their ages, although, the myopic child's thresholds were at the top of the normal range. We suppose that the ocular conditions of these infants may have damaged their S cone systems.

4. Discussion

The results of the first experiment indicate that the achromatic noise masking technique is effective in reducing the salience of achromatic stimuli and leaving the salience of chromatic stimuli unaffected as early as 6 months, supporting the notion that the technique permits the measurement of thresholds associated with chromatic mechanisms at this young age. The masking effects on luminance patterns observed though seemingly large are about 75% of those previously observed in normal adult observers at similar noise contrast values (Barbur, Cole, & Plant, 1997).

Our subsequent results demonstrate two phases of variation of chromatic sensitivity over the life span, one associated with development and the other with aging. Each phase is approximately linear in double log coordinates with the magnitude of the slope slightly less than 1.0. In other words, chromatic sensitivity is nearly linear with the reciprocal of years during development and approximately linear with years during aging. The higher thresholds overall along the tritan axis in this

color space indicate that the slope on a linear scale is greater along this axis, the rate of change faster, than along the other axes, as reported by Hollants-Gilhuijs, Ruijter, and Spekreijse (1998). The similar slopes along the three axes in logarithmic coordinates, however, demonstrate that the sensitivities in the equiluminant plane tend to change proportionately along all directions. Our results are indecisive as to whether the slope along the tritan axis is different or not, although the direction of difference is consistent with those studies that found a slower development along this axis (Teller & Lindsey, 1993). The differences that we found are not large, in any case. Our results, thus, are not inconsistent with the idea of uniform change among color mechanisms across the life span, both in the developmental (Allen, Banks, & Norcia, 1993) and aging phases (Werner & Steele, 1988) and support the hypothesis of Werner (1996), Werner and Steele (1988) that constancy of color appearance over the life span is maintained by such synchronous variation.

We cannot directly address the question of whether there are differences in development between luminance and chromatic sensitive mechanisms (Allen et al., 1993; Morrone, Burr, & Fiorentini, 1993; Kelly, Borchert, & Teller, 1997) since our observations were at equiluminance. However, the literature suggests that whether or not one sees different rates of development may depend on the spatio-temporal parameters of the stimuli (Dobkins, Lia, & Teller, 1997; Kelly et al., 1997). Indeed, Dobkins et al., provide data to suggest that chromatic temporal modulation in infants as young as 3 months is processed through a band-pass channel with the same characteristics as the one that processes luminance temporal modulation. The transformation from band-pass to low-pass chromatic modulation sensitivity with age results in differential change as a function of temporal frequency. One interpretation of their data is that chromatic and luminance modulations are processed by a luminance sensitive channel that passes transients in response to chromatic modulation, as do cells in the M pathway (Lee, Martin, & Valberg, 1988). If chromatic and luminance signals were sharing the same pathway in the infants that we tested, we might have expected to see significant masking of chromatic stimuli by luminance noise in the first experiment, which we did not at ages as young as 6 months. However, since we only tested a single spatio-temporal condition, we cannot exclude that differential change would appear with our technique with a change in stimulus conditions.

We found that the estimate of the age at which thresholds are minimal depends on the function used to describe the data. The four-parameter bilinear equation yielded estimates systematically lower (about 11–16 years) than those from the sum of two powers (18–22 years) equation. The minimum of the latter function is

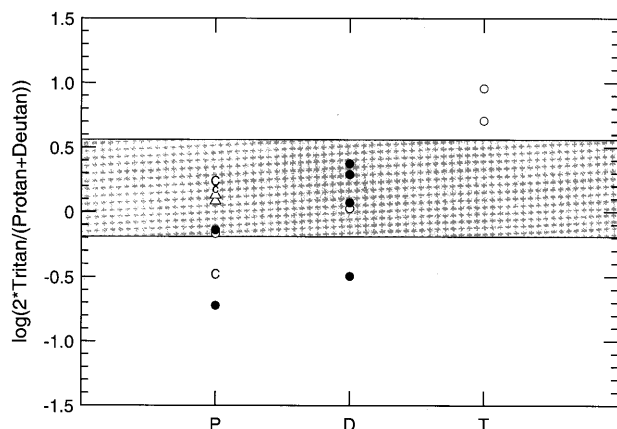


Fig. 9. The ratio of thresholds along the tritan to mean thresholds along protan and deutan axes is plotted for a selected set of observers known (solid symbols) or candidates (open circles and triangles) to be color defective or carriers of a color defective gene ('C' and 'c' symbols).

