



## M- and L-cones in early infancy: II. Action spectra at 8 weeks of age

Michelle L. Bieber<sup>a,\*</sup>, Kenneth Knoblauch<sup>b</sup>, John S. Werner<sup>a</sup>

<sup>a</sup> *Department of Psychology, University of Colorado, Boulder, CO 80309-0345, USA*

<sup>b</sup> *Institut de l'Ingénierie de la Vision, Université Jean Monnet, Saint Etienne, France*

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### Abstract

Field sensitivities were measured under conditions of M- and L-cone isolation for seven infants (8–12 weeks-old) and two adults, using silent-substitution and the visually evoked potential (VEP). The efficacy of the receptor-isolation conditions were first verified by measuring psychophysical and VEP-derived action spectra from two color-normal adults under conditions of M- and L-cone isolation. M- and L-cone action spectra obtained from the two methods were found to be similar to the Smith and Pokorny M- and L-cone fundamentals, respectively. The VEP-derived action spectra obtained from infants and adults were well fit by the Smith and Pokorny M- and L-cone fundamentals. These data, in conjunction with our previous study, confirm that M- and L-cones are operating by 8 weeks and possibly as early as 4 weeks of age. © 1998 Elsevier Science Ltd. All rights reserved.

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### 1. Introduction

In a previous paper [1], we reported data that support the hypothesis that both M- and L-cones are functional in early infancy. We used a double silent-substitution technique to create stimuli that modulate only M- or L-cones, while holding the rod response constant. Under the assumption that photoreceptor responses are univariant, the silent-substitution technique [2,3] allows one to drive the response of a single receptor type in isolation while maintaining a constant output from the remaining receptor types. We measured the amplitude of the visually evoked potential (VEP) from 4- and 8-week-old infants as the mean luminance of an M- or L-cone modulating stimulus was increased over a 30 s period. Nearly all infants in both age groups demonstrated increases in VEP amplitude as the mean luminance of the stimulus increased. In addition, four male infants (4- and 8-weeks-old) were classified as suspects for a red/green color vision deficiency based on poor responses to only one of the cone-isolating stimuli, as well as a maternal history of

color vision deficiency [4,5]. While both of these findings are highly suggestive of functional M- and L-cones as early as 4 weeks, the evidence is not unequivocal, principally because of the possibility that infant spectral sensitivities differ from those of an average adult.

The validity of the silent-substitution technique relies on accurate knowledge of the spectral sensitivities of the photoreceptors/mechanisms held constant. If the stimuli are not adequately equated for these photoreceptors, isolation of a given receptor class can not be achieved. We have previously [6] detailed a number of factors (e.g. optical density differences, the Stiles–Crawford effect, etc.) that could render the infant photoreceptor sensitivities different from those of adults [16,18–20] and presented arguments that these factors would have minimal effect under our testing conditions. Nevertheless the clearest signature of a visual mechanism (e.g. a receptor class) is its spectral sensitivity, the reciprocal of the radiance needed to yield a criterion response. In previous experiments it has been possible to measure the spectral sensitivities of rods [7–9,17] and S-cones [10] in infants, but not to distinguish that of the M-cones from the rods and the L-cones, due to their overlapping sensitivities. Thus, in order to be certain that the M- and L-cones are indeed functional, one

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\* Corresponding author. Tel.: +1 303 4923304; fax: +1 303 4922967; e-mail: mbieber@psych.colorado.edu.

must measure the spectral sensitivities of these receptors.

To obtain action spectra, we have modified our previously described double silent-substitution technique [1,4,11]. Test stimuli with fixed cone contrast and overall luminance were used to obtain M- or L-cone isolation, while a superimposed monochromatic background field of variable wavelength (500–670 nm) was gradually increased to determine the number of quanta required to reduce the VEP response by a criterion voltage. A similar procedure was used by Estévez et al. [2] (but with silent-substitution for only a single receptor class at a time), to measure action spectra from both color-normal and dichromatic adult observers. If adult-like M- and L-cones are truly being modulated in infants, then the spectral sensitivities measured under both M- and L-cone isolation should correspond to the M- and L-cone spectral sensitivities, respectively. This is indeed what the results of the present study show. These data unequivocally confirm the functioning of M- and L-cone receptors in early infancy.

