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**"Development of contrast sensitivity and acuity
of the infant colour system"**

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Development of contrast sensitivity and acuity of the infant colour system

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SUMMARY

We have monitored the development of infant colour vision by measuring chromatic contrast sensitivity and acuity in eight young infants over a period of 6 months. Steady-state visual evoked potentials (VEPs) were recorded in response to both chromatic (red-green) and luminance (red-black or green-black) patterns that were reversed in contrast over time. For most infants, no response could be obtained to chromatic stimuli of any size or contrast before 5 weeks of age, although luminance stimuli of 20% contrast gave reliable responses at that age. When responses to chromatic stimuli first appeared, they could be obtained only with stimuli of very low spatial frequency, 20 times lower than the acuity for luminance stimuli. Both contrast sensitivity and acuity for chromatic stimuli increased steadily, more rapidly than for luminance stimuli. As the spectral selectivities of infant cones are similar to those of adults, the difference in rate of development of luminance and chromatic contrast sensitivity and acuity stimuli probably reflects neural development of the infant colour system.

1. INTRODUCTION

The development of contrast sensitivity, spatial acuity, temporal resolution, stereopsis and many other aspects of the infant visual system has been studied extensively over the past two decades by a variety of techniques (see, for example, Atkinson 1984; Banks & Danner-miller 1987; Mohn & Van Hof 1990). Infant colour vision has been studied less extensively, but it is fairly certain that infants are trichromatic by three months of age with adult-like spectral sensitivity (at least over the middle- to long-wavelength range), and that they can make colour discriminations of large targets by two months (see review of Teller & Bornstein (1987)). In this longitudinal study we apply the technique of recording visual evoked potentials (VEPs) to investigate how the spatial characteristics of the infant colour system develops over the first six months.

2. METHODS

The stimuli for our experiments were plaid patterns modulated sinusoidally both horizontally and vertically, made by summing red and green sinusoidal plaids of equal but opposite contrast (see equation (1) in caption to figure 1). Following the procedure used by Mullen (1985), the ratio of the red:total mean luminance (r in equation (1)) could be varied from 0 to 1, where $r = 0$ defined a green-black pattern, $r = 1$ a red-black pattern and intermediate values a red-green pattern. For each observer there exists a value of r (near 0.5 for colour normals) where the red and green luminances are exactly matched, making the pattern iso-luminant. To produce steady-state VEPs, the patterns were

reversed in contrast at frequencies from 2 to 5 Hz. Electroencephalograms were recorded with surface electrodes (O_z , C_z , with earth halfway between), suitably filtered (1–50 Hz), amplified, and fed into a computer for real-time analysis.

VEPs were first measured as a function of r . In adults, VEPs were qualitatively similar at all values of r , modulating with each pattern reversal (i.e. at the second harmonic of counter-phase frequency), although amplitude usually varied with colour ratio. For stimuli of moderate contrast, second-harmonic amplitude varied with colour ratio symmetrically about a minimum, usually at a ratio near 0.5 (that corresponded closely to the iso-luminant point evaluated by flicker-fusion photometry).

3. RESULTS

Figure 1*a* shows VEP amplitudes of a 7-week-old as a function of colour ratio. Although the response to both red and green luminance stimuli was strong and reliable, no reliable VEPs could be recorded at the colour ratio 0.55 (the iso-luminant point for his mother). The curve is symmetrical about the minimum, with red and green gratings producing VEPs of similar amplitude, reinforcing existing evidence that red and green stimuli that are equally effective for adults are also equally effective for infants of this age (Dobson 1976; Peebles & Teller 1978; Moskowitz-Cook 1979; Maurer *et al.* 1989). The existence of a point (presumably the iso-luminant point for the infant) where no VEP could be elicited indicates that the infant had no response to purely chromatic stimuli at this age. This particular infant was tested extensively over this period (almost daily), and for no spatial or temporal frequency (down to 1 Hz, 0.05 cycles per degree could