rather broad, however, and taking that into account, perhaps, the estimates for the duration of the developmental phase are not really all that different. A late age for the attainment of optimal sensitivity is not inconsistent with a number of studies on contrast sensitivity (Beazley et al., 1980) and color vision (Verriest, 1963; Verriest et al., 1982; Knoblauch et al., 1987), as well as a number of electrophysiological observations (Spekreijse, 1978; De Vries-Khoe & Spekreijse, 1982; Crognale, Kelly, Weiss, & Teller, 1998). Bradley and Freeman (1982) reported that optimal contrast sensitivity was attained by 8 years of age, somewhat younger than we find here. Their data may not be inconsistent with ours, however. They grouped all adults together and in their adult sample, contrast sensitivity for the one 16-years-old was the highest observed in the study.

It would be difficult to argue that criterion differences across age are not present in our data. Infants and toddlers were tested with preferential looking; observers who could follow verbal instructions responded directly to the stimuli. Despite these procedural differences, a uniform rate of variation of threshold is observed across all axes tested. Even if there are inherent criterional factors affecting the data, however, the observation that the ratio of thresholds tends to be invariant across the life span signifies that age differences can be factored out by evaluating the ratio of thresholds across color directions (Knoblauch, Vital-Durand, & Barbur, 1997). This finding suggests that such criterional factors, if present, can be considered fixed within an age group. The results from the infants from families with a history of color deficiency would further support this suggestion if we could confirm their diagnoses, independently. These observations are, in any case, consistent with other studies that have demonstrated that color deficiency can be detected well before infants are verbal (Bieber, Knoblauch, & Werner, 1997; Bieber, Werner, Knoblauch, Neitz, & Neitz, 1998).

Based on a model of the optical and sampling properties of the early visual system, Banks and Bennett (1988) calculated that these factors account for a 350-fold difference in quantum catch efficiency between a 5-days-old infant and an adult. If photon noise were the sole determinant of sensitivity, then one would predict proportional losses between luminance and chromatic mechanisms with the loss of sensitivity equal to the square root of the proportional loss of quantum catch or a factor of 18.7. If we assume that the trends observed in our data can be extrapolated back to 5 days, then using the observed parameters of the fitted curves, we can estimate the age at which a threshold decrease of this magnitude would occur. For example, for the bilinear fit, we observe that in the protan direction, the threshold declines by 0.262 on a

log scale with each doubling of age. At this rate, it will take $\log(18.7)/0.262 = 4.9$ doublings for threshold to decrease by 18.7. If the initial age is 5 days, then the expected threshold decline will occur at an age of $2^{4.9} \times 5 = 145$ days. A similar calculation along deutan and tritan directions yields values of 147 and 227 days, respectively.

For the second equation, we suppose that threshold is proportional to age, A , raised to a power, α . Then, the age at which a decrease of threshold by a factor of 18.7 occurs will be given by solving $18.7 = (5/A)^\alpha$ for A or $A = (1/18.7)^{1/\alpha} \times 5$. For the protan direction, $\alpha = -0.928$, $A = 117$ days. A similar calculation along deutan and tritan directions yields values of 121 and 170 days, respectively. The values for both equations fall far short of the minima in our data. Even with the uncertainty in the parameters, it would be impossible to account for the long period of development that we observe were photon noise the sole determinant of sensitivity.

Criterional factors as a result of procedural differences in measuring infant and toddler thresholds would probably have resulted in higher thresholds than by obtaining responses directly from an observer. Supposing that to be the case in our data, the true infant thresholds would be lower, the estimated slopes of the developmental phase would be lower and concomitantly the overall developmental change in sensitivity would be reduced. In order for such an effect to accommodate the quantum efficiency hypothesis, the slopes of the developmental limbs would have to be reduced by about a factor of two.

