



Development of the Temporal Properties of Visual Evoked Potentials to Luminance and Colour Contrast in Infants

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We have studied the development of the temporal characteristics of the pattern visual evoked potentials (P-VEPs) in response to contrast reversal of patterns of low spatial frequency (0.1 c/deg) of either pure luminance contrast (yellow–black plaid patterns) or pure colour contrast (equiluminant red–green plaid patterns) in 15 infants between 6 and 30 weeks of age. High contrast patterns were modulated temporally either sinusoidally at various temporal frequencies to elicit steady-state responses, or abruptly at a low temporal frequency to elicit transient responses. Analysis of both the transient and steady-state responses suggests the existence of three different mechanisms contributing to the infant and adult P-VEP responses at low, medium and high temporal frequencies. The responses at the three different temporal frequency ranges have different time constants, and develop at different rates. The low frequency response predominates at 8 weeks, where it spans the range 1–6 Hz with an apparent latency of about 230 msec, for both colour and luminance stimulation. This response increases in bandwidth and decreases in latency progressively with age, at a similar rate for luminance and colour contrast, up to 14 weeks.

After 14 weeks, the luminance response undergoes major changes, with the emergence of a new response with a shorter latency (about 100 msec) and a peak activity near 10 Hz. This mid-frequency response matures further with age, until it dominates the whole response of the adult P-VEP to luminance contrast. It also makes a contribution to the chromatic response at frequencies above 10 Hz, generating the characteristic double-peaked amplitude response in adults. However, its contribution is very limited below 10 Hz, where the response latency is 140 msec in adults, as it was at 14 weeks of age.

A third component is evident at very high temporal frequencies of the luminance response as early as 6 weeks, extending up to 15 Hz in 8-week-olds and up to 25 Hz for older infants. It remains apparent up to 18 weeks, thereafter being swamped by the major mid-frequency response. The apparent latency of response over this frequency range is about 70 msec at all ages.

The development of transient P-VEPs paralleled that of the steady-state P-VEPs. At all ages there was an early negative component (N70) at about 70 msec, corresponding to the fast steady-state response at high frequencies for luminance contrast. Before 14 weeks, the luminance and chromatic transient response had the same morphology, with a single major peak of similar latency to the apparent latency of the low temporal frequency response. After this age, the morphology of the luminance response changed, particularly in the first 100 msec, consistent with the emergence of the mid-frequency response. We discuss whether the high-frequency component may represent pre- or early post-synaptic cortical activity, already mature by 8 weeks, and how the different maturation rates of the mid and high-frequency components may reflect different intra-cortical circuitry for colour and luminance. Copyright © 1996 Elsevier Science Ltd.

Infant visual development Visual evoked potentials (VEPs) Colour vision Temporal frequency
Response latency

INTRODUCTION

The temporal responses of the visual system to patterned stimuli are immature at birth and undergo a rapid

development during the first year of life. Between 4 and 6 months of age, psychophysical measures of contrast sensitivity for patterns of 1 c/deg increase considerably, especially for fast temporal modulation (at 8 or 17 Hz), leading to an overall change in the shape of the function, from low-pass to band-pass (Swanson & Birch, 1990). At very low spatial frequencies (0.1 c/deg), a similar course of development takes place, but at a

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much earlier age: the temporal contrast sensitivity function is lowpass at 1.5 months and bandpass at 3 months (Teller *et al.*, 1992; Hartmann & Banks, 1992; Dobkins & Teller, 1996). The behavioural changes are accompanied by changes of the response curve of the pattern visual evoked potential (P-VEP) as a function of the temporal frequency: the bandwidth and the optimal temporal frequency of the temporal response curves increase over the first 6 months (Moskowitz & Sokol, 1980), and the peak latency of transient P-VEPs and the apparent latency evaluated by the steady-state VEP response decrease considerably from 250 msec at 4–6 weeks of age to about 100 msec, after 8 months, near that of adult responses (Sokol & Jones, 1979; DeVries-Khoë & Spekreijse, 1982; Moskowitz & Sokol, 1980; Porciatti, 1984; Aso *et al.*, 1988; McCulloch & Skarf, 1991). It is worthwhile to note that the limits in temporal bandwidth and in peak latency of the P-VEP at each age are not imposed at a retinal level, given that simultaneous measurements of the retinal response (P-ERG) and VEP show an early maturation of the retinal responses (Fiorentini & Trimarchi, 1992). Critical flicker-fusion frequency thresholds (evaluated from VEPs in response to temporally modulated homogeneous light) show three subsequent phases of development, with a rapid phase between the second and the fifth month postnatally, where the flicker fusion increases from 20 to about 50 Hz. Thereafter adult values (60 Hz) are reached slowly by 6–9 months after birth (Apkarian, 1993).

In the adult, strong P-VEPs can be elicited by equiluminant patterns whose chromatic contrast is modulated temporally (Regan, 1973; Regan & Spekreijse, 1974; Murray *et al.*, 1987; Fiorentini *et al.*, 1991; Morrone *et al.*, 1993; Fiorentini *et al.*, 1996). For sinusoidal temporal modulation of equiluminant patterns, most of the P-VEP power is at the second harmonic of stimulus temporal frequency. As with luminance contrast modulation, the psychophysical chromatic contrast threshold can be evaluated by extrapolating to zero amplitude the contrast response curve (see Campbell & Maffei, 1970). The spatial and temporal characteristics of P-VEPs to equiluminant patterns differ from those in response to temporal modulation of luminance contrast, the most obvious differences being the lower spatial and temporal resolution of the equiluminant P-VEP, the steeper gain of the contrast response curve of the equiluminant stimuli and a clear advantage of the chromatic response to very low spatial (0.1–0.7 c/deg) and temporal (1–4 Hz) frequencies (Fiorentini *et al.*, 1991; Morrone *et al.*, 1993).

We have previously studied the development of the human infant P-VEP in response to red–green patterns alternating in colour contrast (Morrone *et al.*, 1990, 1993). No response to pure colour contrast was recordable in infants prior to 5–7 weeks of age, given the limitations of the cone contrast obtainable with standard monitors. After its onset, however, the chromatic P-VEP increases rapidly in optimal contrast sensitivity and in spatial resolution, improving at a higher rate than the P-

VEP responses to luminance contrast. The spatial contrast sensitivity functions of both the luminance and the colour P-VEP increase in bandwidth with increasing age, but the rate of change of their shape is different for colour than it is for luminance, at least for young infants (Morrone *et al.*, 1993). The low spatial frequency (0.1–0.5 c/deg) reached the adult-like ratio of luminance to chromatic sensitivity very early, by 11 weeks of age, while at higher spatial frequencies the final ratio was not obtained until 20 weeks for 1 c/deg, and 30 weeks for 5 c/deg (Morrone *et al.*, 1993). These findings suggest independent development of post-receptoral mechanisms responsible for equiluminant contrast sensitivity. Although this hypothesis was initially challenged by contrary VEP evidence (Allen *et al.*, 1993), recent electrophysiological data have confirmed our initial report, showing a deficit of the chromatic contrast sensitivity at some spatial frequencies, of a similar amount to that shown in our early studies (Kelly *et al.*, 1995, 1996). Forced choice preferential looking evaluations of contrast sensitivity also confirm VEP studies, showing that the ratio of luminance to chromatic sensitivity is adult-like by 12 weeks at low spatial frequency (Dobkins & Teller, 1996). However, the picture is less clear when directional thresholds are evaluated by OKN techniques. There seems to be a clear advantage for colour (compared with the adult) at 12 weeks, indicating a differential maturation of colour and luminance thresholds (Dobkins & Teller, 1996; Brown *et al.*, 1995). On the other hand, the luminance equivalent contrast required to balance the motion of an equiluminant grating is adult-like, even in very young infants (Teller & Lindsey, 1993; Teller & Palmer, 1996), suggesting a common limiting factor for the discrimination of the direction of motion of both luminance and chromatic stimuli [see also Banks & Bennett (1988)].

The present study reports the early development of the temporal characteristics of the P-VEPs in response to patterns of low spatial frequency (0.1 c/deg) of either pure luminance contrast (yellow–black plaid patterns) or pure colour contrast (equiluminant red–green plaid patterns). Stimuli of constant high contrast were used, contrast-reversed either sinusoidally at various temporal frequencies (eliciting steady-state responses), or abruptly at a low temporal frequency (eliciting transient responses). The two types of response characteristics were compared within each infant.