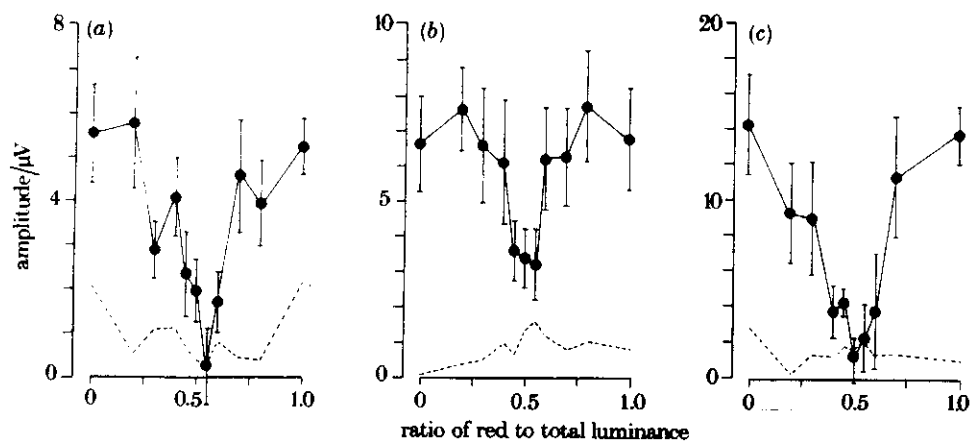


Figure 1. Amplitude of second-harmonic modulation of visual evoked potentials as a function of the ratio of red: total mean luminance for infant PAB. The spatial frequency was 0.1 cycle per degree for (a) and (b), and 0.4 cycle per degree for (c). The temporal frequency of counter-phase modulation was 2 Hz for (a) and 3 Hz for (b) and (c) and contrast was always 0.9. Curve (a) was measured at 7.2 weeks, and (b) and (c) at 8.5 weeks. The error bars show the standard error of the mean of at least four separate (vectorial) estimates of amplitude, and the dashed lines show the amplitude of the second harmonic of VEPs averaged at 1.1 times stimulus rate. Both these measures give an indication of signal reliability. At 7 weeks, no reliable VEPs could be recorded from stimuli with colour ratio near 0.5, at any spatial frequency (down to 0.05) and temporal frequency (down to 1 Hz). The records near colour ratio 0.5 are averaged from 250 sums, and the others 100 sums. The stimulus was a plaid pattern, modulated sinusoidally both horizontally and vertically, with the instantaneous red and green luminances $L_R(x, y, t)$ and $L_G(x, y, t)$ at position x, y and time t given by:

$$\begin{aligned} L_R(x, y, t) &= r \cdot L_0 \{1 + \frac{1}{2} m \cdot S(t) [\cos(2\pi f_s x) + \cos(2\pi f_s y)]\}, \\ L_G(x, y, t) &= (1-r) \cdot L_0 \{1 - \frac{1}{2} m \cdot S(t) [\cos(2\pi f_s x) + \cos(2\pi f_s y)]\}, \end{aligned} \quad (1)$$

where $S(t)$ is the temporal (square wave) modulation function, periodic in $L(O, T)$.

$$S(t) = \begin{cases} 1 & \text{for } 0 < t < \frac{1}{2}T \\ -1 & \text{for } \frac{1}{2}T < t < T \end{cases}$$

where T is the temporal period. L_0 is the total mean luminance (always 16.5 cd m^{-2}), r the ratio of red: total mean-luminance ($L_R/L_R + L_G$), m the Michelson contrast and f_s spatial frequency. $r = 0$ defined a red-black plaid pattern, $r = 0.5$ a green-red pattern and $r = 1$ a red-black pattern. Every $T/2$ s, the contrast of the pattern was reversed: when $r = 1$ the red and black blobs were exchanged; when $r = 0.5$ the red and green blobs were exchanged. The stimuli were displayed on the face of a Barco high resolution oscilloscope by modulating the red and green guns. The peak spectral response for the red phosphor was at 628 nm, with CIE coordinates $x = 0.618, y = 0.35$; the green phosphor peaked at 531 nm, with CIE coordinates $x = 0.28, y = 0.605$. The visible screen was 40 cm wide and 20 cm high, viewed from 30 to 150 cm, depending on spatial frequency.