The aging component is more gradual than the developmental phase, in that a smaller absolute change in sensitivity extends over a considerably longer linear time period. If we consider, however, the natural unit of time a doubling of age, as was convenient for development, then aging extends over less than three such doublings, and the smaller absolute change simply reflects that. The different equations evaluated indicate rather different rates of aging, however, Eq. (1) indicates a loss of nearly the square root of two with each doubling of age. Eq. (3) indicates approximately a doubling of threshold with each doubling of age along all three directions. Thus, our data do not seem to constrain very tightly the rate of aging. We conclude that some care must be exercised in comparing our results with other studies of chromatic sensitivity and aging (Johnson & Marshall, 1995; Werner, Schwarz, & Paulus, 1995) which show similar aging trends but arrive at slightly different interpretations as to the differential rate of aging along different color directions. The interpretation of previous results may have depended on the equation used to describe the data, the scale and the range of ages over which they were fit.

In contrast with our results and those of Hollants-Gilhuijs et al. (1998), Petzold and Sharpe (1998) found no differences in hue discrimination between 4 and 25 years. Their test involved comparisons between saturated stimuli whereas we and Hollants-Gilhuijs et al. required a discrimination of a chromatic from an achromatic stimulus. Aside from methodological differences between these studies, it may be that chromatic detection is subject to different constraints than chromatic discrimination.

The slower rate of increase in chromatic thresholds with age is qualitatively similar to the observed changes in the light scattering characteristics of the eye (Hennelly, Barbur, Edgar, & Woodward, 1998). A detailed analysis of the effects of scattered light on chromatic discrimination thresholds along each color confusion line suggests that normal levels of scattered light in the eye and the typical increase in scatter with age do not affect significantly these thresholds (Barbur, Harlow, & Williams, 1997). Alternatively, the level of intrinsic noise in the visual system might increase as adult's age. Vertical shifts in the increment threshold curves of older adults for detection of chromatic targets are consistent with either such an elevation or a reduction in the ability

of cones to capture quanta (Scheffrin, Werner, Plach, Utlaue, & Switkes, 1992; Scheffrin, Shinomori, & Werner, 1995; Shinomori, Scheffrin, & Werner, 1997).

Such effects are generally less evident if the retinal illuminances are sufficient so that subjects are operating in the Weber region. Based on the tables published by Le Grand (1972) relating luminance and retinal illuminance, we estimate the average retinal luminance of the screen to be about 270 trolands in our experiments, for an average adult observer. For comparison, the average retinal illuminance of a colored chip from the FM 100-hue test under a standard MacBeth Easel Lamp (200 lux) is about half of this value. Knoblauch et al. (1987) found that from 180 to 1800 lux, total error scores and axes of errors did not depend upon age except for observers in the oldest group tested (70–79 years). Working the calculation backwards, our screen level would have been equivalent to a FM 100-hue test under an illuminant of 350 lux, or in other words in the range of values under which adult observers perform nearly optimally.

Acknowledgements

We gratefully acknowledge the critical comments on an earlier version of this article provided by Rita Demanins, John Kelly, Davida Y. Teller and John S. Werner. This research was supported in part by a Fellowship from the Région Rhône-Alpes to K. Knoblauch and a grant from the Neuroscience Programme of the European Science Foundation.