When compared with the temporal frequency characteristics of P-VEP in adults, it seems that there are three different response components in the low-, medium- and high-temporal frequency range, that have different (apparent) latencies and develop at different ages. The high frequency component of short latency is a response to luminance contrast and is present, with a temporal resolution exceeding 10 Hz, even in 8-week-old infants. The low frequency component is present in the adult for particular conditions (Simon, 1992; Fiorentini *et al.*, 1996) and in all infants in response both to stimuli of pure luminance or pure colour contrast, and develops earlier

than the medium frequency component, which is still immature 20–25 weeks after birth. The results suggest the existence of different neural mechanisms involved in processing luminance and colour patterns, that develop at different rates.

METHODS

Stimuli

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. 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 30 cm.

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 Eq. (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 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:

$$L_R(x, y, t) = rL_0\{1 + 0.5s \cdot m\cos(2\pi f_t)[\cos(2\pi f_s x) + \cos(2\pi f_s y)]\}$$

$$L_G(x, y, t) = (1 - r)L_0\{1 + 0.5 \cdot m\cos(2\pi f_t)[\cos(2\pi f_s x) + \cos(2\pi f_s y)]\} \quad (1)$$

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. $s = +1$ for luminance stimuli, and -1 for chromatic stimuli. 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 plaid. This factor should be borne in mind when comparing responses to one-dimensional gratings. The value of r was chosen to give equiluminance, near 0.5 for all adult observers with normal vision, and all the infants in our sample.

VEP recording

EEGs were recorded with surface electrodes (O_z , C_z , with earth halfway between), pre-amplified (500-fold) by a small pre-amplifier (HDX-82 Oxford Medical Systems) on the infant's head, filtered between 0.1–200 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 artefacts, the computer averaged on-line the EEG at a frequency 10% higher than the stimulation frequency, to compare with the synchronized averages. For the steady-state VEPs, 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 < 1 , the 20-trial packet was rejected from the final analysis. The purpose of this procedure was to minimize contamination by artefacts, such as gross head movements or blinks. As an independent measure of reliability of the steady-state VEPs, 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. As an additional estimate of possible artefacts correlated to the stimulus frequency, on each session we made a recording with the screen covered with a diffuser, for several temporal frequencies. When (on very rare occasions) we noted a small synchronized response (usually caused by poor electrode contact), the entire session was discounted, and new data collected after eliminating the artefact signal.

Phase analysis

Response latencies were calculated by measuring phase as a function of temporal frequency, and estimating the slope of this relation (Regan, 1966; Spekreijse *et al.*, 1977). The slope was calculated by least-squares linear fit of the phase data, weighting each point by the inverse of its standard error (evaluated by scatter of phase of the packets). To estimate the error associated with the slope of the regression, the regression was re-estimated repeatedly using only two-thirds of the data points (in all possible combinations), and the error taken to be the standard deviation of these independent estimates (Efron & Tibshirani, 1991). When the data were fit with more than one segment, χ^2 was calculated for both the single segment fit (χ_1^2) and multiple segment fits (χ_2^2), and the more complex fit was accepted if the decrease in χ_1^2 was significant by the following F test:

$$F(k, N) = (\chi_1^2 - \chi_2^2)/(k\chi_2^2/N) \quad (2)$$

where k is the increment of fit parameters (two for each additional segment) and N is the degree of freedom of the multiple segment fits.

The phases of the averaged evoked potentials were calculated by discrete Fourier analysis from the arctangent of the ratio of the sine-to-cosine amplitude. As the arctangent is bounded between $\pm \pi$, these values are not unique, but there exist an infinite set of phases separated by 2π radians with the same tangent. To choose the appropriate phase, one must assume that the phases advance or retard in an orderly fashion with temporal

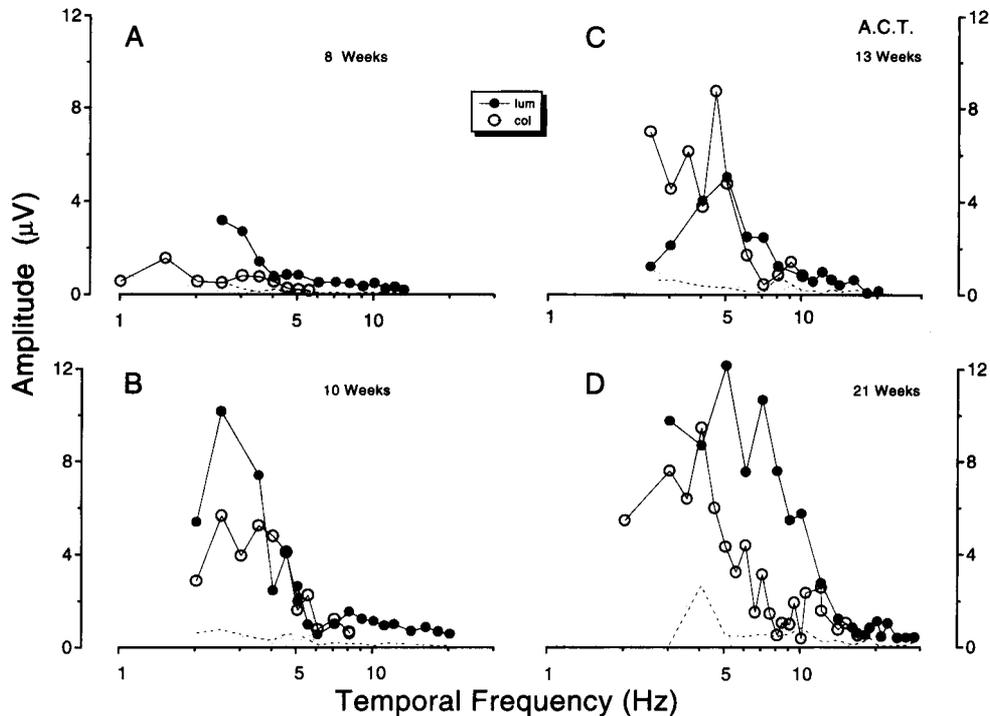


FIGURE 1. P-VEP second harmonic amplitude of infant ACT as a function of stimulus temporal frequency for plaid patterns with pure luminance contrast (yellow–black, ●) or pure chromatic contrast (equiluminant red–green pattern, ○), sinusoidally reversed in contrast. Stimulus contrast: 90%, spatial frequency 0.1 c/deg. Dashed and dotted lines indicate noise amplitudes for patterns with luminance- and chromatic-contrast, respectively.

frequency, and add or subtract multiples of 2π radians to the raw data to produce maximum orderliness.

RESULTS

Steady-state P-VEP to sinusoidal reversal of colour or luminance contrast

In previous papers (Morrone *et al.*, 1990, 1993) we have described in detail our technique of establishing for each subject the equiluminant colour-ratio, the ratio of red-to-total luminance yielding a pattern with pure colour contrast. Basically, we record P-VEPs as a function of colour ratio to find the value where the amplitude is either minimal or locally maximal, and the phase is maximally different from the phase of the P-VEP obtained with green–black and red–black patterns of pure luminance contrast (colour ratios 0 and 1). Most (10 out of 15) of the infants participating in the present experiment were first tested to determine the equiluminant ratio for each of them. The average ratio was 0.5 ± 0.03 (standard deviation). The remaining five were tested at this average ratio. All the results of this study were obtained from each subject with red–green patterns corresponding to the estimated equiluminant ratio of that subject (colour P-VEP) and with yellow–black patterns of the same mean luminance and average chromaticity (luminance P-VEP). The stimulus patterns were of maximum contrast (90%) and very low spatial frequency (0.1 c/deg).

Longitudinal study: Amplitude

Figure 1 shows the amplitude of the responses (second harmonic) to patterns of pure luminance contrast (solid circles) or pure chromatic contrast (open circles) as a function of temporal frequency, in an infant at four different ages. At 8 weeks [Fig. 1(A)] the responses to colour contrast are very small and are significantly above noise levels only at low temporal frequencies, while the responses to luminance contrast are considerably larger in amplitude and significantly above noise up to about 12 Hz. During the next 2 weeks [Fig. 1(B)], the colour responses increase substantially over the entire range (from < 2 to 5–6 μV). Luminance responses also increase in amplitude, reaching a temporal resolution of *c.* 20 Hz. At 10 and 13 weeks, the colour and luminance responses show a similar dependence upon temporal frequency in the range 2–6 Hz, although the luminance response extends to far higher frequencies than the colour response. Eight weeks later [Fig. 1(D)], however, the temporal frequency functions of the two responses become clearly dissociated, with the luminance curve being displaced towards higher temporal frequencies with respect to the colour curve. While the colour response still peaks at 3–4 Hz, the peak of the luminance response is now at 5–7 Hz. In addition, the colour response has developed a high frequency limb, with a peak beyond 10 Hz, and a temporal resolution exceeding 15 Hz, nearly half the resolution of the luminance response, now close to 30 Hz.