we obtain a response to chromatic stimuli before 8 weeks of age. We also attempted using red-blue stimuli (spectrally more separated), to no avail. At $8\frac{1}{2}$ weeks (figures 1b), the response to a 0.1 cycles per degree stimulus was reliable at all colour ratios, showing that the colour system had started to develop. However, at this age, there was no response to chromatic stimuli of 0.4 cycles per degree, implying low chromatic acuity.

To quantify the development of colour vision, we monitored both contrast sensitivity and acuity of eight young infants, using the extrapolation technique of Campbell & Maffei (1970), illustrated in figure 2 for two infants of two different ages. VEPs for both chromatic and luminance stimuli were recorded as a function of contrast and of spatial frequency, and the amplitude response curves fit with a polynomial (up to third order). Extrapolation of the curve to zero response (on log-linear axes) gave an estimate of contrast thresholds or of spatial acuity, along with an error estimate. With adults, the contrast sensitivity and acuity estimates were close to those evaluated directly

by psychophysical means, giving us confidence in the VEP threshold estimates (as previously observed for luminance stimuli by Campbell & Maffei (1970) and for chromatic stimuli by Regan (1973); see also Fiorentini *et al.* (1990)). For example, at 0.3 cycles per degree and 4 Hz, the mean of four VEP estimates of chromatic contrast sensitivities for observer MCM was $29.4 (\pm 0.05 \text{ log units})$ whereas the mean psychophysical estimate (method of adjustment) $32.2 (\pm 0.07 \text{ log units})$. It has also been shown that VEP estimates are similar to behavioural estimates of contrast sensitivity in infants (Atkinson & Braddick 1989).

Figure 3 shows how contrast sensitivity and acuity developed over the first few months of life. Contrast sensitivity (a) was measured at 0.1 cycles per degree, to favour the colour system which prefers lower spatial frequencies (Mullen 1985), and to minimize chromatic aberrations (Flitcroft 1988). Before 4-7 weeks (varying from infant to infant) there was no response to chromatic stimuli, even at 90% contrast. At the same time, however, contrast sensitivity to luminance stimuli