References

- Abramov, I., Gordon, J., Hendrickson, A., Hainline, L., Dobson, V., & LaBossiere, E. (1982). The retina of the newborn human infant. *Science*, *217*, 265–267.
- Abramov, I., Hainline, L., Turkel, J., Lemerise, E., Smith, H., Gordon, J., & Petry, S. (1984). Rocket-ship psychophysics. *Investigative Ophthalmology and Visual Science*, *25*, 1307–1315.
- Allen, D., Banks, M. S., & Norcia, A. M. (1993). Does chromatic sensitivity develop more slowly than luminance sensitivity. *Vision Research*, *33*, 2553–2562.
- Banks, M. S., & Bennett, P. J. (1988). Optical and photoreceptor immaturities limit the spatial and chromatic vision of human neonates. *Journal of the Optical Society of America A.*, *5*, 2059–2079.
- Banks, M. S., & Crowell, J. A. (1993). Front-end limitations to infant spatial vision: examination of two analyses. In K. Simons, *Early visual development normal and abnormal* (pp. 91–116). New York: Oxford University Press.
- Barbur, J. L., Birch, J., & Harlow, A. J. (1993). Colour vision testing using spatiotemporal luminance masking. In B. Drum, *Colour vision deficiencies XI* (pp. 417–426). Dordrecht: Kluwer Academic Publishers.
- Barbur, J. L., Harlow, A. J., & Plant, G. T. (1994). Insights into the different exploits of colour in the visual cortex. *Proceedings of the Royal Society of London B*, *258*, 327–334.
- Barbur, J. L., Harlow, A. J., & Williams, C. (1997). Light scattered in the eye and its effect on the measurement of colour constancy. In C. R. Cavonius, *Colour vision deficiencies XIII* (pp. 439–448). Dordrecht: Kluwer Academic Publishers.
- Barbur, J. L., Cole, V. A., & Plant, G. T. (1997). Chromatic discrimination in subjects with both congenital and acquired colour vision deficiencies. In C. R. Cavonius, *Colour vision deficiencies XIII* (pp. 211–233). Dordrecht: Kluwer Academic Publishers.
- Beazley, L. D., Illingworth, D. J., Jahn, A., & Greer, D. V. (1980). Contrast sensitivity in children and adults. *British Journal of Ophthalmology*, *64*, 863–866.
- Bieber, M. L., Volbrecht, V. J., & Werner, J. S. (1995). Spectral efficiency measured by heterochromatic flicker photometry is similar in human infants and adults. *Vision Research*, *35*, 1385–1392.
- Bieber, M. L., Knoblauch, K., & Werner, J. S. (1997). Detecting color vision deficiency in 4- and 8-week-old human infants. In C. R. Cavonius, *Colour vision deficiencies XIII* (pp. 277–282). Boston: Kluwer Academic Publishers.
- Bieber, M. L., Werner, J. S., Knoblauch, K., Neitz, J., & Neitz, M. (1998). Comparison of genotypic and phenotypic markers of color vision in infants and adults. *Vision Research*, *38*, 3293–3297.
- Bradley, A., & Freeman, R. D. (1982). Contrast sensitivity in children. *Vision Research*, *22*, 953–959.
- Brown, A. M. (1990). Development of visual sensitivity to light and color vision in human infants: a critical review. *Vision Research*, *30*, 1159–1188.
- Brown, A. M. (1993). Intrinsic noise and infant visual performance. In K. Simons, *Early visual development normal and abnormal* (pp. 178–196). New York: Oxford University Press.
- Crognale, M. A., Kelly, J. P., Weiss, A., & Teller, D. Y. (1998). Development of the spatio-chromatic visual evoked potential (VEP): a longitudinal study. *Vision Research*, *38*, 3283–3292.
- De Vries-Khoe, L. H., & Spekreijse, H. (1982). Maturation of luminance and pattern EPs in man. *Documenta Ophthalmologica Proceedings Series*, *31*, 461–475.
- Dobkins, K. R., Lia, B., & Teller, D. Y. (1997). Infant color vision: Temporal contrast sensitivity functions for chromatic (red/green) stimuli in 3-months-old. *Vision Research*, *37*, 2699–2716.