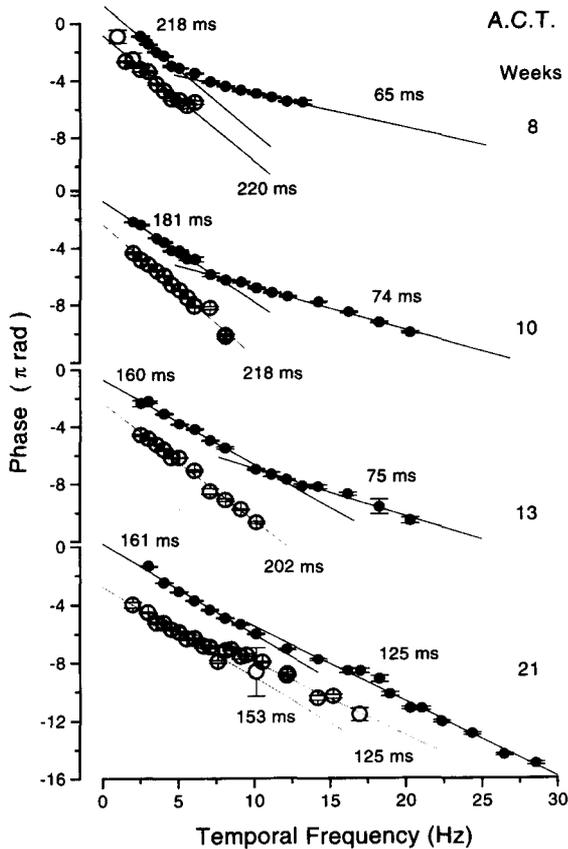


FIGURE 2. P-VEP second harmonic phase as a function of stimulus temporal frequency (linear scale), for infant ACT, tested at various ages. Bars indicate the error associated with the phase estimates. Apparent latencies, estimated from the slope of the regression lines, are indicated in msec. Other symbols are as for Fig. 1. The F tests for the significance of the two segment fits for the luminance data are: $F(2,9) = 99$, $F(2,15) = 152$, $F(2,11) = 35$ and $F(2,16) = 9.3$ for 8, 10, 13 and 21 weeks, respectively; for the colour data at 21 weeks $F(2,18) = 17.4$. All the tests are significant with $P < 0.001$ except the luminance fit at 21 weeks that is significant with $P < 0.005$.

These findings point to different stages in the development of the colour and luminance responses. For both of them there is an increase in the temporal frequency bandwidth with age. However, their relative amplitudes are considerably different in the very young infant, to become more similar during the third and fourth months. After that, they diverge again at 5 months, especially in the mid temporal-frequency range (between 4 and 10 Hz).

The majority of the curves for the luminance P-VEPs in Fig. 1 tend to be bimodal, with a secondary peak in the higher frequency range after a dip to near noise levels. For the luminance responses, the response minima between the two peaks change with age from 3 Hz at 8 weeks to 17 Hz at 21 weeks. For the colour responses, a secondary peak becomes evident only after 20 weeks [Fig. 1(D)]. Local minima such as these between two distinct lobes in a response function often signify the action of multiple separate mechanisms (Regan, 1978; Nakayama & Mackeben, 1982).

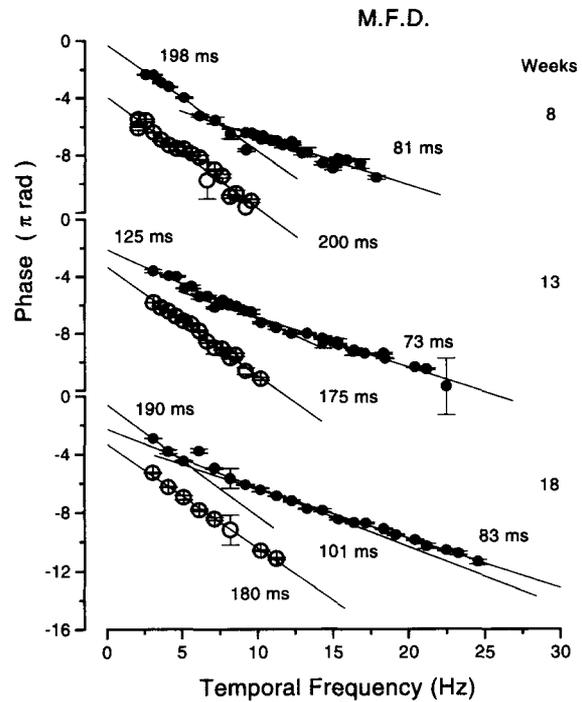


FIGURE 3. Same as Fig. 2 for infant M.F.D. The F test for the multiple fit of the luminance data are: $F(2,25) = 73$, $F(2,25) = 21$ and $F(4,15) = 26$ at 8, 13 and 18 weeks, respectively. All tests are significant ($P < 0.001$).

Longitudinal study: Phase

The bimodal distribution of luminance response amplitudes is also reflected in the way the phases of the responses vary with temporal frequency. This is shown in Fig. 2, which plots the phases of the second harmonic of the responses of Fig. 1 against temporal frequency on a linear scale. Note that the phases of the luminance responses vary linearly, but with different slopes at lower and higher temporal frequencies. The intersection between the steeper and the shallower branches of the phase distributions shifts with age towards an increasingly high temporal frequency. The slope of the steeper, low frequency branch decreases progressively, while the slope of the shallower branch does not change appreciably (except for the data at 21 weeks of age).

The responses to colour do not show the two limbs of phase responses, except at the latest age, after the range of temporal frequencies yielding significant amplitudes and reliable phases, extends beyond 10 Hz. The slope of the phase to colour stimuli below 10 Hz decreases significantly with age, paralleling the change of the phase slope for luminance stimuli of low temporal-frequency. Similar developmental changes in the phase of the responses to luminance and colour contrast were observed in another infant tested longitudinally over the same age period (Fig. 3). For this infant, there were two distinct notches in the amplitude curves at the oldest age, so the phase curves were best fit by three distinct regression lines.

From the slopes of the regression lines of response

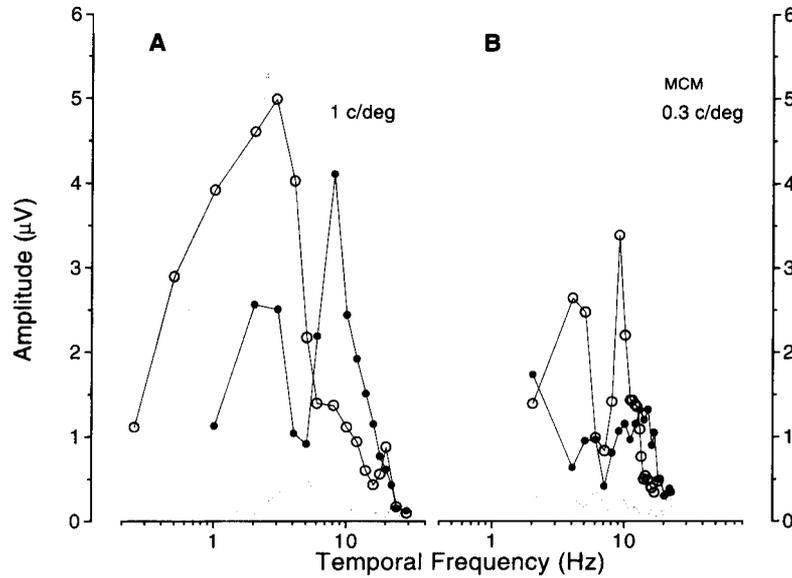


FIGURE 4. P-VEP second harmonic amplitude as a function of stimulus temporal frequency for an adult subject for stimuli of 1 c/deg (A) and 0.3 c/deg (B). Other conventions as for Fig. 1.

phase vs temporal frequency it is possible to evaluate the *apparent latency* of the second harmonic P-VEP (Regan, 1966; Spekreijse *et al.*, 1977). The curves in Figs 2 and 3 are labelled with the apparent latencies (in msec) corresponding to the different branches of the phase curves. The knee point between the two different regression lines was evaluated from the notch frequency of the amplitude response curve. In all cases, the fit of the multiple regression was better than the single regression, as evaluated by the *F* test described in the Methods (see captions for values).

