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# Development of Infant Contrast Sensitivity to Chromatic Stimuli

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**We have monitored the development of contrast sensitivity to equiluminant red–green chromatic patterns by monitoring visual evoked potentials (VEPs) in 13 infants. The results confirm our previous report [Morrone, Burr and Fiorentini, *Proceedings of the Royal Society B, 242* (1990a)] that, before 7–8 weeks of age, there was no response to purely chromatic stimuli, while at the same age luminance stimuli of 20% contrast produced reliable responses. At all ages (even before the onset of a chromatic response) the colour mixture to yield equiluminance was similar to that of adults, suggesting that the relative proportion and efficacy of medium- and long-wave cones is similar for infants as for adults. For both luminance and chromatic stimuli, amplitude increased roughly linearly with log-contrast, so sensitivity thresholds could be predicted by linear extrapolation to the abscissa. Detailed contrast sensitivity curves were measured for four infants at various ages. The results show that luminance and chromatic contrast sensitivity develop independently at different rates, probably reflecting differential development of postreceptoral neural mechanisms.**

Development Colour Contrast sensitivity Acuity Chromatic aberrations

## INTRODUCTION

The human visual system is very immature at birth, both structurally and functionally, and continues to develop postnatally until complete maturity is reached. The time course of postnatal development, however, is different for different visual functions. For instance, "for both rod and cone vision, the spatial properties of visual performance [visual acuity] develop more gradually and over a more protracted time course than do overall contrast sensitivity ... [suggesting that] ... the infant's visual system possesses different immaturities of visual sensitivity and spatial scale" (Brown, 1990, p. 1170). Compared with visual acuity, binocular functions (in particular steroacuity) have a later onset and a different developmental course. Orientation discrimination, on the other hand, is present to some degree very early in life and is fully developed a few months after birth (see Atkinson & Braddick, 1989 for review).

Colour vision seems to develop early in infants. Behavioural experiments provide evidence for the emergence of colour vision in infants between 1 and 3 months from birth (Hamer, Alexander & Teller, 1982; Clavadetscher, Brown, Ankrum & Teller, 1988; Varner, Cook, Schneck, McDonald & Teller, 1985; see Teller & Bornstein, 1987 and Brown, 1990 for review). The infant performance in colour discriminations seems to have the general characteristics of trichromatic vision, but to require relatively large stimuli (Packer, Hartmann & Teller, 1984).

Using a visual evoked potential (VEP) recording technique, we have shown that both acuity and contrast sensitivity (at low spatial frequencies) develop independently for luminance and colour vision in human infants (Morrone, Burr & Fiorentini, 1990a). The results showed important differences in the time course of development of VEP responses to luminance and chromatic patterns, both in the age of onset and in the rate of maturation. No significant responses could be obtained from equiluminant patterns in infants younger than 6–8 weeks, even at the highest colour-contrast, while at this age luminance patterns of only 20% contrast gave strong and reliable responses. After the onset of responses to equiluminant patterns, contrast sensitivity and spatial acuity improved rapidly with age, more rapidly than to luminance contrast.

This study examines in more detail the development of colour vision in human infants, by monitoring the development of contrast sensitivity for luminance and chromatic patterns in 13 infants. As in the previous study, the equiluminant point for the chromatic stimuli was established for each infant and for each spatial frequency, by measuring VEPs for various colour mixes. In 4 infants, the contrast sensitivity function (CSF) for equiluminant red–green patterns was obtained from VEPs recorded at various ages and was compared with the CSF relative to red–black or green–black patterns with pure luminance contrast. At all ages the equiluminant CSF was found to differ from the luminance CSF both in absolute sensitivity and in cutoff frequency, but

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the differences steadily decrease with age. The results reinforce the previous findings that colour contrast sensitivity has a later onset, but a more rapid development, compared with luminance contrast sensitivity. Some of these results have been reported in abstract form (Morrone, Burr & Fiorentini, 1989; Morrone, Fiorentini & Burr, 1990b).

## METHODS

### *Stimuli*

The stimuli for our experiments were tartan patterns (sometimes referred to as plaids) modulated sinusoidally both horizontally and vertically, made by summing red and green sinusoidal tartans of equal but opposite contrast. The patterns were generated by framestore (Cambridge Research VSG), and displayed on the face of a colour monitor (Barco CDCT 6551), by modulating the red and green guns. The peak spectral response for the red phosphor was at 628 nm (CIE co-ordinates: $x = 0.618$, $y = 0.35$) and that of the green phosphor 531 nm (CIE co-ordinates: $x = 0.28$, $y = 0.605$). The visible screen was 40 cm wide and 20 cm high, viewed from 15 to 150 cm, depending on spatial frequency.

Following the procedure introduced by Mullen (1985), the ratio of colours was varied by varying the relative contribution of the red and green stimuli. The ratio of the red-to-total-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 chromatic pattern. The patterns were reversed sinusoidally in contrast, at frequencies ranging from 2 to 5 Hz.

The instantaneous red and green luminances $L_R(x, y, t)$ and $L_G(x, y, t)$ at position $x, y$ and time $t$ are given by:

$$\left.\begin{aligned} L_R(x, y, t) &= rL_0\{1 + 0.5m\cos(2\pi f_t t)[\cos(2\pi f_s x) + \cos(2\pi f_s y)]\} \\ L_G(x, y, t) &= (1 - r)L_0\{1 - 0.5m\cos(2\pi f_t t)[\cos(2\pi f_s x) + \cos(2\pi f_s y)]\} \end{aligned}\right\} \quad (1)$$

$L_0$ is the total mean-luminance (16.5 cd/m$^2$), $r$ the ratio of red-to-total luminance [$L_R/(L_R + L_G)$], $m$ Michelson contrast, $f_s$ spatial frequency and $f_t$ temporal frequency. Note that the contrast $m$ is multiplied by 0.5, indicating that half the total contrast comes from the horizontal and half from the vertical component of the two-dimensional tartan. This factor should be borne in mind when comparing absolute sensitivity with previous data that used one-dimensional gratings.

The response of the long and medium wavelength cones is readily calculated from the CIE values of the oscilloscope phosphor and human cone fundamentals (Smith & Pokorny, 1975). These calculations show that with this particular stimulus, L cones do not modulate at $r = 0.43$ and M cones do not modulate at $r = 0.68$ (points of silent substitution). For $r = 0.5$, the response of L and M cones is equal and opposite. The equiluminant point for all adult observers with normal vision was near this ratio.

### *VEP recording*

EEGs were recorded with surface electrodes ($O_Z$, $C_Z$, with earth half way between), pre-amplified 500-fold, filtered between 1–100 Hz, re-amplified a further 100-fold, and fed into the D/A input of a PC computer for real-time analysis. The computer averaged the EEG in synchrony with stimulus contrast reversal, and calculated second-harmonic amplitude and phase of the average by discrete Fourier analysis. An experimenter observed the infant at all times, and interrupted EEG averaging whenever gaze wandered from the screen, or the infant was unsettled.

To estimate background noise and artifacts, the computer also averaged on-line the EEG at a frequency 10% higher than the stimulation frequency, and calculated the second-harmonic amplitude of this average. For each *packet* of 20 sums (20 periods of stimulus presentation) the signal-to-noise ratio was calculated as the ratio of the synchronous to asynchronous amplitude. If this ratio was less than 1, the 20-trial packet was rejected from the final analysis. The purpose of this procedure was to minimize contamination by artifacts, such as gross head movements or blinks.

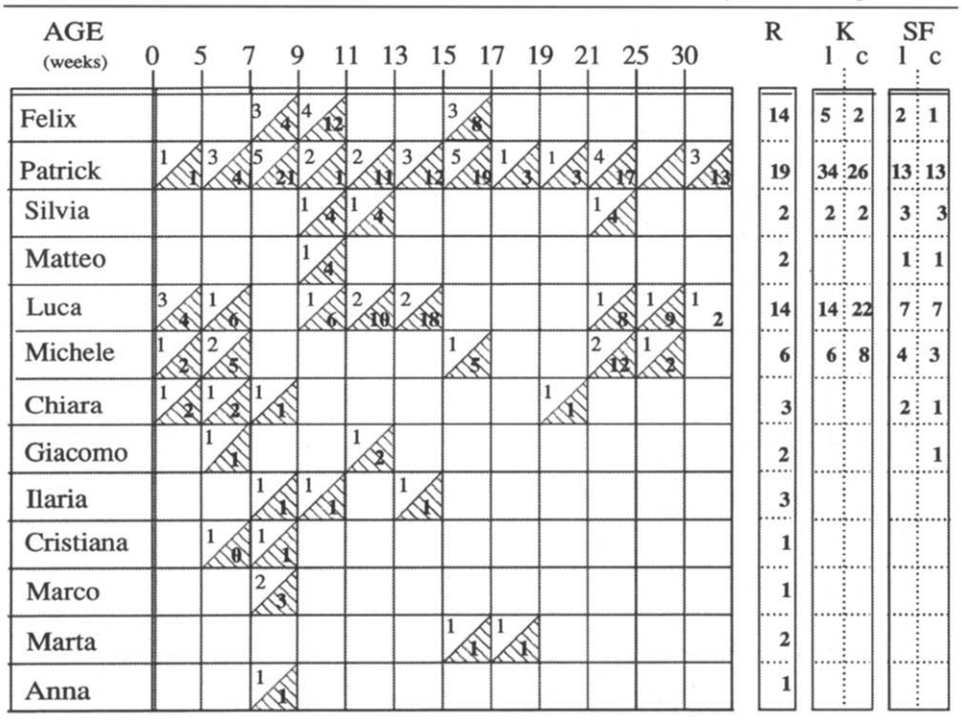
As an independent measure of reliability, we calculated the standard error of our estimates of amplitude and phase from the two-dimensional scatter in amplitude and phase of the individual (non-rejected) 20-sum packets.

### *Infants*

A total of 13 infants were examined at various ages. Table 1 indicates the number of recording sessions for each infant at each age (upper left numbers in each square), and the number of complete graphs (amplitude and phase curves as a function of colour-ratio, contrast or spatial frequency) obtained during those sessions (lower right number). The numbers in the right-hand columns indicate the total number of curves as a function of colour-ratio, contrast or spatial frequency. As each curve typically comprised about 8 data points, each made up of between 100–300 sums at between 2 and 5 Hz, the data set represents about 40 hr of actual averaged potentials (reflecting much longer actual recording, of course).

The order of measurement of VEPs was such as to minimize adaptation. For contrast response curves, the lowest contrasts were measured first, and for colour-ratio curves, the ratios around 0.5 were measured first, progressively moving to the more saturated ratios. For spatial frequency, the order was pseudo-random. After completion of a given curve, we allowed a period for recovery from adaptation, and repeated all measurements at least once, concentrating on conditions where the results were least clear.

TABLE 1. Summary of testing of the 13 infants involved in this study at various ages.




The numbers in the upper (unshaded) triangles indicate the number of testing sessions during the given period, and those in the bottom triangle the total number of complete curves recorded during those sessions. Each session typically lasted a full morning or afternoon, and with Patrick and Luca, the full day. The columns on the right indicate the total number of each type of curves collected for each infant, as a function of colour-ratio (R), contrast (K) or spatial frequency (SF), for either luminance (l) or chromatic (c) stimuli. The total number of curves were 253, each comprising an average of about 8 data points, each with about 200 sums.