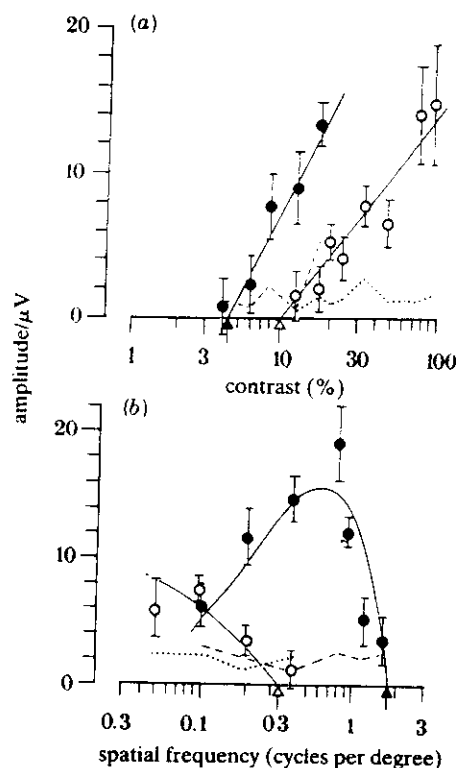


Figure 2. Illustration of the method of estimating contrast sensitivity and spatial acuity from VEP amplitude response curves for two different infants of different ages. (a) Plot of VEP amplitudes (second harmonic) of infant SP (22 weeks) as a function of contrast; (b) plots of VEP amplitudes of infant PAB (8.5 weeks) as a function of spatial frequency. The closed symbols refer to luminance stimuli ($r = 1$), and the open symbols to chromatic stimuli ($r = 0.55$ for (a) and 0.50 for (b), chosen to given minimum response). The dashed and dotted lines indicate the asynchronous noise levels for the luminance and chromatic stimulation (respectively). Temporal frequency was 5 Hz for (a) and 3 Hz for (b). Spatial frequency for (a) was 0.1 cycle per degree, and the contrast for (b) 0.9. The curves passing through the data are best fitting polynomials (up to third order), fitted by least squares fit (weighting the data by both standard error and signal:noise ratio). The intercepts at zero amplitude give estimates of contrast sensitivity and visual acuity (see arrows). In adults, these estimates were close to those obtained by direct psychophysical means.

was 5–8 (threshold of 12–20% contrast). Both chromatic and luminance sensitivity increased with age, first rapidly then more slowly. Over the first 20 weeks, chromatic sensitivity increased 0.073 log units per week, whereas luminance sensitivity increased at 0.060 log units per week. As the standard errors of measurement were about 0.001, the difference in slope is clearly significant. By about six months, both chromatic and luminance contrast sensitivity levels approached those of adults.

At the earliest age at which chromatic VEPs could be recorded, only very low spatial frequencies (around 0.1 cycles per degree) would elicit a response (figure 3b). During this period, the acuity for luminance stimuli was around 2 cycles per degree, 20 times higher. Like contrast sensitivity, chromatic and luminance acuity developed at a different rate over the first 20