Adult amplitude and phase

In spite of the considerable modification of the responses and increase in the bandwidth of the amplitude curves for both luminance and colour, the developmental process is far from being complete at the age of 20 weeks. Figure 4 shows for comparison the amplitude of the second harmonic of the steady-state P-VEPs recorded from an adult subject as a function of temporal frequency, for stimuli of two spatial frequencies, 1 and 0.3 c/deg. At the very high contrast used in the present experiment, both the luminance and the chromatic P-VEPs show a bimodal dependence upon temporal frequency, that is more evident for the luminance P-VEP at 1 c/deg and for the chromatic P-VEP at 0.3 c/deg. For luminance P-VEPs, the first peak occurs at 2–3 Hz, and the second one at 8–10 Hz, or even higher at 0.3 c/deg. It is important not to confuse the two peaks observed here with those of the young infants. Here, the second peak occurs for both luminance and chromatic stimuli, and is usually higher than the first, at least for luminance. The notch frequency occurs around 7–10 Hz, compared with 17 Hz for 21-week-olds. There is also a major difference in the apparent latency estimated from the phase response of the high temporal frequency limb, faster in the infant than in the adult.

Figure 5 shows the phases of the adult responses, as a function of temporal frequency. The chromatic responses show two clear limbs, breaking at a similar frequency as the amplitude notch. The low-frequency limb has an

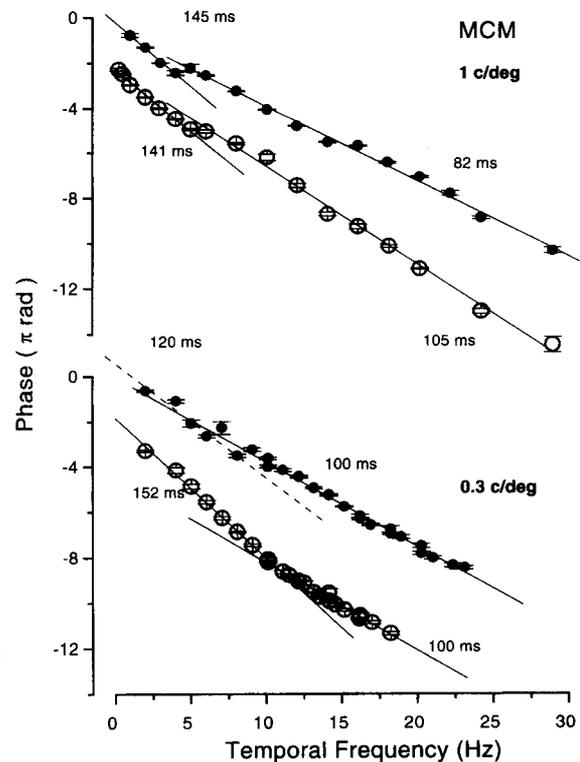


FIGURE 5. P-VEP second harmonic phase as a function of stimulus temporal frequency (linear scale) for the adult subject of Fig. 4 at 1 c/deg (top) and 0.3 c/deg (bottom). Other conventions are as for Fig. 2. The *F* test for significance of the fit with multiple segments are $F(2,14) = 4$ for luminance and $F(2,13) = 4.5$ for colour at 1 c/deg ($P < 0.05$) and $F(2,22) = 90$ ($P < 0.001$) for colour at 0.3 c/deg. The double segment fit of luminance data at 0.3 c/deg did not yield a significant improvement, and hence is illustrated by a dashed line.

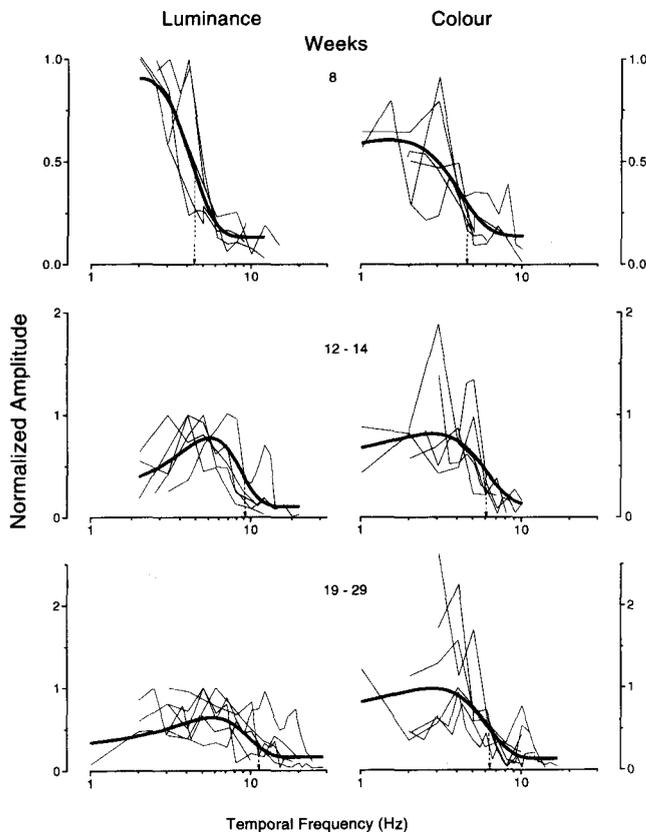


FIGURE 6. Amplitudes of second-harmonic of steady-state P-VEP as a function of temporal frequency for infants of three age groups. Thin lines show curves of individual subjects, and thick lines the means. For each infant, both colour and luminance curves were normalized to the peak luminance amplitude. The arrows indicate the temporal frequency at half-height of the average curves.

apparent latency of about 140–150 msec, very close to those obtained from 20-week-old infants. The apparent latency of the high-frequency limb is about 100 msec, somewhat faster than the corresponding latency in the 20-week old infant. At 0.3 c/deg, the luminance response is seemingly well fitted by a single regression line of about 100 msec, as is typical for stimuli of this luminance and contrast [for review see Regan (1989)]. However, on careful analysis across subjects, it is clear that the first few data points of low temporal frequency amplitude lobe are fit better by a regression line of steeper slope. At 1 c/deg, the slope at these low frequencies is 145 msec, very similar to the apparent latency of the colour response. This behaviour is far clearer in infants, at all ages.

Cross-sectional study: Amplitudes of steady-state P-VEP

In order to compare the development of the temporal frequency characteristics of colour and luminance P-VEP amplitudes, the infants examined in this study were subdivided into three age groups. The amplitude vs temporal frequency functions of the infants were averaged within each group separately for luminance and colour. Figure 6 shows the individual amplitude

curves (thin lines) normalized for both luminance and colour to the peak of the luminance curve, together with the average of these individual records (thick lines) for the three age groups. Note that the amplitude curves reported here have been truncated to the notch frequency to highlight the development of the low temporal frequency lobe.

The figure shows clearly the different developmental modification of colour and luminance P-VEP responses. For luminance, the average curves are low-pass at 8 weeks and then change to band-pass, with the peak and the cut-off frequency shifted progressively towards higher temporal frequencies. For colour the shape of the curves remains substantially low-pass and the increase in cut-off frequency is less marked. The colour amplitude is smaller relative to luminance at the earliest age, and larger at 5–6 months. The curves are quite similar at 8 weeks, both in optimal temporal frequencies and cut-off, while they diverge at older ages, as the luminance curve shifts considerably to higher temporal frequencies as compared with the colour curve (noted above for the infant of Fig. 1).

The phase data of the infant population fit by a single regression line up to the notch at high frequencies (the equivalent frequency range of the amplitude curves shown here) also point to a progressive differentiation of colour and luminance steady-state P-VEPs. These will be discussed later, together with the latencies of transient P-VEPs (see Fig. 12).

Transient P-VEPs in response to luminance and colour contrast reversal

Further information about the development of the temporal properties of the P-VEP can be obtained from the changes in the morphology and the peak latency of the transient responses to contrast reversal.