## RESULTS

### *Red–green equiluminance for infant vision*

In adults, VEP responses to sinusoidal reversal of red–green patterns depend upon the colour-ratio, the ratio of the red-to-total luminance (Regan, 1973; Regan & Spekreijse, 1974; Murray, Parry, Carden & Kulikowski, 1987; Fiorentini, Burr & Morrone, 1991). At all colour-ratios, most of the VEP power is in the second harmonic, but second-harmonic amplitude varies considerably with colour-ratio. Figure 1 illustrates two typical examples of how second-harmonic amplitude and phase may vary with colour ratio. The curve at left (6.2 Hz, 90% contrast) shows a maximum, and that on the right (7.5 Hz, 30% contrast) a minimum at colour-ratios near 0.47, which was the colour-ratio to produce minimal flicker with this observer for these stimuli. The phase of the second-harmonic for colour-ratios close to equiluminance is usually less than that at colour-ratios near 0 (pure green pattern) or 1 (pure red pattern). The phase lag of the equiluminant response (with respect to that to pure luminance) corresponds to a difference in latency of about 40 msec, consistent with that estimated by Fiorentini *et al.* (1991) from the slope of the temporal response phase-curves.

To establish the equiluminant point in infants, we recorded from infants VEPs for tartan patterns of low spatial and temporal frequency as a function of colour-ratio. In agreement with our previous report, for all infants younger than 7–8 weeks, the amplitude of the responses were near noise levels for colour-ratios close to 0.5, while good responses were obtained at colour-ratios of 0 or 100.

The records of infant Michele (Fig. 2) illustrate this point. At 4 weeks of age, there was a strong response to luminance stimuli (colour-ratio 0), at both 0.1 and 0.5 c/deg (upper curves). This is clear not only from the strong second-harmonic modulation of the response (at an amplitude well in excess of the asynchronous noise), but also from the associated polar plot. The amplitudes and phases (shown by solid symbols) of the partial (20 sum) packets are grouped reasonably closely, suggesting that the signal is reliable. For chromatic stimuli (colour-ratio 0.5), however, there was no reliable response. At neither frequency do the records show any tendency for second-harmonic modulation, only random fluctuation of amplitude similar to that of the asynchronous noise. The partial-sum packets are broadly scattered, and closer to the origin than the packets of the luminance response, again consistent with the absence of a reliable stimulus-driven response.

At 6 weeks of age, the response to chromatic stimuli began, but only at the lower spatial frequency. At 0.1 c/deg, the response at colour-ratio 0.5 was as strong and as reliable as that at colour-ratio 0. However, at the higher spatial frequency (0.5 c/deg), there was no response to the chromatic stimulus, while the response to the luminance stimulus was larger than at 0.1 c/deg.

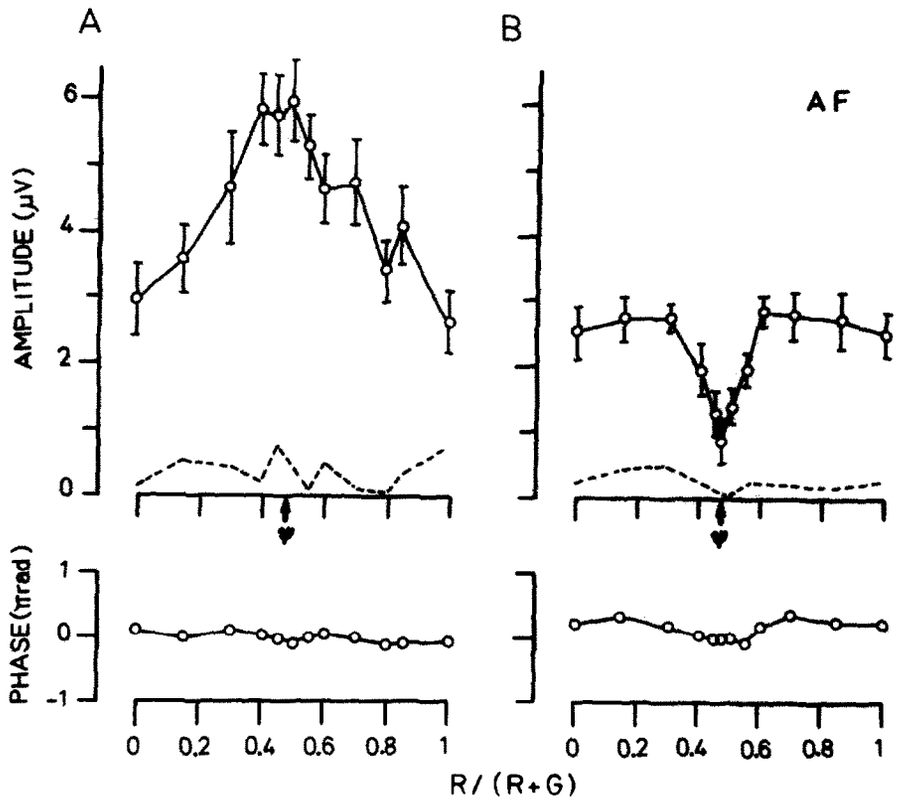



FIGURE 1. Amplitude and phase of VEPs recorded from an adult subject (AF) for plaid patterns of various colour-ratios. Colour-ratio 0 represents a green–black pattern, and 1 a red–black pattern, both of pure luminance contrast. The arrow indicates the ratio of red-to-total luminance corresponding to the equiluminance value evaluated psychophysically. Each point is the mean of 240 and 400 sums for (A) and (B) respectively, with the vertical bars indicating standard error. The amplitude of the asynchronous noise estimates are represented by the broken line. Stimulus spatial frequency: 1 c/deg, temporal frequency 6.2 Hz (A), 7.5 Hz (B). Contrast 90% (A), 30% (B). One condition leads to a local maximum in amplitude, the other to a local minimum.

Again this agrees with our earlier work (Morrone *et al.*, 1990a) in showing that the development of chromatic acuity lags that for luminance acuity.

Figure 3 shows second-harmonic amplitude and phase as a function of colour-ratio for another infant, Felix. At 8 weeks of age, there was a clear minimum in the curve (measured with maximum contrast), with no reliable response at colour-ratios 0.45 and 0.5. There the amplitude was at noise levels, and the standard errors large, both for amplitude and phase.

At 9 weeks, there was a good response at ratio 0.5, which dipped to noise levels at adjacent ratios before reaching maxima for pure luminance ratios. Here there was clearly a response at the previously established equiluminant point, so we presume that chromatic mechanisms are now operating. The dips on either side of this minimum may simply result from vector summation of colour and luminance mechanisms, discussed in a later section.

After 9 weeks the response to chromatic stimuli grew steadily stronger and more reliable. At 10 weeks [Fig. 3(C)], it was well above the noise levels at colour-ratios near 0.5. At 100% contrast (solid symbols), the minimum amplitudes were around 0.5, the established equiluminance point. However, at 50% contrast, there was a peak response at equiluminance, with two strong dips symmetrically either side [like Fig. 3(B)]. This behaviour (discussed in more detail later) was not at all atypical, but usually occurred only at particular contrasts.

At 15 weeks [Fig. 3(D)] the response was much like that at 10 weeks. At high contrasts, amplitudes were lower around equiluminance, but at 50% contrast, the curve was flat. Although the precise shape of the curve may depend to some extent on contrast, there is clearly a response to chromatic stimuli.

Note how rapidly the response at equiluminance develops. At 8 weeks the response did not differ significantly from noise, whereas 1 week later the response was clear and reliable, with amplitude around two-thirds of that to pure luminance stimuli. At 10 weeks the response continued to improve at equiluminance, being almost as strong as that to luminance at certain contrasts.

It is important to observe that in order to be certain that the amplitude is at noise levels at equiluminance, the range of colour-ratios around 0.5 has to be sampled finely. For instance, in the range 0.4–0.6, there are only two colour-ratios in Fig. 3(A) at which the VEP amplitude was near noise, and only one point in Fig. 3(B) where the VEP amplitude was significantly different from zero.

Figure 4 shows some other examples of second-harmonic amplitude curves that demonstrate no response at equiluminance. The dashed line indicates the average noise level for that particular session. In each case, at colour-ratios around 0.5, the response was at or

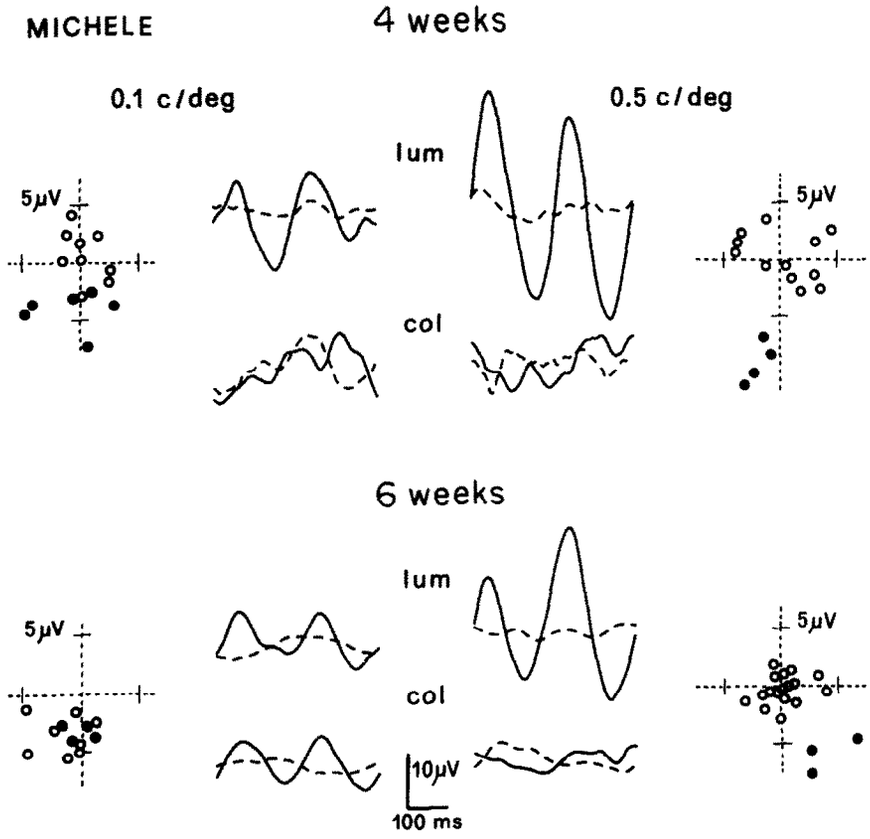



FIGURE 2. Examples of VEP records for luminance and equiluminant stimuli from infant Michele at 4 and 6 weeks to two different spatial frequencies. The continuous traces show the VEP averaged in synchrony with the stimulus reversal rate, and the dashed lines that averaged at 1.1 times the stimulus rate (which provides an estimate of noise). The adjacent polar plots show the amplitude (norm) and phase (argument) of partial (20 sum) packets, with solid symbols for the luminance stimuli and open symbols for the chromatic stimuli, both of 100% contrast. These give an indication of the variability of the response (from which the standard errors of all subsequent plots were calculated). While the response to luminance was reliable at all conditions (shown both by the relative amplitude of the signal to noise in the averaged records and by the relatively close clustering of the partial packets), only at 0.1 c/deg and 6 weeks did the chromatic stimulus produce a reliable response.

below the noise level. For the low spatial frequency range (0.1–0.2 c/deg), the infants with no chromatic response were all young, $<8$ weeks. But at higher spatial frequencies (0.7–0.1 c/deg), infants as old as 14 weeks showed no response at equiluminance.