## 2. Methods

### 2.1. Subjects

Fifteen full-term infants were recruited from birth announcements in the local newspaper to participate in this study. Informed consent was obtained from a parent before testing commenced. Data were successfully collected from seven infants (six 8-week-olds, one 12-week-old). Each infant participated in 1–5 testing sessions that lasted  $\approx 45$ –60 min. Testing was completed within a 3-week period for each subject. The parents of all infants reported no history of color vision deficiency on the maternal side of the family. We were unable to collect data from eight infants due to crying, inattention or sleeping.

Two female adults (24 and 43 years-old) served as control observers. Both displayed normal color vision when tested with the Neitz anomaloscope, Farnsworth panel D-15 and the American Optical HRR pseudoisochromatic plates. Each adult subject participated in 5–10 VEP testing sessions that lasted  $\approx 2$  h.

### 2.2. Stimulus and optical system

Stimuli were rear-projected as a 6° disk using an optical system that provided mixtures of four monochromatic ( $\leq 8$  nm bandpass) lights. Channels 1–3 gave rise to the receptor-isolating component of the stimulus. For L-cone isolation, this portion of the stimulus consisted of a 540/640 nm mixture (channels 1 and 2) alternating at 15 Hz in square-wave counter-phase with a 570 nm light (channel 3), producing an

L-cone contrast of 0.38. M-cone isolation was achieved using a 540/645 nm mixture alternated with a 580 nm light, producing an M-cone contrast of 0.42. To isolate the response of one receptor class, e.g. the L-cones, the ratio of the radiances of the 540/610 nm mixture in one field and the radiance of a 570 nm light in a second field were adjusted so that each field produced equal quantal absorptions in M-cones and rods, respectively. When presented successively to the same retinal area, the substitution of one field for the other should be silent for M-cones and rods; any response obtained would then be due to the modulation of only the L-cones. The same logic is used to isolate responses originating in M-cones. See Ref. [1] for the computational procedures used in determining the isolation conditions. The addition of a fourth channel was used to create a steady, 6° monochromatic background field (520–670 nm) that could be superimposed onto the receptor-isolating field in order to measure field sensitivities.

### 2.3. Recording system

Bipolar VEPs were recorded with conventional EEG electrodes placed 1 and 3 cm above the inion for infants, and 2 and 8 cm above the inion for adults. A vector voltmeter was used to extract the phase-independent amplitude of the VEP in real time as a function of the mean luminance of the background field. See Ref. [1] for a detailed description of the recording procedures used in the present experiment. Ancillary measurements demonstrated that the amplitude of the fundamental component of the VEP was greater than the second harmonic, under our testing conditions (see Ref. [12], Appendix 3 for details).

### 2.4. Infant and adult VEPs

No dark adaptation period was used. After the electrodes were positioned, the infants were seated on a parent's lap 32 cm from the stimulus in the shielded chamber. Adult subjects were positioned 32 cm from the stimulus via a chin and forehead rest. At the beginning of each testing session, the mean luminance of the flickering receptor-isolating field (generally  $\approx 5$ –10  $\text{cd/m}^2$ ) was adjusted to produce a strong VEP response from the subject. This intensity level was maintained for the receptor-isolating component throughout the test session. The amplitude of the fundamental component of the VEP was then measured while continuously increasing the radiance of the superimposed monochromatic field for 45 s, over a 2 log unit range. The wavelengths of this field were selected in random order. Infants were viewed throughout the testing session on a video monitor (via an infrared illumination system) so that recording could be interrupted if the infant moved or turned away from the

stimulus. As the radiance of the monochromatic background field increases both the perception of flicker and the amplitude of the VEP are reduced. The reciprocal number of quanta needed to reduce the VEP amplitude by a criterion voltage at each wavelength defined the action spectrum of the mechanism(s) driving the VEP.

### 2.5. Psychophysics

Psychophysical action spectra (under M- and L-cone isolation) were collected from the two adult subjects following 5 min of dark adaptation. The observer's task was to locate their threshold for flicker using the method of adjustment. The observers were instructed to first increase the radiance of the monochromatic background field (starting at a point where flicker was apparent) until flicker was first abolished. The subject then decreased the radiance of the monochromatic background (starting at a point where the flicker was not detectable) until flicker was just detected. Both points defined a range, the geometric mean of which was used as the criterion. The wavelength of the background field was presented in a random order once through the entire series of wavelengths tested, and then repeated in reverse order for each testing session. Both adults participated in six 45-min sessions, three each for the L- and M-cone isolation conditions.