The P-VEP in response to a square-wave reversal of luminance contrast is known to change progressively after birth, first increasing in amplitude and decreasing in peak latency, then passing from a relatively simple waveform with a single positive peak to an increasingly complex waveform (Sokol & Jones, 1979; Moskowitz & Sokol, 1980; Aso *et al.*, 1988). In the present experiment we have investigated the development of the transient P-VEP both to luminance contrast reversal and colour contrast reversal.

Figure 7 shows the results of the longitudinal study in infant ACT. The first and third columns present P-VEPs in response to reversal of patterns with luminance contrast of 90% (left) or 20% (right). The second column shows the transient P-VEPs for equiluminant red–green patterns with colour contrast of 90%. The luminance P-VEPs change with age in agreement with previous findings. At their first appearance around 8 weeks the colour P-VEPs are very small compared with the luminance responses (Ruddock & Harding, 1994). They then increase progressively in amplitude and decrease in peak latency, so that at the latest age tested, their positive peak is higher than the luminance response. Comparison

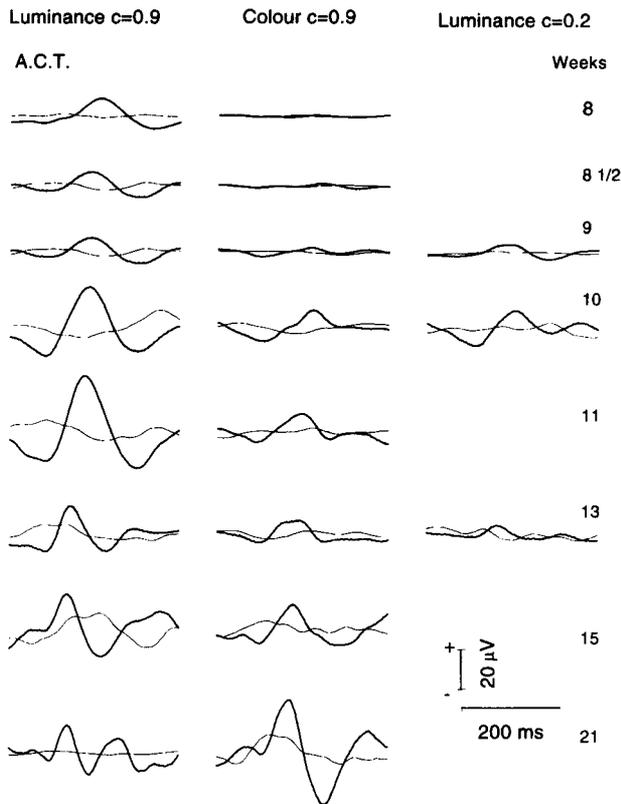


FIGURE 7. Transient P-VEPs recorded from infant ACT at various ages (thick lines) in response to 0.75 Hz square-wave reversal of luminance or colour contrast. Stimulus contrast was 90% for the first two columns, and 20% for the third column. Thin lines indicate noise (see Methods). Records averaged over 100–200 stimulus periods.

with the records obtained with luminance contrast of 20% (similar to the cone contrast of the red–green pattern) shows that the differential development of colour and luminance transient P-VEPs cannot be accounted by the lower effective cone contrasts of the chromatic stimuli. Indeed, at 9 weeks the colour P-VEP is smaller, while at 13 weeks it is larger than the P-VEP in response to a luminance contrast of 20%.

These longitudinal findings are representative of those obtained from the other infants. Figure 8 presents the normalized transient P-VEPs (thin lines) of all the infants tested, subdivided in four age groups. The average responses (thick lines) of each group show developmental changes very much like those observed in infant ACT, with a decrease in peak latency and a change in waveform morphology with increasing age. More important for this study is the change in *relative* amplitudes of luminance and colour responses: as observed above for the longitudinal data of ACT, the colour P-VEPs are smaller than the luminance P-VEPs in the first three age groups, but are larger in the oldest group. Note also that the waveforms of the two responses are very similar in the younger infants, but different in the older ones. This seems to result mainly from the change in waveform of the luminance response that in the oldest

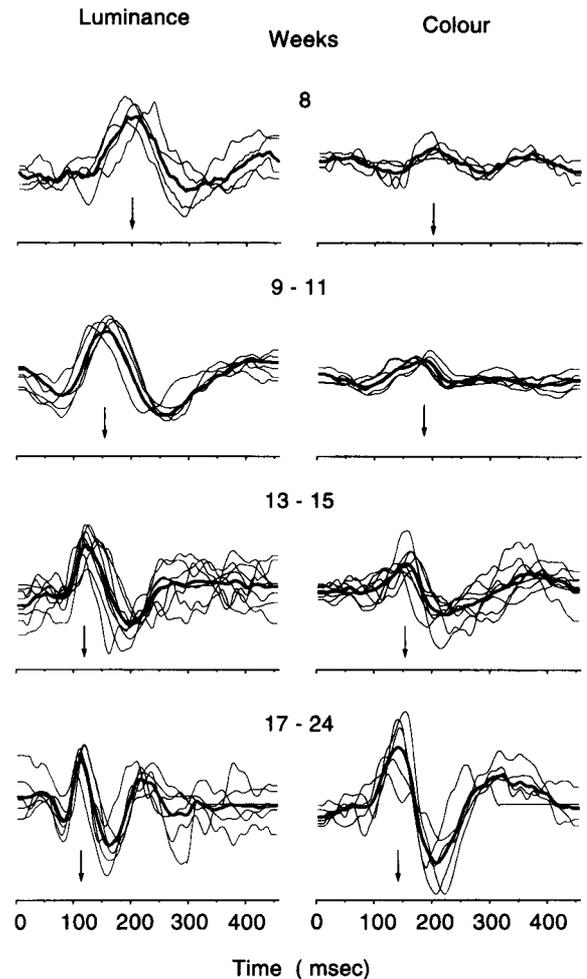


FIGURE 8. Individual (thin lines) and average waveforms (thick lines) of transient P-VEPs for luminance and colour contrast reversal in infants of four age groups. The arrows indicate the latency of the main positive peak. For each infant both the colour and luminance responses were normalized (by the same factor) to yield a peak activity of the luminance response of unity.

group shows a pronounced negative wave with latency < 100 msec.

In order to illustrate better the age-dependent evolution of the transient responses, the average waveforms of the four age groups, normalized to unity, have been reproduced in Fig. 9(A) with their peaks aligned. Note the similarity in shape of the luminance and colour responses at all ages except the oldest. This observation was pursued more quantitatively by analysis of principal components of the waveforms of the two oldest age groups, where the difference in latency of the major peak is quite small at the various ages. The responses of each infant to luminance and colour were normalized and decomposed into their first two major components, PC₁ and PC₂, illustrated in Fig. 9(B) using the singular value decomposition algorithm [see Maier *et al.* (1987) for general methods, and Press *et al.* (1988) for algorithm]. These two components account for 80% of the variance of the data. PC₁ was surprisingly similar for the two age

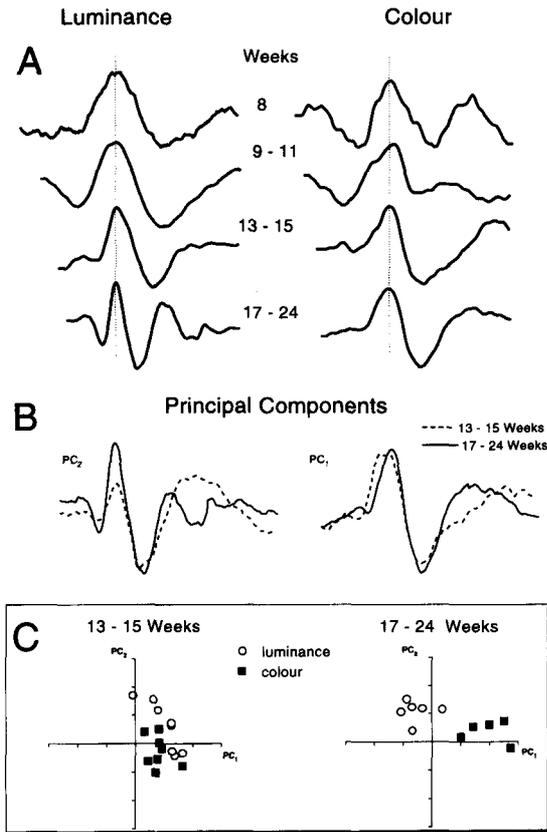


FIGURE 9. (A) Average transient P-VEPs replotted from Fig. 7 with their main positive peaks aligned and normalized. (B) First and second principal components PC₁ (right) and PC₂ (left) for the waveforms relative to the two older age groups. (C) Scatter diagram of the individual principal components of luminance (○) and colour (■) responses for the infants of the two older age groups.

groups, suggesting little variation of that component with age. However, PC₂ changes form, with the first positive peak increasing considerably.