- Dobson, V. (1976). Spectral sensitivity of the 2-month infant as measured by the visually evoked potential. *Vision Research*, 16, 367–374.
- Efron, B. (1982). The jackknife, the bootstrap and other resampling plans. *CBMS-NSF regional conference series in applied mathematics*, vol. 38. SIAM.
- Efron, B., & Tibshirani, R. J. (1993). *An introduction to the bootstrap*. New York: Chapman & Hall.
- Gegenfurtner, K., & Kiper, D. (1993). Contrast detection in luminance and chromatic noise. *Journal of the Optical Society of America A*, 9, 1880–1888.
- Geisler, W. S. (1989). Sequential ideal-observer analysis of visual discrimination. *Psychological Review*, 96, 267–314.
- Hays, W. L. (1973). *Statistics for the social sciences* (second ed.). New York: Holt, Rinehart and Winston.
- Hendrickson, A. E. (1994). Primate foveal development: a microcosm of current questions in neurobiology. *Investigative Ophthalmology and Visual Science*, 35, 3129–3133.
- Hennelly, M. L., Barbur, J. L., Edgar, D. F., & Woodward, E. G. (1998). The effect of age on the light scattering characteristics of the eye. *Ophthalmic and Physiological Optics*, 18, 197–203.
- Hill, A. R., Heron, G., Lloyd, M., Lowther, P. (1982). An evaluation of some colour vision tests for children. In: G. Verriest, W. Junk, *Colour vision deficiencies VI, documenta ophthalmologica proceedings series*, vol. 33 (pp. 183–187). The Hague.
- Hollants-Gilhuijs, M. A. M., Ruijter, J. M., & Spekreijse, H. (1998). Visual half-field development in children: detection of colour-contrast-defined forms. *Vision Research*, 38, 560–645.
- Hurvich, L. M. (1972). Color vision deficiencies. In D. Jameson, & L. M. Hurvich, *Handbook of sensory physiology, visual psychophysics*, vol. VII/4. Berlin: Springer.
- Johnson, C. A., & Marshall, D. (1995). Aging effects for opponent mechanisms in the central visual field. *Optometry and Visual Science*, 72, 75–82.
- Kelly, J. P., Borchert, K., & Teller, D. Y. (1997). The development of chromatic and achromatic contrast sensitivity in infancy as tested with the sweep VEP. *Vision Research*, 37, 2057–2072.
- Knoblauch, K., Saunders, F., Kusuda, M., Hynes, R., Podgor, M., Higgins, K. E., & de Monasterio, F. M. (1987). Age and illuminance effects in the Farnsworth-Munsell 100-Hue test. *Applied Optics*, 26, 1441–1448.
- Knoblauch, K., Vital-Durand, F., & Barbur, J. L. (1997). Age-matched comparisons of chromatic thresholds between normal and strabismic observers. In C. R. Cavonius, *Color vision deficiencies XIII* (pp. 271–276). Dordrecht: Kluwer Academic Publishers.
- Kraft, J. K., & Werner, J. S. (1994). Spectral efficiency across the life span: flicker photometry and brightness matching. *Journal of the Optical Society of America A*, 11, 1213–1221.
- Le Grand, Y. (1972). *Optique physiologique tome II, lumière et couleurs* (second ed., p. 72). Paris: Masson & CIE.
- Lee, B. B., Martin, P. R., & Valberg, A. (1988). The physiological basis of heterochromatic flicker photometry demonstrated in ganglion cells of the macaque retina. *Journal of Physiology*, 404, 323–347.
- MacAdam, D. L. (1942). Visual sensitivities to color differences in daylight. *Journal of the Optical Society of America A*, 32, 247–274.
- McKee, S. P., Klein, S. A., & Teller, D. Y. (1985). Statistical properties of forced-choice psychometric functions: implications of probit analysis. *Perception and Psychophysics*, 37, 286–298.
- Morrone, M. C., Burr, D. C., & Fiorentini, A. (1993). Development of infant contrast sensitivity to chromatic stimuli. *Vision Research*, 33, 2535–2552.
- Moscowitz-Cook, A. (1979). The development of photopic spectral sensitivity in infants. *Vision Research*, 19, 1133–1142.
- Mullen, K. T., & Losada, M. A. (1994). Evidence for separate pathways of color and luminance detection mechanisms. *Journal of the Optical Society of America A*, 11, 3136–3151.
- Petzold, A., & Sharpe, L. T. (1998). Hue memory and discrimination in young children. *Vision Research*, 38, 3759–3772.