From the various colour sweeps under various conditions, we obtained many estimates of the equiluminant point for our infants. Equiluminance was usually defined as the minimum of the curve, but sometimes as a local maximum, flanked by symmetric minima. Where there was a variation of phase with colour-ratio (see Fiorentini *et al.*, 1991), the point of symmetry of the phase plot also helped to define equiluminance. Figure 5(A) shows the distribution of equiluminance for twenty-seven estimates of eleven of our infants (excluding Patrick) over a range of ages and spatial frequencies (all $<1$ c/deg). The peak is clearly at colour-ratio 0.5, with very little scatter around this point (SD = 0.03). This result agrees with previous measures of equiluminance using different techniques (Maurer, Lewis, Cavanagh & Anstis, 1989), and would suggest that none of the infants in our sample (including 7 boys) had colour anomalies. Figure 5(B) shows the distribution of seventeen different estimates of isoluminance of one infant (Patrick), at different ages and spatial frequencies. The scatter in the estimates of this single observer is similar to the scatter in the population estimates.

*VEP contrast response curves*

After the second month, the VEP response to equiluminant patterns of low spatial frequencies improved rapidly. Figures 6 and 7 give some indication of how the response to both luminance and colour stimuli as a function of contrast develops with age. For all curves, the open squares refer to luminance and the solid squares to chromatic patterns.

Figure 6 shows luminance and colour contrast response curves at 0.2 c/deg for infant Patrick, at three successive ages. At 8.5 weeks, there was no clear response at equiluminance at any contrast, while luminance stimuli gave a strong response at all contrasts down to 10%. By 14 weeks, the situation had changed, showing a strong response to equiluminant stimuli over a range of contrasts, with the magnitude of the response increasing monotonically with contrast. The response range increased further by 18 weeks, while the range of contrasts to elicit responses from luminance stimuli increased relatively little over the same period.

Figure 7 shows results from another infant, Luca, all measured at the same age (11 weeks), at three different

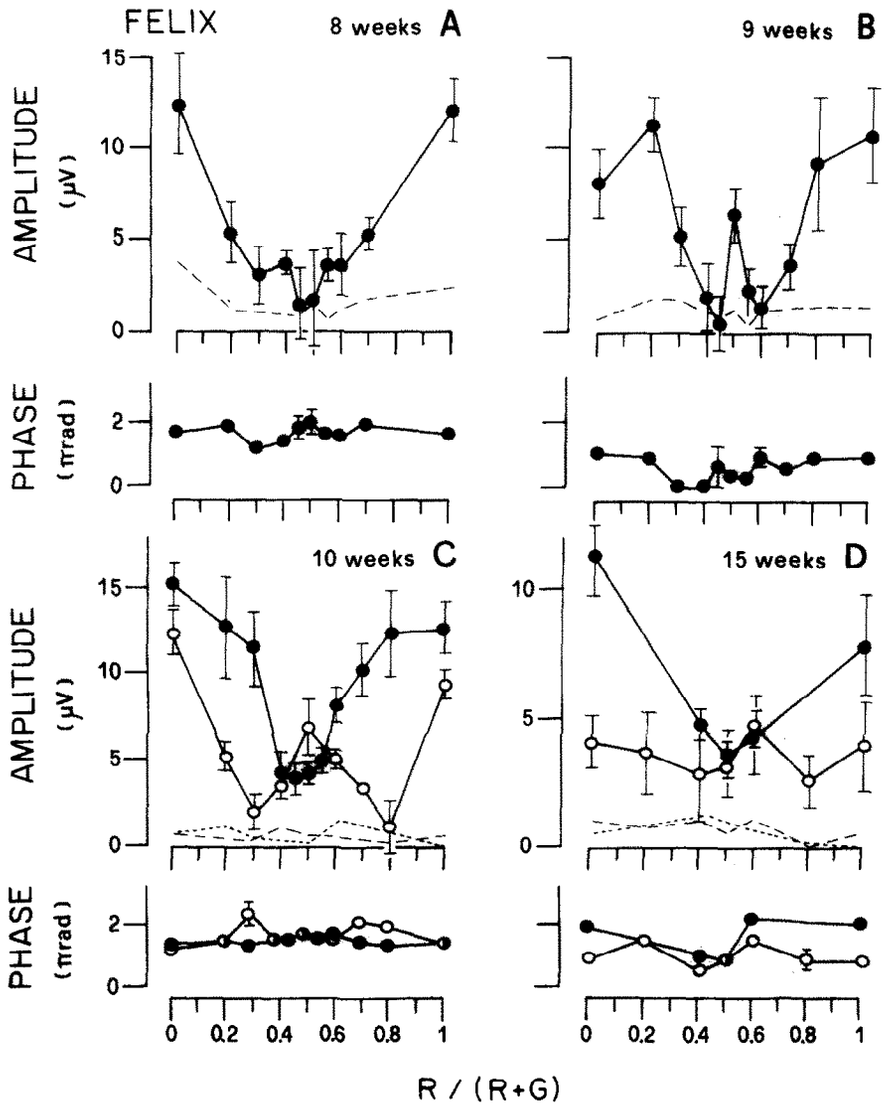



FIGURE 3. Amplitude and phase of VEPs as a function of colour-ratio, recorded from infant Felix at the age of 8 (A), 9 (B), 10 (C) and 15 (D) weeks. Each point is the mean of 200 sums in (A) and (C), and 140 in (B) and (D). The stimulus was 0.3 c/deg and 3 Hz: the solid circles refer to contrasts of 100%, and the open circles to contrasts of 50%.

spatial frequencies. At these relatively low spatial frequencies (0.1–1 c/deg), the range of luminance contrasts that evoke a response does not vary greatly, while the range of effective equiluminant contrasts is strongly dependent on spatial frequency. At 0.1 c/deg, the chromatic response is as strong as the luminance response at high contrasts, and remains similar at moderate contrasts. At higher spatial frequencies, however, the response to chromatic stimuli is greatly reduced at all contrasts, to disappear almost completely at 1 c/deg: there is a response at the very highest contrast, but as pursued later, this might result from chromatic aberrations.

Note that in all six data sets of Figs 6 and 7, response increased monotonically with contrast, except for a response saturation at 0.1 c/deg [Fig. 7(A)]. Furthermore, the relationship between amplitude and log-contrast could be well approximated by linear regression (up to the saturation point). Therefore, it was possible to estimate contrast sensitivity to both luminance and chromatic contrast by the extrapolation technique of Campbell and Maffei (1970). The curves (up to saturation) were fitted by linear regression (weighting each point by amplitude standard error and signal-to-noise ratio), and contrast threshold taken to be the intersection of the regression line with the abscissa. Note that in this study the extrapolation was linear, up to the saturation point, whereas in our previous study (Morrone *et al.*, 1990a), the extrapolation used a third order polynomial fit. However, both techniques yielded very similar results, suggesting that the exact nature of the fitting procedure is not crucial. The results of these extrapolations are summarized in a later section.

*Independent VEP generators for luminance and colour stimuli*

The absence of a reliable VEP at equiluminance in infants at high spatial frequencies, together with a systematic and symmetrical increase in amplitude as the colour-ratio moves from equiluminance, suggest that the response at all colour-ratios may be generated entirely by mechanisms sensitive to *luminance* contrast,

independent of *chromatic* contrast. That is to say, the response may be accounted for entirely by mechanisms which sum M and L cone output (ignoring for the present S cone and rod output), without the existence of any chromatic opponent mechanisms.

To test this idea more quantitatively, we compared VEP amplitudes recorded as a function of colour-ratio to those predicted by the response to luminance alone. To minimize data fluctuation, all measurements were recorded from the same infant in the same recording session. We first measured VEP amplitudes and phases for a stimulus of 0.4 c/deg as a function of colour-ratio. These results are illustrated by the open symbols of Fig. 8(A). We next measured the amplitude and phase response for luminance (red–black) patterns as a function of contrast, to produce the contrast response curves of Fig. 8(B). From these data we predicted what the amplitude and phase of the colour-ratio response should be if it were determined entirely by the luminance contrast of the stimulus. For each colour ratio, the value of *luminance contrast* was calculated by assuming that it varies linearly from 1.0 at colour-ratios 1.0 and 0, to zero at the equiluminant point. The data measured as a function of contrast [Fig. 8(B)] were then replotted as a function of colour-ratio [solid symbols in Fig. 8(A)], by calculating the colour-ratios that produce that particular luminance contrast. Each contrast value corresponds to two colour-ratios, symmetric about the equiluminance point.

Both the amplitudes and the phases predicted from the contrast response are very similar to those measured directly, at all colour contrasts. Both sets of amplitude data decrease steadily to zero as colour-ratios approach equiluminance, and in both cases the phases increase near equiluminance. This strongly reinforces the suggestion that the responses at this spatial frequency result entirely from mechanisms sensitive to luminance contrast.

The strength of the VEP response at equiluminance depends strongly on stimulus spatial frequency (Morrone *et al.*, 1990a; see also Fig. 7). Figure 8(C) shows measurements in the same infant at the same age, made at 0.1 c/deg. Here there is a significant response at equiluminance, and as the contrast response curve on the right shows [solid squares, Fig. 8(D)], the response could also be obtained at moderate contrasts. At the highest