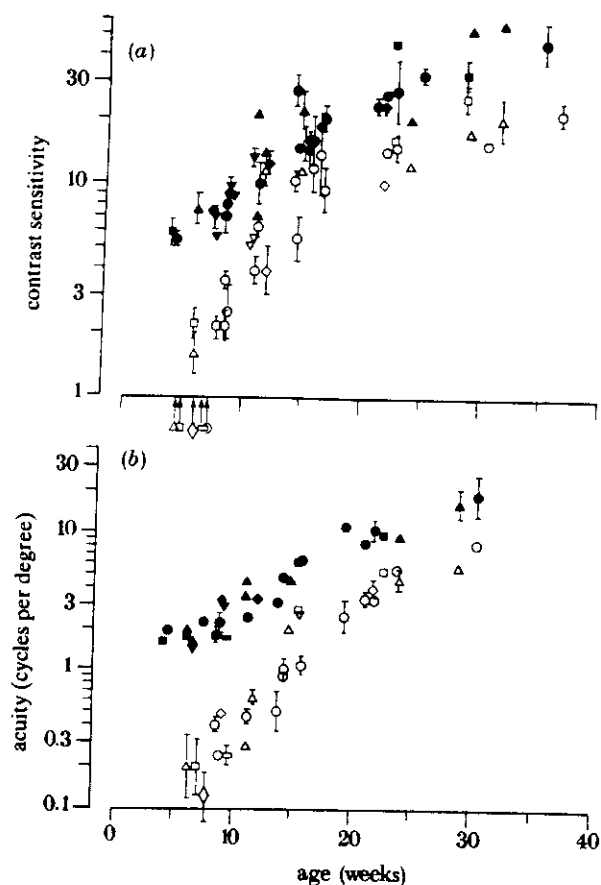


Figure 3. (a) Development of contrast sensitivity (the inverse of contrast threshold) for chromatic stimuli (open symbols) and luminance stimuli (filled symbols). The different symbol types refer to longitudinal measurements of the eight infants. Contrast sensitivity was estimated by the fitting procedure described in figure 2, with the error bars indicating the standard error associated with the fit. The arrows below the abscissa indicate the latest recording session at which no-response could be elicited by chromatic stimuli at 90% contrast. Spatial frequency was always 0.1 cycles per degree, and temporal frequency varied with age, chosen to yield maximal response to chromatic stimuli: 2 Hz from 4 to 7 weeks, 3 Hz from 7 to 20 weeks, and 5 Hz thereafter. Both chromatic and luminance sensitivities increased with age, fairly rapidly up to 15 weeks, and more slowly thereafter. The first section of both curves (up to 20 weeks) were fitted by linear regression (weighting each point with the standard error): chromatic sensitivity increased at the rate of 0.073 ± 0.001 log-units (LUs) per week, and luminance sensitivity at 0.060 ± 0.001 LUs per week. (b) Development of acuity for chromatic and luminance stimuli (open and closed symbols respectively). Contrast was always 0.9, and temporal frequency varied with age (see above). Again the first section of both curves (up to 20 weeks) were fitted by linear regression to yield estimates of slope. Chromatic sensitivity increased at the rate of 0.138 ± 0.002 LUs per week, and luminance sensitivity at 0.045 ± 0.001 LUs per week.

weeks: chromatic acuity at 0.138 log units per week and luminance acuity at 0.045 log units per week (the latter rate consistent with previous studies (Pirchio *et al.* 1978; Marg *et al.* 1976; Sokol 1978). Again the standard errors were around 0.001 log units per week, so the differences are significant. By six months chromatic acuity was one third the luminance acuity,

ratios similar to those observed with adults (Mullen 1985).

As detailed in the legend to figure 3, the temporal frequency of the stimuli for the contrast sensitivity and acuity measurements varied with age from 2 to 5 Hz. These frequencies were chosen to be below the preferred temporal frequency for luminance stimuli (which increases with age (Moskowitz & Sokol 1980; Fiorentini & Trimarchi 1989)), thereby favouring chromatic sensitivity (which is higher at lower temporal frequencies (Kelly 1989)). However, from 8 to 20 weeks (the range over which the slopes of the curves were measured), temporal frequency was constant at 3 Hz. If the increase in temporal frequency after 20 weeks had any effect on the relative sensitivities, it should favour luminance rather than chromatic contrast sensitivity (Kelly 1989), contrary to what we find.

It is important to appreciate that lack of response to chromatic stimuli before 4–7 weeks does not necessarily imply that infants of that age have no mechanisms for processing colour information. Because human cones have a broad and largely overlapping spectral sensitivity, the chromatic stimuli used here produce a lower contrast in the cones than do luminance stimuli of the same physical contrast. The maximum cone contrast produced by the iso-luminant stimuli of this study (calculated from the integral of the product of the cone and phosphor spectral curves) was about 15% for long-wavelength (L) cones, and 33% for medium-wavelength (M) cones. Depending on the assumptions of combination of L and M cone output, the effective contrast of the chromatic stimuli should be one third to one sixth the luminance stimuli. As the absorption spectra of infant cone photopigments are similar to those of adults (Brown & Teller 1989), and the media transmission above 500 nm is also similar (Powers *et al.* 1981; Hansen & Fulton 1989), the effective cone-contrast of the chromatic stimuli in young infants should also be one third to one sixth the luminance stimuli. Averaging across all infants, we found that on the latest recording session for which there was no response to chromatic stimuli of 90% contrast, the luminance contrast thresholds were on average 17.5%, by about one-fifth. As this factor is within the range predicted from the cone-contrast for these stimuli, we cannot exclude the possibility that the earliest chromatic responses are limited by the effective contrast of the stimuli, rather than by a deficit of neural mechanisms for colour analysis.

However, although effective cone-contrast may limit the onset of colour vision, it cannot be responsible for the differential rate of development of contrast sensitivity, nor the fact that chromatic acuity is so low in young infants. The ratio of luminance-to-chromatic contrast sensitivity decreases from a factor of 6–7 (the limit of the cone-contrast estimate) to 3–4 at six months (and in adults for temporally modulated stimuli), while the cone-contrast of the stimuli should remain unaltered. The ratio of luminance-to-chromatic acuities varies even more, from over 20 in very young infants to the adult value of 3 at 7 months. The greater differences in acuity could not result from pre-neural factors such as cone size or inter-cone spacing, as these

should affect both luminance and chromatic acuity to the same extent. Nor could the low chromatic acuity simply reflect low chromatic contrast-sensitivity, as the difference in development rates of acuity was greater than that for contrast sensitivity, whereas the steepness of the contrast sensitivity curve would predict the opposite.