## 3. Results

Fig. 1 shows mean VEP amplitude versus radiance functions obtained from an adult (upper panel) and an infant (lower panel) observer during one testing session under conditions of M-cone isolation. Relative VEP amplitude is plotted as a function of the log radiance of the background field. These data are typical of those obtained from all subjects. For all observers, mean amplitude versus radiance functions were measured for each background wavelength tested in a given session, yielding a series of mean amplitude versus radiance functions like those presented in Fig. 1. Mean functions are based on 3–11 records for adults and 1–4 records for infants in any given test session.

The VEP amplitude of each of these functions starts out high and then declines as the radiance of the superposed background light is increased. There is an initial plateau in the VEP response before the amplitude begins to decline. The initial plateau corresponds to the VEP amplitude in response to the flickering receptor-isolating component of the stimulus. The point of the initial decline varies as a function of wavelength, in correlation with the sensitivity of the residual mechanism mediating the response.

### 3.1. Data analysis

Fluctuations in the amplitude of the VEP response can be seen at the beginning of the VEP functions during which the initial receptor-isolating stimulus intensity was constant. Some of this random fluctuation in VEP amplitude was eliminated by averaging the records obtained at each wavelength, especially for the adult observers who provided more data. For the infants, however, much of this noise still remained after averaging because the means were based on only 1–4 VEP records. To eliminate this noise in the data, mean amplitude versus radiance functions were normalized at the initial mean plateau of the VEP response.

The plateau for each mean function was determined using a least-squares, curve-fitting algorithm. Fig. 2 shows an example of how the mean amplitude versus radiance functions were fit. Relative VEP amplitude is plotted as a function of radiance. Amplitude versus radiance functions were fit by either a bilinear (upper panel) or a trilinear (lower panel) function. Most records were fit with the former, while some records, because they also displayed a terminal plateau (as a

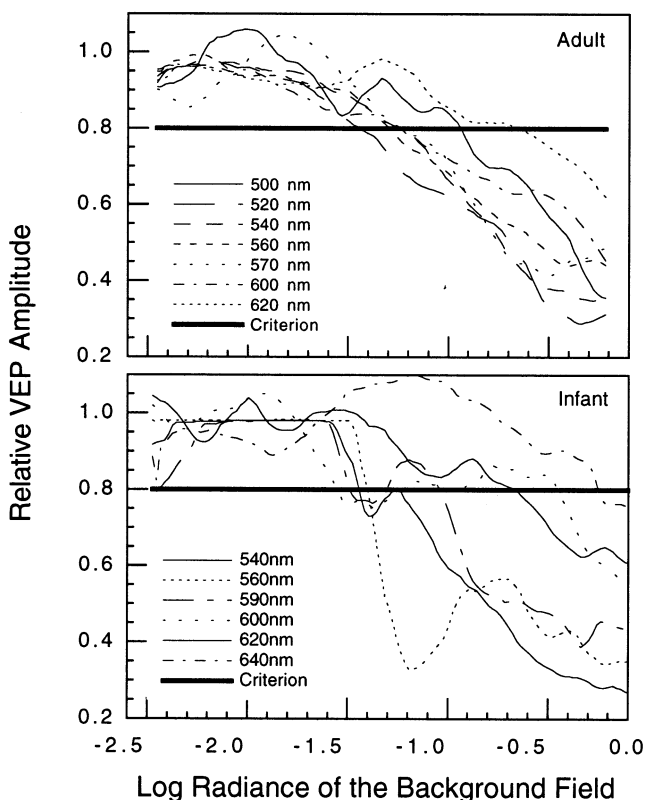


Fig. 1. Relative VEP amplitude is plotted as a function of the log radiance of the background field. Different curves show mean response functions obtained from an adult (upper panel) and an infant (lower panel) with different monochromatic background fields superimposed on the M-cone isolating stimulus. The bold line represents a possible criterion reduction in the VEP response that might be used to calculate action spectra.