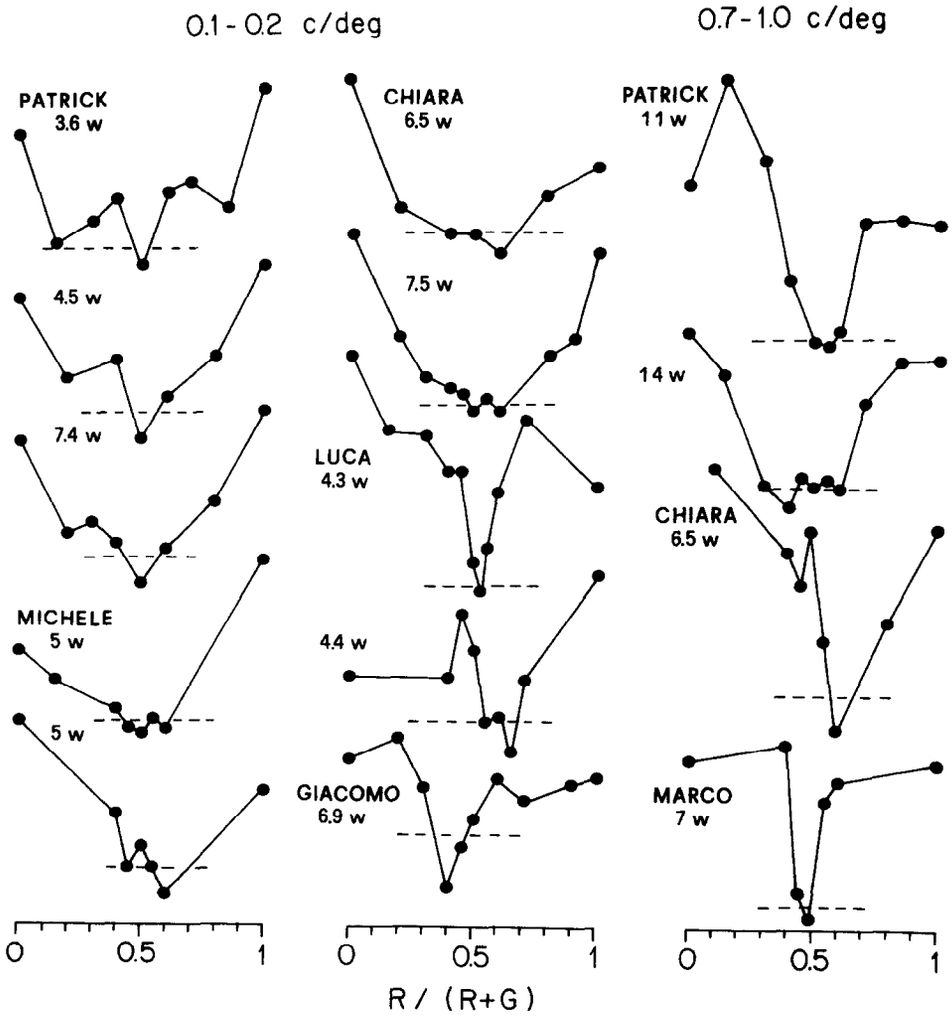



FIGURE 4. Further examples where there was no reliable response at equiluminance, at 0.1–0.2 c/deg (two left-hand columns) and 0.7–1.0 c/deg (right-hand column). The amplitudes have been scaled arbitrarily to accommodate all the curves on the figure. The dashed line shows the average asynchronous-noise for all colour-ratios in that session.

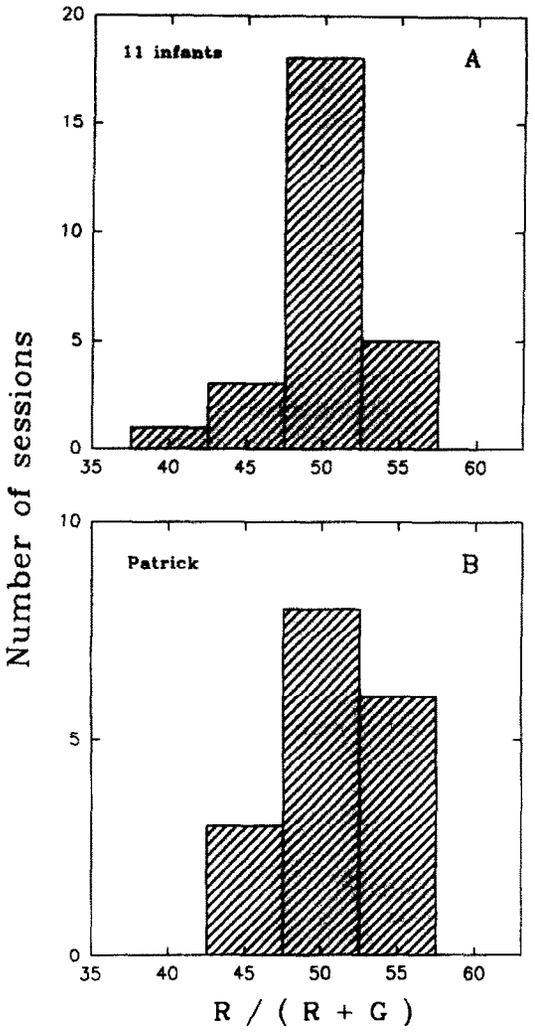



FIGURE 5. Distribution of colour-ratios producing equiluminance (defined as either a local minimum or maximum in the amplitude vs colour-ratio functions). (A) Shows 27 separate estimates from 11 of the infants (discounting Patrick), and (B) shows 17 separate measurements of equiluminance for Patrick. The estimates were made at various ages, temporal frequencies and spatial frequencies (all < 1 c/deg).

contrast, the colour and luminance responses were similar in amplitude and phase. At lower contrasts, however, the responses to equiluminant patterns drop to noise levels for colour contrast below 50%, while the responses to luminance contrast remain reliable down to contrasts of 15%.

At this spatial frequency, the colour-ratio response curves [open circles in Fig. 8(C)] clearly do not result solely from a luminance response, but must also reflect the action of mechanisms sensitive to chromatic contrast. Chromatic contrast is maximal at equiluminance, and decreases linearly to zero at colour-ratios 0 and 1. We assume that the VEP response to chromatic contrast is independent from that to luminance contrast, and the two separate responses will sum linearly. By a similar procedure to that outlined above, we predicted from the contrast response curves the amplitude and phase for each colour-ratio from the vector sum of luminance and chromatic response. The predictions from the vector-sums are depicted by the solid circles in Fig. 8(C), together with the experimental data (open symbols). Again the two sets of data follow each other reasonably well, both in amplitude and in phase, consistent with the simple hypothesis of linear summation of independently generated VEP signals.

In Fig. 3, two of the curves (at 9 and 10 weeks) did not vary monotonically with colour ratio, but showed secondary dips at either side of the equiluminance point. The open symbols of Fig. 9(A) illustrate another example of this type of result for infant Michele at 22 weeks. The contrast response curves measured during the same session are shown in Fig. 9(B). Following the procedure described above, the predicted amplitude and phase was calculated by vector summation of the purely luminance and chromatic responses of appropriate contrasts, and plotted as a function of colour-ratio (solid symbols) in Fig. 9(A). As before, the vector sums are very similar to the measured data, both in amplitude and in phase. In particular, they predict that amplitude should drop to near zero at ratios either side of the equiluminance point, as was observed in this and other examples. The reason for this is that at those points the luminance and chromatic response are roughly equal in amplitude, but opposite in phase, so they null each other.

*Development of contrast sensitivity for equiluminant patterns*

The section on contrast response showed how contrast sensitivity can be estimated by extrapolating contrast response curves to zero amplitude. Estimating contrast sensitivity at various spatial frequencies produces sensitivity functions for both luminance and chromatic patterns at various ages. Figure 10 shows an example of luminance and chromatic sensitivity functions for an adult. For comparison the psychophysical estimates of threshold (measured under the same conditions by method-of-adjustment) are shown by open squares. At all frequencies they are similar. It is therefore likely that the same technique used with infants will provide reasonable estimates of infant luminance and colour sensitivity.

Examples of infant contrast sensitivity curves are shown in Figs 11 and 12. The last point on each graph is an estimate of spatial acuity, determined separately by measuring VEPs to a high contrast stimulus of increasing spatial frequency, and extrapolating the amplitude curve to zero (Morrone *et al.*, 1990a). The curves show that the contrast sensitivity curves for equiluminant stimuli improve rapidly with age, both in absolute sensitivity and in resolution. The sensitivity curves for luminance stimuli also improve with age, but to a lesser extent.

Movshon and Kiorpes (1988) suggest that at all ages, contrast sensitivity curves can be well fit by the same function (sum of exponentials) that simply scales both in sensitivity and in resolution (see also Wilson, 1988). On double logarithmic coordinates, multiplicative scaling implies a simple translation. Our data for both luminance and chromatic sensitivity are consistent with this idea, but the degree to which the function must scale is different for luminance and chromatic sensitivity.

Figure 13 makes this point more clearly. The sensitivity data of Patrick (taken from Fig. 11) have been replotted with rigid translations along both axes to minimize the variability of the luminance data (shift factors given in caption). With this rescaling of both resolution and sensitivity, the data of all ages tend to follow a common curve (as Movshon and Kiorpes observed with monkeys). However, if the chromatic functions are scaled by the same amount, the data do not overlap. There is a clear and consistent tendency for the data of the earlier measurements to be less sensitive and have lower resolution than that predicted by the rigid shift, reinforcing the suggestion that colour vision develops later than luminance vision. This tendency can also be seen with the data of Luca (which the reader can verify by photocopying Fig. 12 onto a transparency and attempting various rigid translations) and other contrast sensitivity functions for Michele and Felix. However, as Movshon and Kiorpes (1988) observed, the amount scaling required varies from infant to infant. The chromatic sensitivities of infants could also be described by a single function which scales both in sensitivity and resolution (again verifiable with transparent photocopies of Figs 11 and 12), but the function must be rescaled by a greater amount over this age range, particularly in resolution.

The age-related improvement in chromatic contrast sensitivity for 4 infants is summarized in Fig. 14, which shows how sensitivity to equiluminant patterns of various spatial frequencies increases with age. At low spatial frequencies (0.1 c/deg), contrast sensitivity for red–green equiluminant patterns is nearly adult-like in infants by 15–20 weeks. However, at this age, where sensitivity to 0.1 c/deg will mature no further, there is virtually no response from chromatic stimuli of 1.5 c/deg. The curves at all spatial frequencies seem to have similar form, simply shifted along the age abscissa and in absolute sensitivity. That is to say, after a response at a certain spatial frequency first appears (at maximal contrast), sensitivity has asymptoted to near adult levels $<10$ weeks later.

One of the most obvious results revealed by the contrast sensitivity functions of Figs 11–13 is that the difference between chromatic and luminance sensitivity (on a logarithmic scale) is greater at high than low spatial frequencies. At all ages, luminance sensitivity exceeds chromatic sensitivity by a factor of two or three at the lower spatial frequencies, but is about ten times higher at the highest measurable spatial frequency.

This fact is pursued further in Fig. 15. The data points show for various infants at various ages the ratio of luminance to chromatic sensitivity at the highest spatial