4. DISCUSSION

Behavioural studies of colour discrimination in infants support our results (Hamer *et al.* 1982; Clavadetschler *et al.* 1988; Teller & Bornstein 1987). For example, 1-month-olds can make Rayleigh colour discriminations for large (4° and 8°) patches but not small (2°) patches, whereas 3-month-olds can also make colour discriminations with 2° patches (Packer *et al.* 1984). Although the behavioural studies were done under slightly different conditions from ours (monochromatic stimuli of lower luminance, colour patches rather than gratings), the general agreement with our study encourages us to believe that the VEP estimates of colour contrast sensitivity and acuity reflect functional limits in colour processing.

Although our results find support from behavioural studies, they are unfortunately at variance with a recent VEP study by Allen *et al.* (1990). They report reliable chromatic responses from infants as young as two weeks from stimuli of 0.8 cycle per degree (eight times finer than the resolution limit of our infants at 7 weeks), from which they concluded that infant colour vision is limited entirely by cone contrast (see also Banks & Bennett 1988). Although there were differences in the techniques of the two studies (Allen *et al.* (1990) used lower luminances and the 'sweep' VEP technique of Norcia *et al.* (1985)), it is difficult to understand how these could account for the order of magnitude differences in results. We can only suggest that a major difficulty inherent to all colour research is the possible contamination by chromatic aberrations, which may induce luminance contrast in the supposed iso-luminant stimuli (see Mullen (1985) for details of how to reduce the problem with adults). In adults the aberrations should be negligible at spatial frequencies below 1 cycle per degree (Flitcroft 1988), but they may well be significant at that frequency in the young infant eye (which has about twice the power of the adult eye). This was one reason why we made the bulk of our measurements at very low spatial frequencies. We also took particular care to identify the iso-luminant point for all infants by finding the colour ratio (not always exactly 0.5) that yielded the minimum response. Colour ratios 5% away from the iso-luminance point introduce 10% luminance contrast, which may produce a response by itself (compare, for example, the response of figure 1a at colour ratio 0.5 with that at colour ratio 0.55).

As cone-contrast is not by itself sufficient to explain the differential development of chromatic and luminance vision, neural factors must be involved. One possibility is that the cones of very young infants are so immature (Hendrickson & Yuodelis 1984) that rods contribute to luminance contrast sensitivity and acuity

in young infants, and this factor diminishes with age as the cones mature. However, it is unlikely that cones do not contribute to luminance sensitivity in young infants, as even at nine weeks of age contrast sensitivity increases with luminance up to at least 200 cd m^{-2} (Fiorentini *et al.* 1980; Norcia *et al.* 1990; see also Fiorentini 1990). Also, if rods were making a major contribution to luminance sensitivity in young infants, it would be hard to explain why their iso-luminant mixes were similar to those of adults (Maurer *et al.* 1989) (our figure 1), and why their spectral sensitivity functions resemble adult photopic rather than scotopic functions (Peebles & Teller 1978).

The rapid development in chromatic acuity most probably reflects maturation in the organization of receptive fields of neurons responding to chromatic stimuli. Several physiologists have suggested that chromatic and luminance patterns are processed, at least in part, through separate visual pathways, (see, for example, Hubel & Livingstone 1987; Shapley 1989). The magno pathway is thought to be largely confined to luminance signals, whereas colour information is processed mainly through the parvo pathway (although important interactions between the pathways certainly exist). If this be the case, our results would suggest different rates of development of the magno and parvo systems. Although speculations of this nature are possibly premature, we can be reasonably certain that differential development of neural mechanisms are implicated in the maturation of chromatic spatial processing.

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