Figure 9(C) plots PC₁ against PC₂ for the colour and luminance records of the two ages. PC₁ seems to provide a good description of the colour response at both ages. The luminance responses tend to cluster along a positive component of PC₂ with the older group, while for the younger group the luminance response does not cluster clearly. This implies that between 15 and 20 weeks, the luminance, but not the colour response, has matured considerably, particularly over the first 100–120 msec.

Adult transient response

Comparison of the infant transient P-VEP with that of the adult (examples shown in Fig. 10) shows that it is not yet mature at 20 weeks. However, the comparison poses some problem, because in adults the waveforms of the transient responses show a larger intersubject variability than in infants, besides varying systematically with spatial frequency (Berninger *et al.*, 1989). At low spatial frequencies (below 1 c/deg) the major response to luminance is formed by two close and overlapping

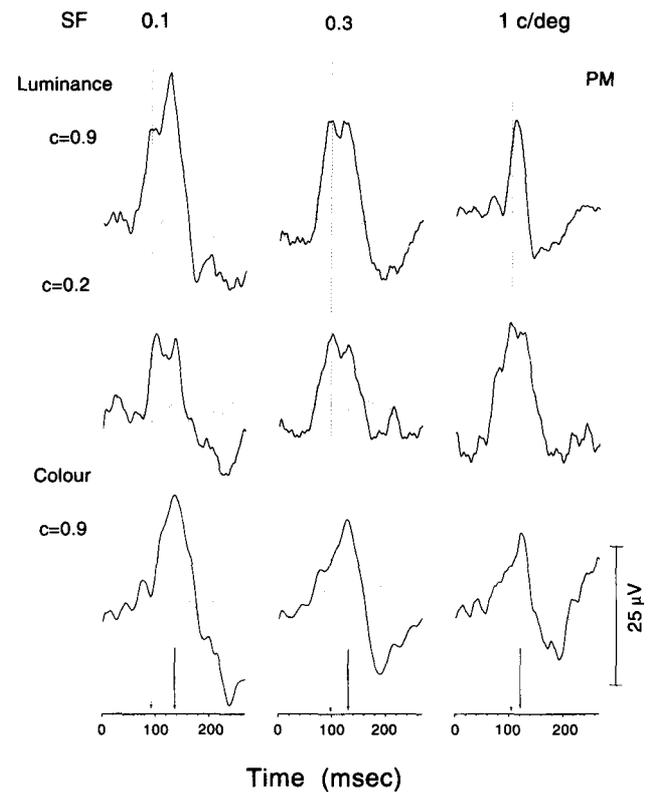


FIGURE 10. Transient P-VEPs from an adult subject for luminance- (top and middle rows) and colour-contrast reversal (bottom row) of plaid patterns of three different spatial frequencies (0.75 Hz). Stimulus contrast was 90% for the top and bottom rows, and 20% for the middle row. Dotted lines show noise traces. The broken and solid arrows indicate the latency of the first peak of the luminance and of the major peak of the colour response, respectively.

positive peaks, one with latency of about 100 msec and another with a latency of about 140 msec. This phenomenon has been described previously (Plant *et al.*, 1983), and occurs over a wide contrast range. The response to colour comprises one single major positive peak, with a latency similar to that of the second luminance peak (around 140 msec).

At higher spatial frequencies (1 c/deg) the two peaks of the luminance response merge into a single peak of intermediate latency, although a hint of a double-peak remains at some contrasts. Here the difference in the early peak latency between luminance and colour is notably reduced, both because the luminance peak is now the average of the two peaks at low spatial frequencies, and because the colour peak becomes more precocious.

It is also interesting that the early negative response (N70) is less obvious here than in the transient response of the infants, agreeing with the observation that the short-latency high-frequency limb of the steady-state phase response is not obvious in adults. Furthermore, while the colour transient responses of adults and infants have very similar shapes, the luminance responses are qualitatively quite different, even at the oldest ages.

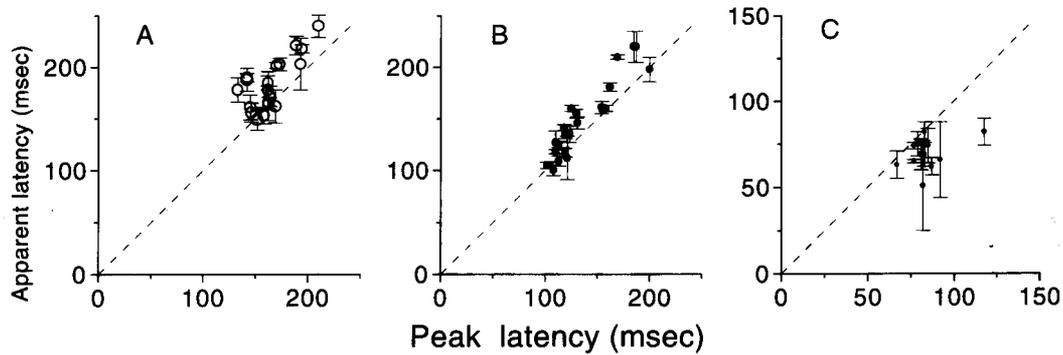


FIGURE 11. Apparent latency of steady-state P-VEPs plotted against peak latency of transient P-VEPs for all infant subjects. (A) Shows the colour responses, (B) the luminance responses of temporal frequencies lower than the notch frequency, and (C) the luminance responses at higher temporal frequencies. The peak latencies in (B) refer to the main positive peak, those in (C), to the early negative peak. Vertical bars indicate the error associated with the fit, evaluated by Montecarlo simulation.

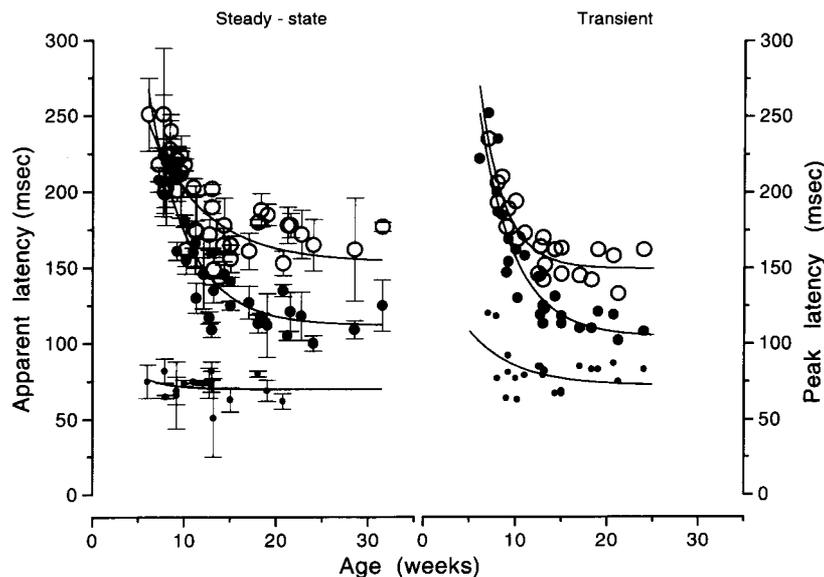


FIGURE 12. Apparent latencies estimated from steady-state P-VEPs (left) and peak latencies of transient P-VEPs (right) as a function of age. Open circles show the colour responses and solid circles the luminance responses. The large solid circles of the steady-state plot (left) refer to apparent latencies of the luminance response for the range of temporal frequencies lower than the notch frequency; those of the transient plot (right) refer to the latency of the main positive peak. The small solid circles indicate apparent latencies relative to the higher temporal frequency range (left) and latencies of the early negative peak (right).

Latency of P-VEP in response to colour or luminance contrast reversal

The average records of Fig. 8 show that at 8 weeks the latency of the positive peak is very similar for luminance and colour responses, while at 21 weeks the former is much faster. For infant ACT (Fig. 2) it was shown that the apparent latency derived from the phase plots in the low temporal frequency range is the same for luminance and colour P-VEPs at 8 weeks of age, while the major responses in adults have different latencies.