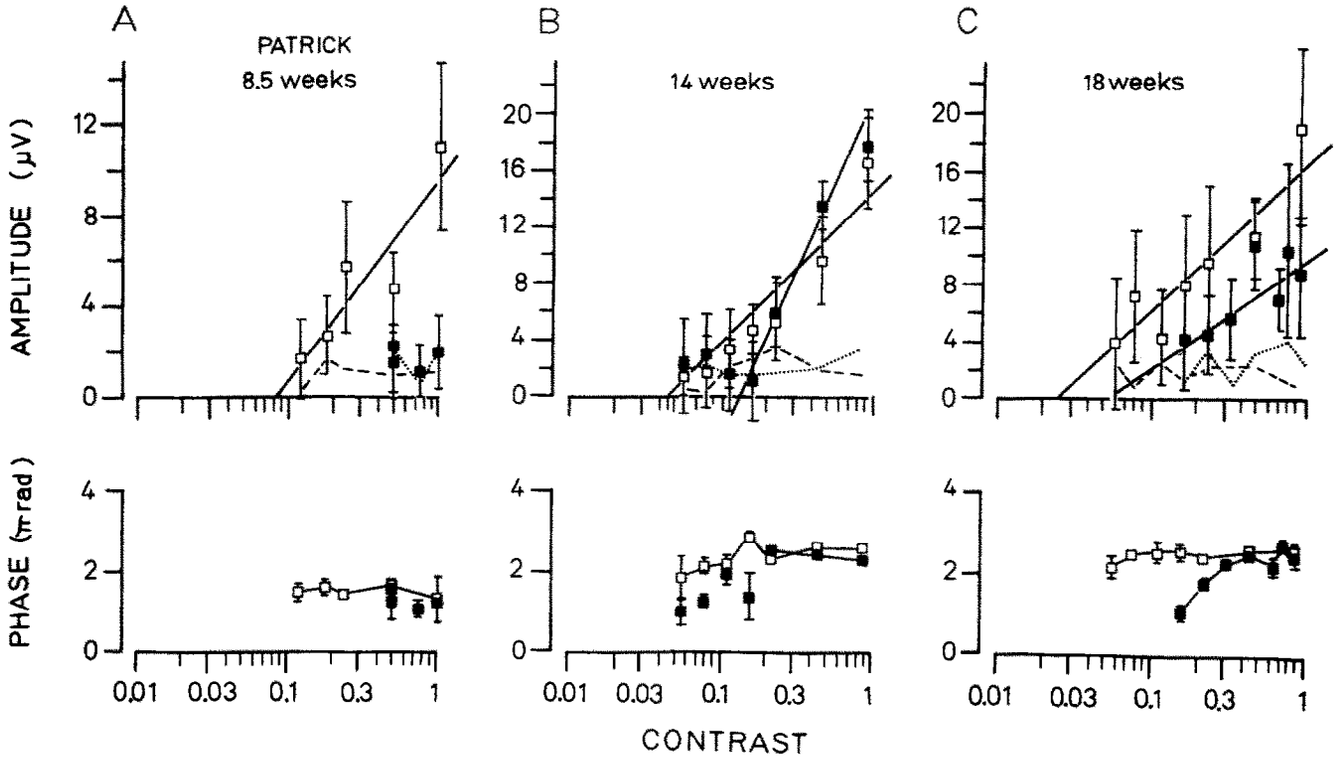



FIGURE 6. Amplitudes and phases of VEPs as a function of contrast for infant Patrick at the age of 8.5 (A), 14 (B), and 18 (C) weeks, for a stimulus of 0.2 c/deg, 3 Hz. Open squares indicate luminance patterns [colour-ratio 1.0 for (A) and 0 for (B) and (C)], and solid squares red–green patterns (colour-ratio 0.5). Each point has between 140 and 280 sums, with vertical bars indicating standard errors, derived from the variation of the partial-sum packets (see Fig. 2). The lines are best fit linear regressions, weighting each point for standard error. Noise amplitudes are indicated by dashed and dotted lines for luminance and chromatic stimuli (respectively). Phase data corresponding to amplitudes larger than noise have been connected by solid lines.

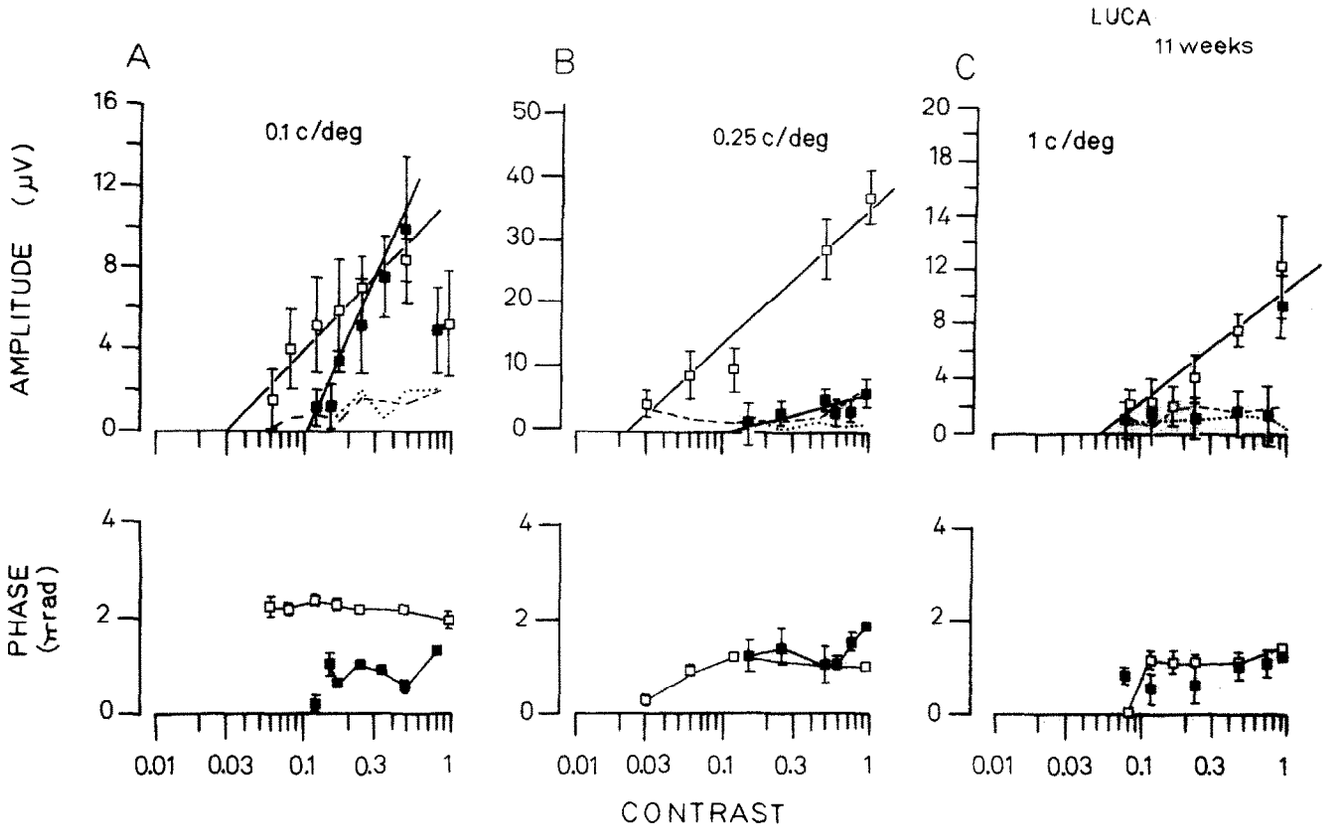



FIGURE 7. Amplitudes and phases of VEPs as a function of contrast for infant Luca, 11 weeks old, for three stimulus spatial frequencies, all measured at 3 Hz: 0.1 (A), 0.25 (B), and 1.0 (C) c/deg. Open squares: green–black pattern (colour-ratio 0), solid squares: red–green pattern (colour-ratio 0.5). Other conventions as for Fig. 6.

frequency at which this comparison could be made. In practise, the highest spatial frequency was the chromatic spatial acuity, and as chromatic sensitivity at this point is 1 (by definition), the ratio reduces to the luminance sensitivity at this point. The points are plotted as a function of chromatic acuity (irrespective of age, which is given in the caption). All points clearly fall near a value of 10, with no systematic tendency for increase or decrease the mean of the regression line $10.5 \pm 0.8$, with slope of $-0.02 \pm 0.04$. The possible significance of this consistency will be discussed later.

*Chromatic aberrations*

In studying colour vision, one is always concerned about chromatic aberrations, which may create spurious luminance contrast, giving an artefactual response where there is in fact none. With adult measurements, special procedures are taken to minimize aberrations, particularly at high spatial frequencies. Typically, monochromatic patterns are displayed on separate monitors (Mullen, 1985), allowing each to be independently magnified to compensate for chromatic differences of magnification, and viewing one of them through a lens of suitable negative or positive power corrects for differences in focus (longitudinal chromatic aberration). However, these procedures require control of head position, and do not lend themselves to infant research. We relied largely on the fact that aberrations are small at low spatial frequencies (Flitcroft, 1989), where most of our measurements were made. We felt it necessary, however, to check how far chromatic aberrations could affect chromatic VEPs in our conditions.

Figures 16(A) and (B) show how chromatic aberrations may influence the infant VEPs. VEPs were recorded as a function of colour-ratio at two spatial frequencies, 0.1 and 2 c/deg. At the 0.1 c/deg, recordings were made at two contrasts, 20 and 80%. There the higher contrast produced a local amplitude maximum at colour-ratio 0.5, and the lower contrast a local minimum at the same point. At both contrasts, the phase plot was symmetrical around this point, presumably equiluminant. At 2 c/deg, however, the amplitude curve was highly asymmetrical, with the minimum displaced to 0.65, well towards the red end of the colour mix. The symmetrical point in the phase data is similarly displaced. A simple explanation for this effect is that the green pattern was better focused than the red, and hence its effective contrast was higher. This effect was observed in four different infants.

In some cases we observed a reliable response at high spatial frequencies for all colour-ratios, when the spatial frequency was clearly beyond the chromatic resolution limit at that age (as there was zero response at moderate spatial frequencies). The response at all ratios may result from fluctuations in accommodation during the session, sometimes favouring one colour and sometimes the other, so there is never a truly equiluminant point. Alternatively, in this condition, the chromatic difference

in magnification may add its own luminance artifacts to the spurious luminance contrast.

Figure 17 illustrates how chromatic aberrations of this and other types may lead to an erroneous estimate of chromatic resolution. The amplitudes of the responses to the red–green patterns are indicated by the open circles. All measurements were made at colour-ratio 0.5, the equiluminant point for a very low spatial frequency (0.1 c/deg). While at this frequency there was a reliable response, at somewhat higher spatial frequencies the amplitude dropped to noise levels, indicating an acuity around 0.3 c/deg. However, at still higher spatial frequencies, there was a rebound, peaking at 1 c/deg and continuing until 4 c/deg. The solid symbols show the response to luminance patterns, measured in the same session. The fact that the high spatial frequency limb in the colour response parallels the trend of the luminance response suggests that the secondary peak is a luminance artifact. And the curves of Fig. 16 suggest that longitudinal aberrations may be a principal cause of the luminance artifact. When using high spatial frequencies, it is therefore fundamental to be certain of equiluminance by sampling colour-ratios very finely: but even then one can never be certain that magnification aberrations do not cause a luminance artifact.