- Pokorny, J., Smith, V. C., Verriest, G., & Pinckers, A. J. L. G. (1979). *Acquired and congenital color vision defects*. New York: Grune and Stratton.
- Press, W. H., Flannery, B. P., Teukolsky, S. A., & Vetterling, W. T. (1988). *Numerical recipes in c: the art of scientific computing* (pp. 305–309). Cambridge: Cambridge University Press.
- Regan, B. C., Reffin, J. P., & Mollon, J. D. (1994). Luminance noise and the rapid determination of discrimination ellipses. *Vision Research*, 34, 1279–1299.
- Scheffrin, B. E., Werner, J. S., Plach, M., Utlaut, N., & Switkes (1992). Sites of age-related sensitivity loss in a short-wave cone pathway. *Journal of the Optical Society of America A*, 9, 355–363.
- Scheffrin, B. E., Shinomori, K., & Werner, J. S. (1995). Contributions of neural pathways to age-related losses in chromatic discrimination. *Journal of the Optical Society of America A*, 12, 1233–1241.
- Schmidt, I. (1955). A sign of manifest heterozygosity in carriers of color deficiency. *American Journal of Optometry*, 32, 404–408.
- Shinomori, K., Scheffrin, B. E., & Werner, J. S. (1997). Age-related declines of chromatic discriminations are the same for equiluminant stimuli lying on tritan and constant S-cone axes. In C. Dickinson, I. Murray, & D. Carden, *John Dalton's colour vision legacy* (pp. 287–297). London: Taylor & Francis.
- Skoczenski, A. M., Banks, M. S., & Candy, T. R. (1993). Contrast sensitivity and equivalent noise in infants and adults. *Investigative Ophthalmology and Visual Science*, 34(Suppl.), 1335.
- Skoczenski, A. M., & Norcia, A. M. (1998). Neural noise limitations on infant visual sensitivity. *Nature*, 391, 697–700.
- Spekreijse, H. (1978). Maturation of contrast EPs and development of visual resolution. *Archives Italiennes de Biologie*, 116, 358–369.
- Teller, D. Y. (1979). The forced-choice preferential looking procedure: a psychophysical technique for use with human infants. *Infant Behavior and Development*, 2, 135–153.
- Teller, D. Y. (1985a). The acuity card procedure: a rapid test of infant visual acuity. *Investigative Ophthalmology and Visual Science*, 26, 1158–1162.
- Teller, D. Y. (1985b). Psychophysics of infant vision: definitions and limitations. In G. Gottlieb, & N. Krasnegor, *Measurement of audition and vision in the first year of life* (pp. 127–143). New Jersey: Ablex.
- Teller, D. Y., & Lindsey, D. T. (1993). Infant color vision: OKN techniques and null plane analysis. In K. Simons, *Early visual development normal and abnormal* (pp. 143–162). New York: Oxford University Press.
- Verriest, G. (1963). Further studies on acquired deficiency of colour discrimination. *Journal of the Optical Society of America*, 53, 185–195.
- Verriest, G., Laethem, J. V., Uvijls, A. (1982). A new assessment of the normal ranges of the 100 hue total scores. In: G. Verriest, W. Junk, *Colour vision deficiencies VI, documenta ophthalmologica proceedings series*, vol. 33 (pp. 199–208). The Hague.
- Vital-Durand, F. (1996). An acuity cards cookbook. *Strabismus*, 4, 89–97.
- Weale, R. A. (1992). *The senescence of human vision* (pp. 220–224). Oxford: Oxford Medical Publications.
- Werner, J. S. (1996). Visual problems of the retina during ageing: Compensation mechanisms and colour constancy across the life span. *Progress in Retinal and Eye Research*, 15, 621–645.
- Werner, J. S., & Steele, V. (1988). Sensitivity of human color mechanisms throughout the life span. *Journal of the Optical Society of America A*, 5, 2122–2130.
- Werner, A., Schwarz, G., & Paulus, W. (1995). Ageing and chromatic contrast sensitivity. In B. Drum, *Colour vision deficiencies XII* (pp. 235–241). Dordrecht: Kluwer Academic Publishers.

Wyszecki, G., & Stiles, W. S. (1982). *Color science: concepts and methods, quantitative data and formulae* (second ed.). New York: Wiley.

Yuodelis, C., & Hendrickson, A. (1986). A qualitative and quantitative analysis of the human fovea during development. *Vision Research*, 26, 847–855.