In order to evaluate the relative change in luminance and colour P-VEP latencies for the whole population of infants studied, we first compared for each subject the peak latency of the transient P-VEPs (main positive wave

for the luminance and colour responses and early negative wave for the luminance responses) with the apparent latencies derived from the steady-state P-VEP phases (slope of the regression lines). For the steady-state estimates, the curves were divided into two limbs (separated by the frequency of the amplitude notch), and latency evaluated separately for each. This means that for the older infants, where there may actually exist three separate limbs, the first two are averaged. The results are presented in Fig. 11. The distributions of the experimental points for all three P-VEP components show a good correlation between the apparent latency of steady-state P-VEPs and the peak latency of the transient P-VEPs.

The apparent latency of the steady-state P-VEPs and the peak latency of the transient responses (main positive peak for the colour and luminance P-VEP and early negative peak for luminance P-VEP) of all infants are plotted in Fig. 12 as a function of postnatal age. The results for luminance P-VEPs confirm previous data indicating a long latency of the positive peak in the second month from birth and a progressive shortening of latency during the next months. Interestingly, the present findings show that in the youngest infants the colour and the luminance responses have approximately the same peak latency (and apparent latency) exceeding 200 msec. The latency of the colour responses decreases progressively with age. So does the latency of the positive peak in the luminance responses, but more rapidly, so that at about 24 weeks from term the latencies are about 40 msec shorter for luminance than for colour. The fast negative component of the luminance response has a relatively stable latency in the age period investigated.

Interestingly, the same pattern of results emerges from the apparent latency estimates from the steady-state potentials. The separation of the luminance and colour latencies after 8–10 weeks suggests the development of a faster neural process, which eventually masks the component in the luminance response at low temporal frequency, which otherwise would be as slow as the colour response.

DISCUSSION

The results of the present experiment supplement previous findings about the postnatal development of the temporal properties of P-VEP responses to luminance pattern reversal and provide the first evidence for age-related changes in the temporal properties of the P-VEP responses to equiluminant colour contrast reversal in infants.

Luminance P-VEP: Development of a short latency component

In measuring the infant responses to luminance contrast reversal an interesting fact has emerged. For patterns of low spatial frequency, the infant P-VEPs contain a high temporal frequency component of small amplitude that extends beyond 15 Hz as early as 10 weeks, reaching 30 Hz at 20 weeks. The phase data indicate that this component has a constant and short apparent latency (70–80 msec) independent of infant age. The latency of this steady-state component is similar to the latency of the early negative component of the transient P-VEP, present in nearly all infants. The colour contrast reversal P-VEP does not have a measurable component in the same range of high temporal frequencies. However, it should be remembered that the effective RMS cone contrast of the chromatic stimulus [Helmholtz's line element theory, see Wyszecki & Stiles (1982)] is about four times lower than the luminance stimulus, possibly too low to generate a response over this range.

It is interesting that in adults a prominent peak in the

temporal frequency range 15–30 Hz is present in the pattern reversal electroretinogram [P-ERG: Porciatti *et al.* (1992); Morrone *et al.* (1993)], but much less pronounced in the P-VEP. Even in 5 month-old infants there is evidence of a P-ERG response to temporal frequencies >10 Hz, which is considerably larger than the P-VEP over this range (Fiorentini & Trimarchi, 1992). The temporal resolution of the fast component compares well with that evaluated by VEPs in response to flickering homogeneous light of around 20 Hz during the second month of life (Apkarian, 1993). One might speculate that the high temporal frequency component observed in our infant data is a sign of presynaptic or early post-synaptic activity in the thalamus-recipient layers of the visual cortex, and owes its short and age-independent latency to an early development of retinal and geniculate temporal resolution.

The suggestion of a nearly mature integration time (apparent latency) and temporal resolution limit of thalamic input is supported by other evidence in monkey. In newborn monkey LGN, both M- and P-neurons have a cut-off frequency (half-height) of around 10 Hz, and an acuity well exceeding this limit (Hawken *et al.*, 1996). It is also interesting to note that the first negative peak in monkey P-VEPs probably reflects the initial depolarization of stellate cells in layer 4C in primary visual cortex (Schroeder *et al.*, 1991). Similarly, in humans, the early P-VEP P60 is thought to be driven by LGN activity, while a cortical circuitry may be involved in the generation of the first negative wave, N70 (Rappaport *et al.*, 1995). Our data suggest that these early components and the underlying neural circuitry generating them are well developed by 8–10 weeks in human infants.

It is interesting that the temporal resolution evaluated psychophysically reaches high values similar to those evaluated by P-VEP by 1 month (Regal, 1981) and is substantially mature by 3 months (Dobkins & Teller, 1996). In addition, the colour and the luminance temporal CSFs are very similar at this age, indicating that they are possibly mediated by the same mechanisms (Dobkins *et al.*, 1996). The similarity of the development course of the fast P-VEP component and the psychophysical evaluation of temporal properties suggest that the mechanisms generating this VEP component might have a behavioural influence even at threshold contrast, favouring the suggestion of an early post-synaptic cortical involvement.

Steady-state luminance and colour P-VEP: Development of the components in the low and medium temporal frequency ranges

In the adult, the temporal contrast sensitivity evaluated from pattern-reversal P-VEPs predicts psychophysical performance well. For luminance contrast, it is a band-pass function with a peak at about 8 Hz. For colour contrast it is low-pass, with a corner frequency at about 5 Hz and a resolution of about 20 Hz [compared with about 30 Hz for luminance; Fiorentini *et al.* (1991)]. For

stimuli of very high contrast, however, the function relating P-VEP amplitude to temporal frequency has multiple peaks, both for luminance and colour P-VEPs (Fig. 4). The relative amplitudes of the two main peaks (at 3 or 6 Hz and 8 or 12 Hz, respectively, for colour and luminance responses) depend on the stimulus spatial frequency. The corresponding phase plots indicate that the response components of different temporal frequency ranges have different apparent latencies, and the discontinuities in the slopes correspond to relative minima in the P-VEP amplitude plots. The phase plot of the low frequency component has longer apparent latency than the medium frequency component. However, the apparent latencies relative to the various temporal frequency ranges are equal or longer for colour than for luminance P-VEPs, in agreement with the small difference (10–20 msec) in colour and luminance latencies measured in the human and monkey retina (Morrone *et al.*, 1994a, b). All these results are consistent with the existence of temporal mechanisms tuned to different temporal frequency bands and with different time delays (Simon, 1992). However, it is important to note that the contribution of the various mechanisms to the determination of the psychophysical threshold is still unknown.

The temporal response curves of infants differ from the adult curves in many respects. In the youngest age range, as soon as the chromatic response is recordable (around 8 weeks), the curves for luminance and colour are very similar in shape and bandwidth in the low-frequency range (< 10 Hz), and the phase responses can be well fit by a single regression, yielding the same apparent latency for both responses. These data suggest that a single mechanism generates both luminance and colour P-VEPs in these infants.

At 12–14 weeks several developmental changes take place. The luminance curves begin to become bandpass, and to extend to a higher range of temporal frequencies, more rapidly than does the colour response. The transition towards a band-pass curve occurs at an age when similar transitions are seen both in the P-ERG (Fiorentini & Trimarchi, 1992) and in the psychophysical contrast sensitivity function (Hartmann & Banks, 1992). The chromatic response remains low-pass (as it is in the adult), and begins to exceed the amplitude of the luminance response over much of its range. Around 14 weeks, the apparent latency of the chromatic response has nearly reached adult levels, while the luminance latency is still much longer than in the adult. At this age the preferential looking temporal sensitivity function for colour is band-pass (while in adult it is low-pass) and very similar in shape to the luminance function (Dobkins *et al.*, 1996). The difference between the psychophysical and P-VEP data suggests that at threshold this component probably does not predominate over the faster component. To elucidate the different component contributions one should study the dependence of phase on the stimulus contrast at various temporal frequencies. The few data reported in the literature seem to indicate that at low

temporal frequencies there is a variation of phase with contrast, particularly for colour [see for example Morrone *et al.* (1993)]. However, the data available at this stage are too sparse to reach a firm conclusion.