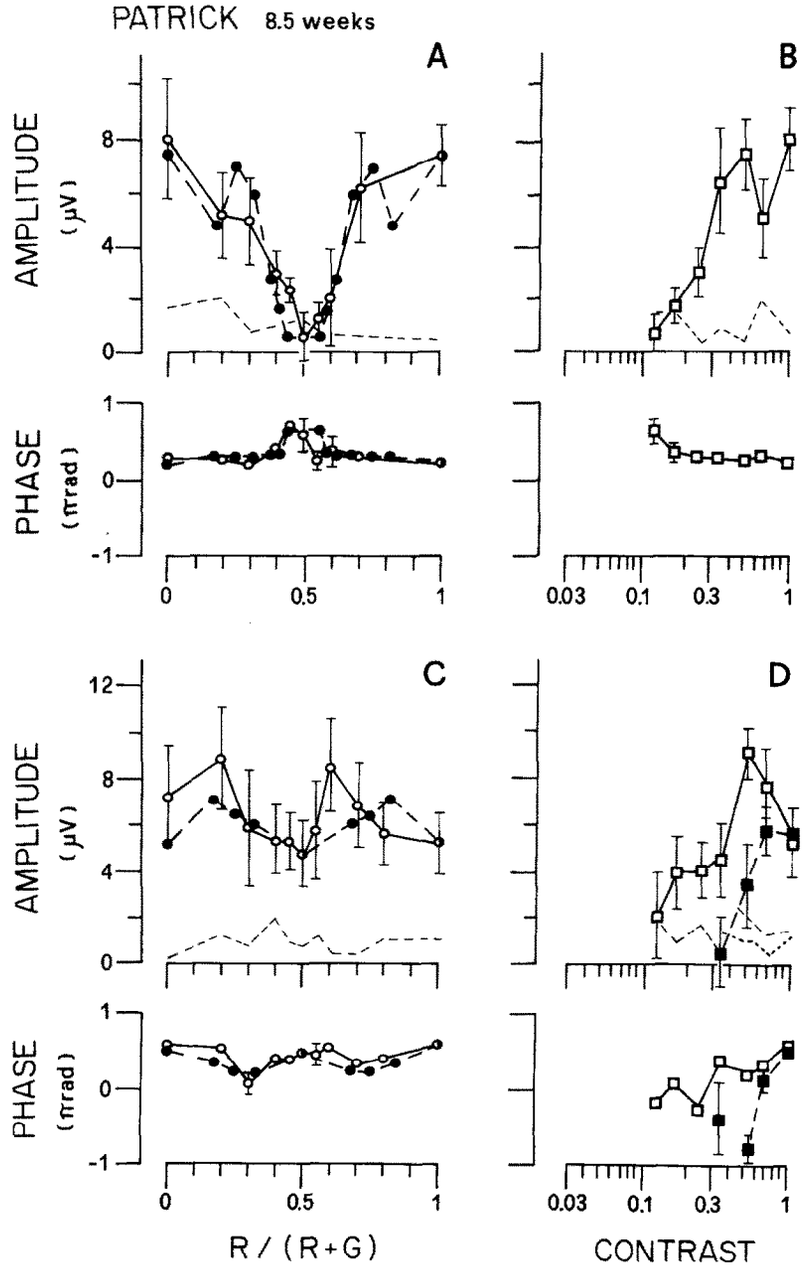



FIGURE 8. (A) and (C) Amplitude and phase of VEPs recorded from infant Patrick at 8.5 weeks of age, as a function of colour-ratio (open circles). The stimulus was 0.4 c/deg [(A) and (B)] or 0.1 c/deg [(C) and (D)], 3 Hz and 100% contrast. In (B) and (D), the amplitude and phase of VEPs are plotted against contrast for a plaid pattern of colour-ratio 1 (red–black, open squares) or 0.5 (red–green, solid squares). Noise amplitudes are indicated by the broken lines, except for those relative to the red–green pattern in (D), indicated by a dotted line. The solid circles in (A) and (C) are amplitudes and phases predicted from the data reported in (B) and (D), respectively, as explained in the text.

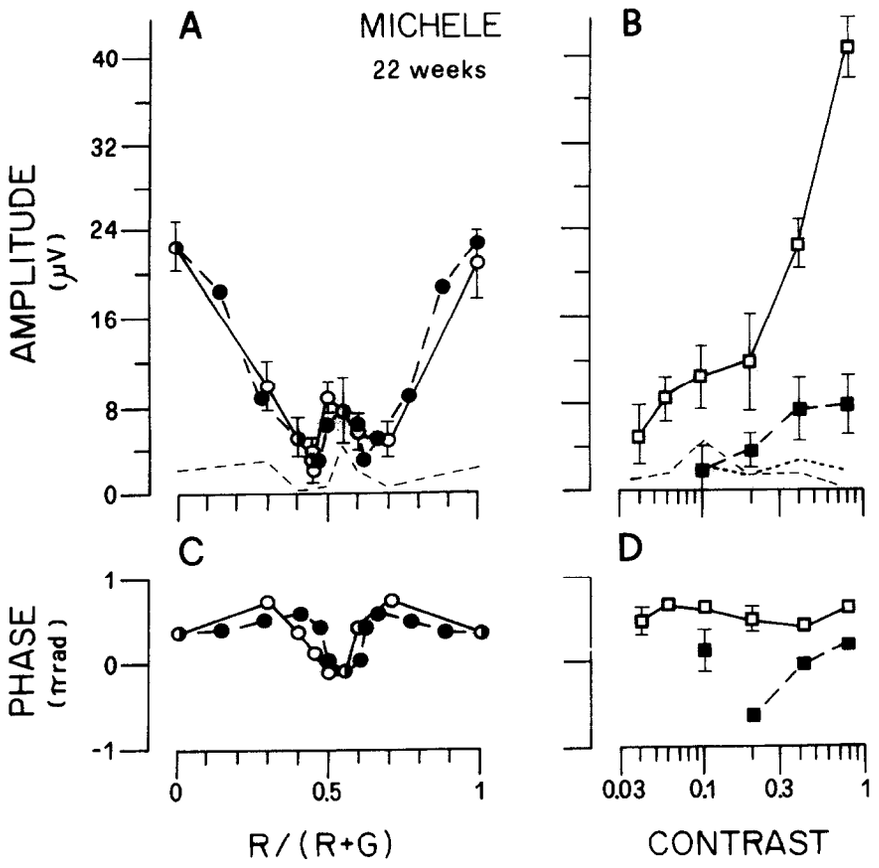



FIGURE 9. Same conventions as Fig. 8, for infant Michele at 22 weeks. The stimulus was 1 c/deg, 5 Hz and for the measurements as a function of colour-ratio, 40% contrast. Equiluminance was evaluated as $r = 0.55$, and this value was considered to give maximal chromatic contrast and zero luminance contrast. Where there were no corresponding measurements of luminance and chromatic response of exactly appropriate contrast, we interpolated linearly between adjacent points.

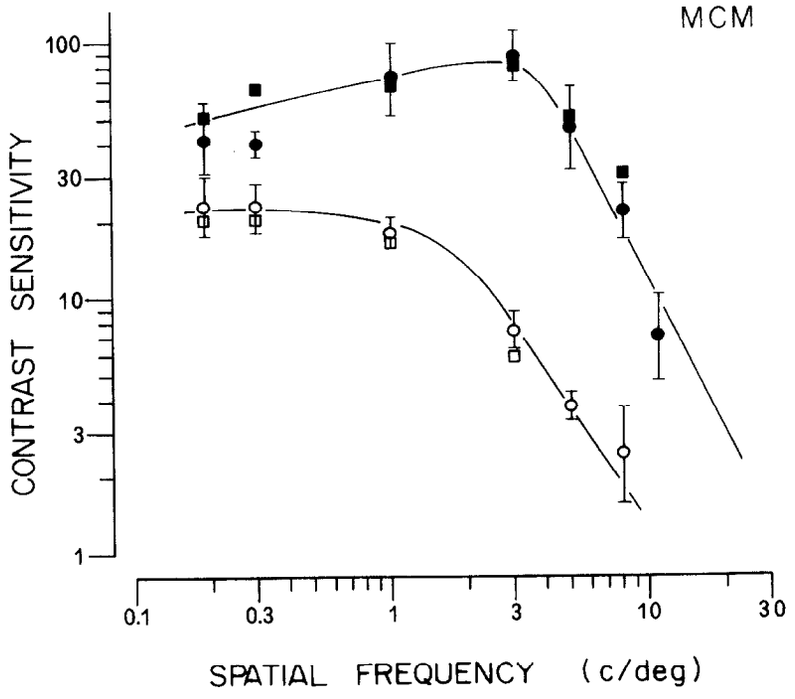



FIGURE 10. Contrast sensitivities as a function of spatial frequency for an adult subject (MCM). The circles indicate estimates from extrapolating VEP contrast response curves, and squares thresholds from direct psychophysical measurement, using standard method-of-adjustment techniques. The solid symbols refer to red–black luminance patterns (colour-ratio 1.0), and open symbols to red–green equiluminant patterns (colour-ratio 0.52). The temporal frequency was 5 Hz in all cases.

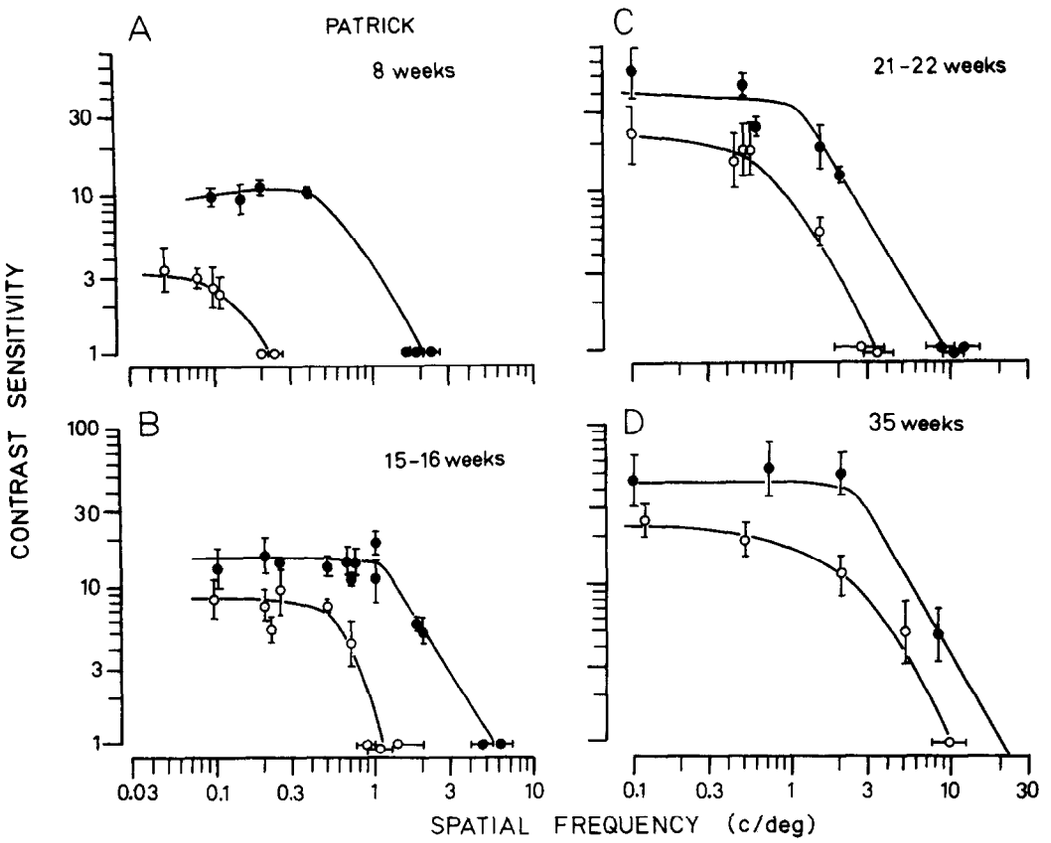



FIGURE 11. Contrast sensitivity estimated from VEPs, as a function of spatial frequency for infant Patrick at ages of 8 (A), 15–16 (B), 21-22 (C) and 35 (D) weeks. Solid circles refer to luminance patterns, and open circles to red–green patterns at equiluminance (colour-ratio between 0.45 and 0.5). The temporal frequency was 3 Hz for (A) and (B) and 5 Hz for (C) and (D). Vertical bars (for contrast sensitivity data) and horizontal bars (for acuity data) indicate standard error.