At 20 weeks, the luminance curve moves to far higher temporal frequencies than the colour curve, and the phase response begins to divide into two limbs with different slope over the low frequency range (see Fig. 3). However, for neither luminance nor colour P-VEPs is there a clearly developed component of steady-state responses peaking around 10 Hz. In the adult, this is the component having an apparent latency of about 100 msec, both for colour and for luminance P-VEPs, and representing the largest peak in the luminance curves for a wide range of spatial frequencies. It seems that the development of this medium-frequency component is delayed with respect to both the high-frequency and the low-frequency components.

In the adult luminance response there is little sign of the high-frequency component of shortest latency (70 msec), and of the low-frequency component of longest latency that are so evident in the amplitude and phase plots of the infants (Figs 1–3). Perhaps these components may be masked in the adult by the now dominant mid-frequency component with apparent latency of 100 msec. For the chromatic response, however, the mid-range component is not sufficiently dominant to swamp the low frequency response, and the phase plot still shows two distinct limbs, even in adults.

Several studies have reported a difference in apparent latency between luminance and colour P-VEPs of about 40 msec (Regan & He, 1993; Fiorentini *et al.*, 1991; Girard & Morrone, 1994), while the difference at the retina (in monkey) is about 10–20 msec (Benardete & Kaplan, 1993; Lee *et al.*, 1994). The difference in the M- and P-response at the cortical level is also of this order (Maunsell & Gibson, 1992; Nowak *et al.*, 1995). The greater difference in apparent latency estimated from the P-VEP (see, for example, Fig. 12) probably reflects the different relative contributions of the two different mechanisms tuned to low and medium temporal frequencies, that become confused within a single regression line. However, when it is possible to disentangle the two mechanisms the difference in latency between colour and luminance mechanisms remains constant at about 20 msec, at least in adults.

In conclusion, the steady-state findings suggest that a high-temporal frequency component of the luminance P-VEP of 70 msec apparent latency is present very early (8 weeks of age) and approaches the adult temporal resolution by 20 weeks. A low temporal frequency component of the colour and luminance P-VEPs is nearly mature by 12–14 weeks, while a component peaking around 10 Hz with apparent latency of 100 msec, is still far from mature at 20 weeks. The data also show that the colour and luminance P-VEPs initially have very similar amplitude distributions and apparent latencies in the low temporal frequency range, and that they differentiate later on.

Development of transient luminance and colour contrast P-VEP

The adult transient responses to luminance contrast reversal for plaid stimuli of low spatial frequencies and high contrast are M-shaped (Fig. 10) with two positive peaks at about 100 and 140 msec. For plaids of 1 c/deg there is one main positive peak at about 120 msec. At a lower contrast (20%), the waveforms are approximately the same, apart from slight differences in the relative amplitudes and latency of the peaks. For colour contrast reversal, there is one main positive peak of latency around 140 msec at low spatial frequencies decreasing to 120 msec at 1 c/deg.

The latencies of the two peaks in the luminance response are comparable to the apparent latencies of the low- and medium-temporal frequency components of the steady-state P-VEP (Fig. 5). For colour, the main peak of the transient responses has approximately the same latency as the low-temporal frequency component of the steady state P-VEP. A contribution to the transient colour response of a medium temporal frequency component (apparent latency 100 msec) is less evident, although it probably contributes to the gradual emergence of the major peak.

Like the steady-state responses, the transient waveforms of the infants show a clear developmental course over the age period investigated. The colour responses resemble the adult waveform and latency by 14 weeks of age, while the luminance transient responses remain quite different, even in the oldest infants tested (Fig. 8). This is due probably to the still immature medium-frequency component that in the adult may correspond to the earlier positive peak of the transient luminance P-VEP. It is noteworthy that the luminance transients P-VEPs of infants at all ages contain a negative component of short latency (< 100 msec) not evident in the adult, and that the latency of the main positive peak decreases with increasing age, both for luminance and colour responses (Figs 7–8, 12). As shown in Fig. 11, the latencies of the peaks in the transient P-VEPs and the corresponding apparent latencies of the steady-state P-VEPs are well correlated.

Comparison between luminance and colour transient responses shows an initial phase of development where the luminance and colour waveforms are practically indistinguishable, apart for a difference in amplitude. This is followed by a progressive differentiation in the waveform of the two responses (Figs 7–8) as confirmed by the principal component analysis (Fig. 9), and by a change of their relative amplitudes. The colour responses are smaller at first, but quickly increase in amplitude to exceed those to luminance contrast. The reduction of the luminance P-VEP amplitude relative to the colour P-VEP with increasing age may reflect changes in waveform resulting from the development of a negative component, that reduces overall amplitude of the positive peak. Similarly, for the steady-state P-VEP the change in amplitude of the colour responses relative to the luminance responses may be a consequence of the

change from low-pass to band-pass of the amplitude curve of the luminance P-VEP. This in turn might be due to the development of inhibitory mechanisms.

The transient P-VEPs therefore confirm and complement the steady-state findings on the development of the temporal characteristics of luminance and colour contrast P-VEPs in infants.

Possible mechanisms underlying the various P-VEP components and their development

There are three phases of development of the temporal frequency characteristics of luminance and colour pattern reversal response, for three response components of high, low and medium temporal frequencies, respectively. These components probably reflect three mechanisms with different temporal frequency tuning and different time constants.

The early developed high frequency component sets a limit to the temporal resolution of the luminance P-VEP, which approaches adult values as early as 3 months (Figs 1–3). The latency of this component corresponds to the latency of the early negative wave of the transient P-VEP. We have suggested that it may represent presynaptic or early post-synaptic activity in thalamus-recipient layers of the visual cortex in the infant, accounting for its early development. It is possible, however, that during the course of development the thalamo-cortical input activity contributes by a decreasing amount to the high temporal frequency, short latency component of the P-VEP, and that this instead starts to reveal cortical postsynaptic responses, possibly reflecting the initial depolarization of stellate cells in layer 4C of the striate cortex, as suggested by Schroeder *et al.* (1991).

The low-temporal frequency component is the major component of the colour P-VEP of the infant, and in the youngest age group (8 weeks) has similar characteristics (bandwidth and apparent latency) for luminance and colour responses. Although this component has a smaller amplitude in the colour response of the youngest infants, it develops rapidly reaching maturity by 13–14 weeks. This component might reflect the activity in response to both luminance- and colour-contrast of a population of cortical cells, not necessarily from V1, preferring relatively low temporal frequencies. The larger amplitude of this component for colour- as compared to luminance contrast in the older age groups (Fig. 6), as well as in the adult (Fig. 4), may suggest that it receives the major contribution from cells on the P-pathway. For luminance P-VEPs this component shows an early development also for patterns of higher spatial frequencies than that employed in the present experiment (Moskowitz & Sokol, 1980; Fiorentini & Trimarchi, 1992).

Values of peak latency around 140–150 msec are not inconsistent with the cortical circuitry subserved by the parvocellular thalamic input, given that the onset latency of 4C β and supragranular neurones (of both V1 and V2) is between 50 and 130 msec, and build to a peak activity 30–60 msec later (Nowak *et al.*, 1995). Developmental studies of the morphology of the neurones of 4C β in the

monkey show a gradual increase in spine density and dendritic complexity over the first 2–4 weeks (Lund & Holbach, 1991). This time course would correspond to about 2–4 months in humans, about the period over which the low temporal-frequency lobe matures.

The third component, largest in amplitude over the range of 10–15 Hz with apparent latency 100 msec or less in the adult, of relatively late development, may represent the response to both luminance- and colour-contrast of a population of cells of the various cortical areas responding best at higher temporal frequencies. It may at first appear strange that the chromatic response extends to high temporal frequencies, possibly suggesting a spurious chromatic response associated with the M pathway, particularly strong at 10 Hz (Hawken *et al.*, 1996). However, the fact that the response over this range of temporal frequencies is as large as at very low temporal frequencies makes this possibility unlikely. Schroeder *et al.* (1991) suggest that the P100 component of the transient pattern-reversal VEP arises from the depolarization of supragranular neurones of the striate cortex, presumably pyramidal cells of layers 2 and 3. If so, our results would indicate a delayed development of the circuitry of the superficial layers with respect to the thalamic input or the initial stage of visual analysis in the striate cortex. It is only after 6 months that several other responses ascribable to later stages of visual cortical processing appear in the infant P-VEP, such as cross-orientation inhibition (Morrone & Burr, 1986). Interestingly, this cortical interaction is also mediated by a fast and transient system, with characteristics similar to the components of medium temporal frequencies.

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