In some infants, we never observed the types of effects shown in Figs 16 and 17. For example with Patrick, the infant most tested in this study, there were never signs of spurious responses at high spatial frequencies. On the other hand, those infants who showed evidence of aberrations (such as Luca) did so consistently. We have no firm explanation of why this should occur, but suggest that some infants may have more refractive error and/or variable accommodation than others.

## DISCUSSION

The present findings confirm our previous report in suggesting that chromatic contrast sensitivity develops after luminance contrast sensitivity. In infants younger than 7–8 weeks, no significant VEP responses could be elicited by contrast reversal of equiluminant red–green tartan patterns, despite the fact that we used stimuli of very low temporal and spatial frequency, to favour the VEP response of chromatic mechanisms (Fiorentini *et al.*, 1991). This probably indicates that signals from different cone types do not combine to generate a chromatically selective mechanism. With these young infants, not only was there no response at equiluminance, but the entire colour-ratio curve could be predicted quantitatively from the VEP response to the luminance component of the stimulus (Fig. 8), strongly suggesting that only luminance responses exist.

Chromatic sensitivity for stimuli of low spatial frequency (below 0.5 c/deg) reaches maturity within 12–15 weeks from birth, but at higher spatial frequencies, full maturity is not reached until at least 20–25 weeks of age. This finding is consistent with behavioural experiments showing that colour discrimination in newborns and 1-month-olds is absent or very weak (and limited to very large stimuli) if luminance difference cues are carefully eliminated (Packer *et al.*, 1984; Clavadetscher *et al.*, 1988; Adams, Maurer & Davis, 1986; Adams, Maurer & Cashin, 1990; for review see Teller & Bornstein, 1987 and Brown, 1990).

### *Infant equiluminance*

The colour-ratio (ratio of red-to-total luminance) at which the VEP of young infants vanishes was $0.5 \pm 0.03$, very similar to the equiluminance point of adults tested psychophysically (for minimum flicker) and with VEPs with the same apparatus. This would imply that even though there is no VEP response to chromatic stimuli at 7 weeks, the relative contribution of long and medium wavelength cones to the generation of luminance VEP responses is similar at that age to adults (see Regan & Spekreijse, 1974). This reinforces the finding by Maurer *et al.*, 1989) that the equiluminance point evaluated behaviourally by the minimum apparent motion technique of Anstis and Cavanagh (1983) is the same for colour-normal adults as for 1–3 months-old infants. Our

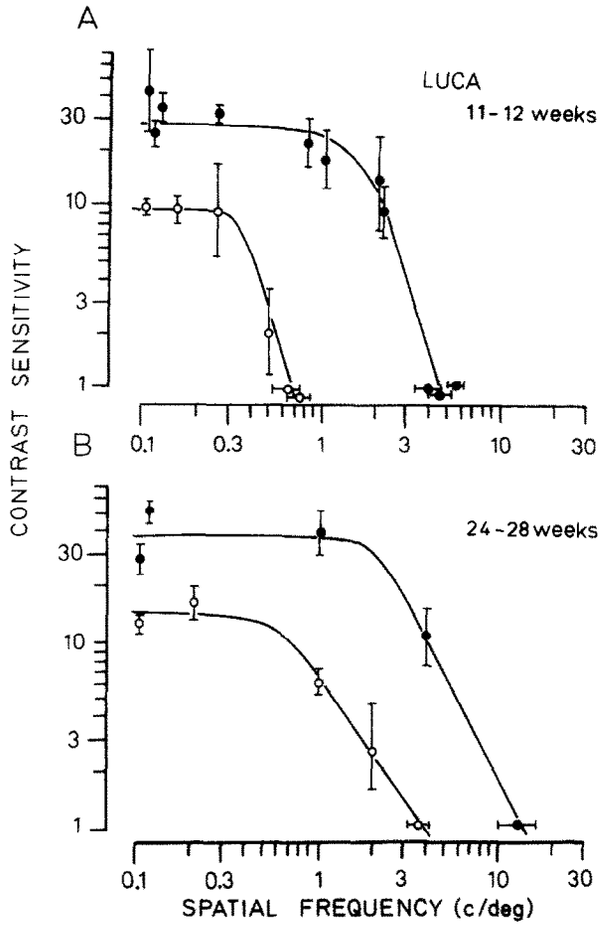



FIGURE 12. VEP contrast sensitivity for infant Luca at 11–12 (A) and 24–28 (B) weeks. Solid circles refer to luminance patterns, and open circles to red–green patterns (colour-ratio between 0.5 and 0.6). The temporal frequency was 5 Hz.

findings add further evidence in favour of the equivalence of the spectral luminous efficiency of adults and newborns for photopic stimuli.

For adults, a small shift of the equiluminance value (from 55 to 50% colour-ratio) has been reported for psychophysical contrast sensitivity at spatial frequencies from 0.1 to 2 c/deg (Mullen, 1985). The infant equiluminance point seems to vary by a similar amount, with no large changes either with age or with spatial frequency over the lower range (0.1–1.0 c/deg). At high spatial frequencies, however, we observed an appreciable shift in the equiluminant point, probably due to chromatic aberration combined with inaccurate or variable accommodation, discussed further in a later section.

*Contrast sensitivity*

In adults, the amplitudes of the equiluminant VEP vary linearly with log contrast (Regan, 1973; Fiorentini *et al.*, 1991), and are therefore well fit by linear regression. In all infants older than 7–8 weeks, reliable responses were recorded to equiluminant patterns, and these curves were also well fit by linear regression on log contrast. At all ages, however, the slopes of the contrast response tended to be steeper for chromatic than for luminance contrast. This was a very general feature of the results (more general than the curves of Figs 6 and 7 suggest), suggesting that the gain of the colour response (as reflected by VEP amplitude) is higher than that of the luminance response, and that these two responses are recorded independently in the VEP response.

The contrast sensitivity functions for both chromatic and luminance patterns change with age, but the two functions do not change at the same rate. For spatial frequencies below 0.5 c/deg, the chromatic contrast sensitivity is about one-third luminance sensitivity by 12–15 weeks, and this ratio is maintained thereafter. However, at higher spatial frequencies, chromatic sensitivity takes much longer to stabilize at this ratio, pointing to clear differences in the rate of luminance and chromatic mechanisms. This is clearly brought out in Fig. 15, which shows that the luminance-to-chromatic sensitivity ratio at the limit of chromatic resolution was always about 10, irrespective of infant age or the spatial frequency of chromatic resolution. At lower spatial frequencies (relative to the chromatic acuity), this ratio was always around 3–4, in both infants and adults. Clearly, the chromatic sensitivity functions cannot be derived from luminance functions merely by scaling for sensitivity.

If one were to scale both sensitivity and resolution (both vertical and horizontal translation on logarithmic plots), the chromatic functions could probably be made to approximate luminance functions reasonably well. However, the amount of scaling necessary to achieve this varies substantially with age. Figure 13 shows that scaling the luminance data in both sensitivity and resolution can cause all the luminance points to fall along a common curve (as shown by Movshon & Kiorpes, 1988). However, the scaling required to align the luminance data does not align the chromatic data, especially at the youngest ages.

Interestingly, however, after a response to a particular spatial frequency appears, sensitivity to that frequency matures almost completely within about 10 weeks (Fig. 14). To compare these results with the development of luminance contrast sensitivity, the reader is referred to Fig. 8 of Norcia, Tyler and Hamer (1990), and advised to rescale absolute sensitivities by a factor of about 7 (0.85 log-units). The rescaling is required to take account of the factor-of-two difference in oriented contrast between tartans and sinusoids [see equation (1)], and a further factor of 3.5 for the square-root of the difference in mean luminance between the two situations (200 compared with 16 cd/m$^2$), assuming that sensitivities approximate a square-root law (Rose, 1948; Barlow, 1964). After this transformation, the absolute sensitivities of Norcia *et al.* (made under similar conditions of spatial and temporal frequency and age) agree reasonably well with those of our own for luminance contrast. If one accepts this form of comparison, then the development of chromatic sensitivity at all spatial frequencies is most like that of the development of luminance contrast sensitivity at about 2 c/deg. This is interesting, as the contrast sensitivity to luminance stimuli of high spatial frequencies, and to chromatic stimuli of all spatial frequencies, are probably mediated by the same class of neural substrate, the parvo-cellular stream

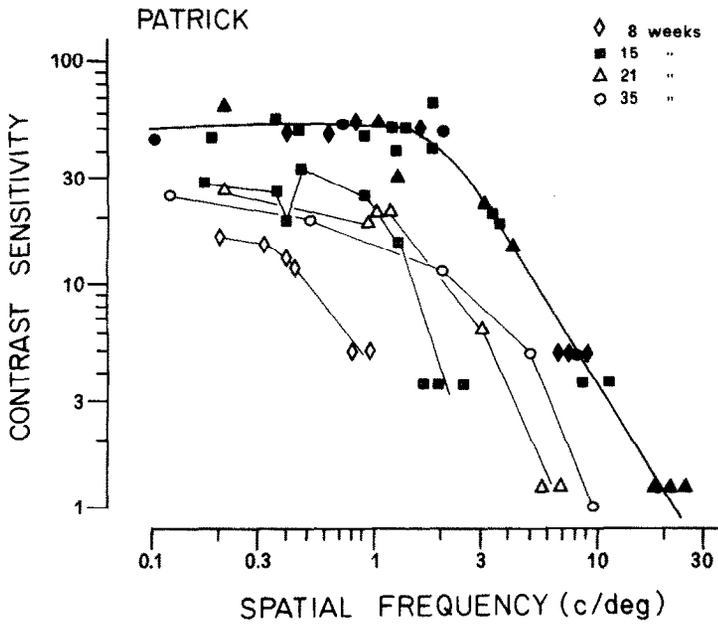



FIGURE 13. Contrast sensitivity for infant Patrick (taken from Fig. 11), where the data from the earlier sessions have been rescaled in both sensitivity and resolution to cause the luminance sensitivities (solid symbols) to fall as near as possible to those measured at 35 weeks. The scaling factors (in log-units) for sensitivity and resolution (respectively) were: 0.7, 0.6 at 8 weeks; 0.55, 0.3 at 15 weeks; 0.1, 0.3 at 21 weeks; and 0, 0 at 35 weeks. Note that while this rescaling aligns the luminance sensitivities along a common curve, the chromatic sensitivities measured at different ages remain quite distinct.

(Merigan & Maunsell, 1990; Merigan, Katz & Maunsell, 1991).

*Chromatic aberrations*

Chromatic aberrations are the bug-bear of all colour studies, as they produce spurious luminance contrast which may produce a stronger response than that to the chromatic content of the stimulus. Because of the longitudinal chromatic aberrations resulting in different foci for different wavelengths, the red patterns of this study would require to an adult eye at least 0.5 D more accommodation than do the green patterns (Le Grand, 1956). There are as yet no measurements of chromatic aberration in the infant eye, but as the axial length is considerably shorter (about two-thirds of adult at 6 months: Larsen, 1971) one would expect the aberrations to be commensurably greater (Hughes, 1979). With sinusoidal gratings, defocus leads to reduced contrast, and this effect depends on spatial frequency. In an ideal optical system defocus produces the greatest loss of contrast at a frequency one half the maximal frequency transmitted (Campbell & Gubisch, 1966). The longitudinal chromatic aberration (with or without the additional effects of inaccurate or variable accommodation), would

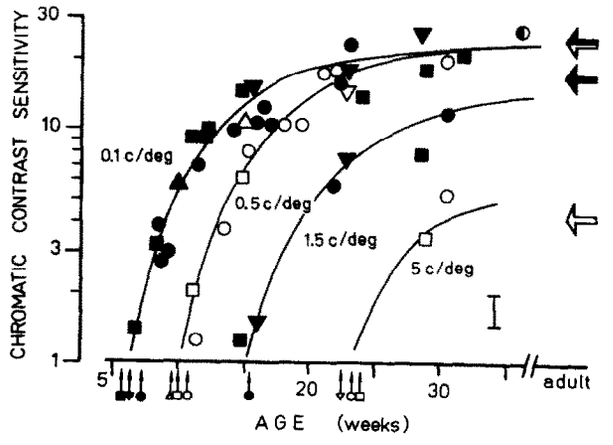



FIGURE 14. Development of contrast sensitivity for red–green patterns of four different spatial frequencies. The different symbols refer to longitudinal measurements of different infants, and adult values are indicated by the arrows on the right. The arrows below the abscissa indicate, for each spatial frequency, the last recording session at which no response could be elicited by chromatic stimuli at 100% contrast. The vertical bar is the average standard error of the experimental points. The symbols refer to different infants: circles, Patrick; squares, Luca; upright triangles, Felix; inverted triangles, Michele.

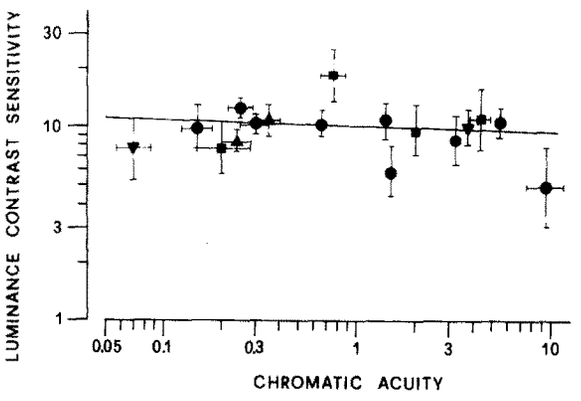



FIGURE 15. Luminance contrast sensitivity at the resolution limit for chromatic response, as a function of the chromatic resolution limit. The vertical and horizontal error bars indicate the standard errors in the two estimations, and the continuous line the linear regression (weighting for standard error). The different symbols refer to different infants: circles Patrick, measured at 7.4, 8, 8.5, 11, 14, 15, 21, 23 and 35 weeks; squares, Luca, 6, 11, 14 and 29 weeks; upright triangles, Felix, 8.5 and 9.2 weeks; inverted triangles, Michele, 6 and 22.5 weeks.

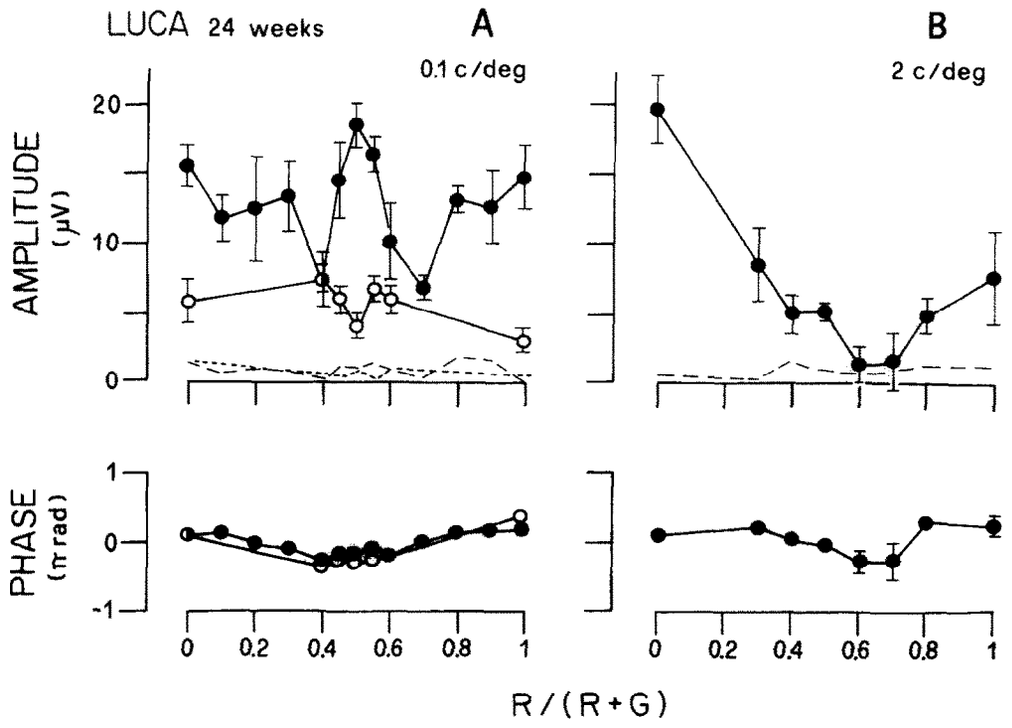



FIGURE 16. Amplitude and phase of VEPs as a function of colour-ratio for infant Luca, 24 weeks of age, at two spatial frequencies, 0.1 c/deg (A) and 2 c/deg (B). Contrast was 80% for the solid circles, and 20% for the open circles, and temporal frequency 5 Hz. Each point is the mean of 200 sums, with vertical bars indicating standard error, and broken lines indicating noise amplitudes.

affect differently the contrast of the red and green components of the tartan pattern, because of their different degrees of defocus. Since the differential effects vary with spatial frequency, the colour-ratio corresponding to equiluminance may also change with spatial frequency. In addition, the chromatic difference of magnification may cause spurious resolutions of red–green patterns, because of size differences between the red and green components [although the transverse chromatic aberrations are probably small in the infant eye, as they are very small in the adult (Ogboso & Bedell, 1987; Thibos, 1987; Simonet & Campbell, 1990)].

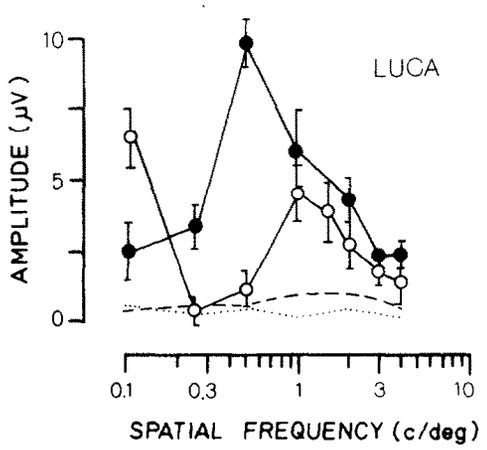



FIGURE 17. VEP amplitudes as a function of spatial frequency for infant Luca, 11 weeks of age. Stimulus contrast was 95%, and temporal frequency 4.3 Hz. Solid circles refer to red–black patterns (colour-ratio 0), and open circles to red–green pattern (colour-ratio 0.5). Each point is the mean of 160 sums. Noise amplitudes corresponding to the red–black and red–green stimulus conditions, are indicated by dashed and dotted lines (respectively).

Figure 16 of our study shows a clear example of how chromatic aberrations may influence VEP results. At low spatial frequencies, equiluminance was demonstrated at colour-ratio 0.5 (the mean for all infants measured), while measurements at 2 c/deg showed a strong dip around colour ratios of 0.65. It is difficult to account for this large change in equiluminance, without suspecting chromatic aberrations. If the infant focus favoured the green stimuli, then more red would have to be added to the mixture to compensate for the attenuation of red by longitudinal aberrations.

In this situation, it would seem that the infant was constantly (or at least on average) under-accommodated, to favour the green stimulus. However, it is also possible that the accommodation fluctuates during a recording session, sometimes favouring red, sometimes green. In this case there will be an aberrant response at all colour-ratios (which will not cancel on vector summation, as it is the second-harmonic being measured), so no null point could be revealed. Figure 17 gives an idea of how this could lead to quite erroneous estimations of chromatic sensitivities.

It should be pointed out, however, that the sort of aberrations shown in Figs 16 and 17 were seen only in some infants, possibly those with the refractive or accommodation errors. For example, we never observed this type of spurious resolution in Patrick, the infant most tested in this study. However, we must accept that the measurements at the higher spatial frequencies may be subject to aberrations, and should therefore be

considered as upper limits of estimates of chromatic resolution. But when no response is recorded, one can be certain that there were no chromatic mechanisms operating.

*Chromatic contrast*

As Allen, Banks, Norcia and Shannon (1993) point out, one would expect sensitivity to chromatic stimuli to be less than that to luminance stimuli, simply on physical grounds. As the cone spectral sensitivities are broad and largely overlapping, stimuli modulated only in chromaticity do not cause complete modulation of the photoreceptors, and therefore produce lower "*cone contrast*". At equiluminance, our stimuli (of 100% contrast) modulate the long wavelength (L) cones by 11%, and the medium wavelength (M) cones by 35%. Sensitivity at equiluminance should therefore be reduced by an amount somewhere between these extremes. The model embraced by Allen *et al.* (from Geisler, 1989) assumes signals to be combined in a way to yield cone contrasts of 20% at equiluminance. However, if this were the only factor limiting chromatic sensitivity, the ratio of luminance to chromatic sensitivity should always be a factor-of-five, and this factor should remain constant with age. Unfortunately, this prediction is supported neither by our previous note (which showed small but significant reduction of this ratio with age) nor by this more complete study.

The clearest evidence against the so-called "ideal observer" theory of development (Banks & Bennett, 1988), are the contrast sensitivity functions (Figs 10–13). Although the luminance functions at all ages could be rescaled in sensitivity and in resolution to fall along a common curve, the same rescaling did not align the chromatic functions. Clearly, reduced cone contrast is not the only limit to infant colour vision.

It is perhaps not surprising that the functions for luminance and colour vision should develop at different rates. It is generally agreed that whereas both magno and parvo streams contribute to luminance sensitivity, chromatic sensitivity is determined primarily by the parvo system (e.g. Merigan & Maunsell, 1990; Merigan *et al.*, 1991). It is not unreasonable to suspect that these two distinct cell classes develop at different rates, and that the differential development will cause independent development of luminance and colour contrast sensitivity.

Although development is not determined by cone contrast in a straightforward way, cone contrast may play a very interesting role. Figure 15 reveals a very curious fact: that at all ages, as a particular spatial frequency becomes resolvable at equiluminance, the contrast threshold is always ten times that of the luminance threshold. These data (which were not collected specifically for this purpose) are remarkably consistent for infant research, with the flat regression line passing through almost all the error bars. What is the significance of this result? It is possible that chromatically opponent units may not develop automatically, but may require reliable cone-signals from chromatic patterns (as most Hebbian-like development models would predict). Interestingly, the maximum of 11% contrast available in the L cones from a chromatic input is very similar to the chromatic luminance sensitivity always observed as a new spatial frequency becomes resolvable chromatically. This may be only a coincidence, but the possibility that the activation of chromatically opponent unit requires *both* cone inputs is appealing, and may merit further investigation.

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