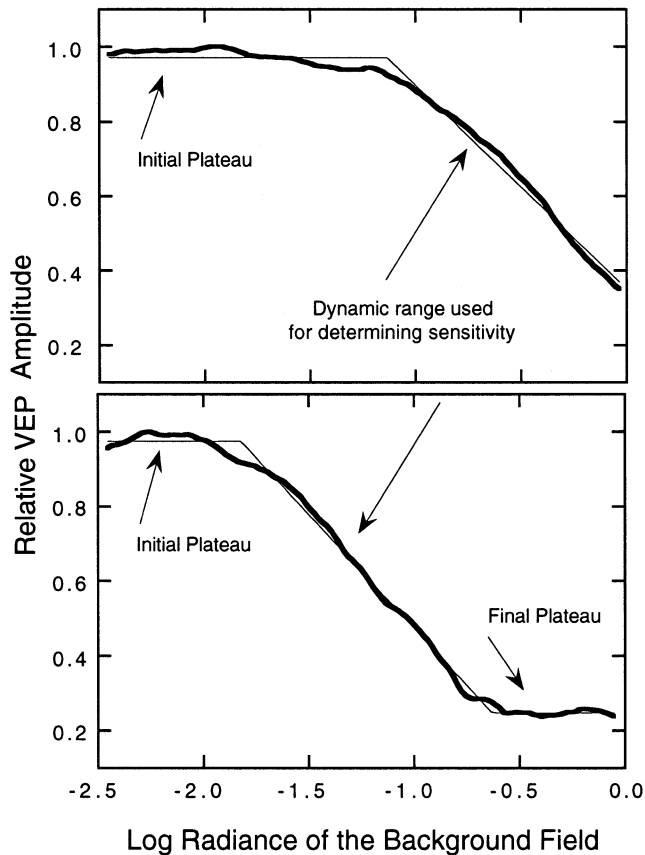


Fig. 2. Relative VEP amplitude is plotted as a function of the log radiance of background field. The upper and lower panels show mean amplitude vs. radiance functions fit with a bilinear and trilinear function, respectively. These functions were fit to each mean amplitude vs. radiance function using a least-squares criterion in order to estimate the plateau.

result of the VEP amplitude being less than the available operating range of the apparatus), were fit with a three-line function. In both cases, the intercept of the first line of zero slope was used to determine the plateau. The slope of the line fitting the descending limb of the VEP response was allowed to vary in order to provide the best fit. All mean amplitude versus radiance functions were then normalized at the mean plateau.

If the VEP response were to adapt within a given intensity scan, it might be difficult to interpret the action spectra obtained with this technique. To test for possible adaptation or saturation of the VEP response, records were obtained from both of the adult subjects, and one infant subject in response to the receptor-isolating stimulus alone (no background), for a 45 s period. If significant adaptation did occur, it would be evident as a gradual decline of the VEP response to the receptor-isolating stimulus, even though the stimulus is not varying in mean luminance. Fig. 3 shows mean amplitude versus radiance functions (thin curves) obtained from an adult (upper panel) and an infant (lower panel) during one testing session. Mean VEP amplitude in response to the receptor-isolating stimulus alone over the 45 s period (bold function), is also shown normalized at the mean

plateau of each data set. The mean VEP function for the infant in response to the receptor-isolating stimulus alone is based on 4 records collected at various times throughout the testing session. The adult function is based on 10 VEP records.

By eye, the functions appear to drift to lower amplitudes over the 45 s period. A test for linear trend [13] was significant in both cases (infant:  $t = 2.11$ ,  $df = 339$ ,  $0.05 > P > 0.01$ ; adult:  $t = 7.95$ ,  $df = 1089$ ,  $P < 0.001$ ). The maximum variation of the two curves is small, however, being  $< 14\%$  (or  $< 0.06$  log units) for the adult and  $< 31\%$  (or  $< 0.12$  log units) for the infant data. While it was not feasible for all infants to obtain VEP responses to the receptor-isolating stimulus alone (because of time restrictions), the analyses performed indicate the magnitude of the adaptation to be small compared with the responses measured in the presence of the background field, over the 45 s scan time. This interpretation is borne out by the data presented below which would be distorted by significant adaptation, showing systematic deviations from the M- and L-cone fundamentals.

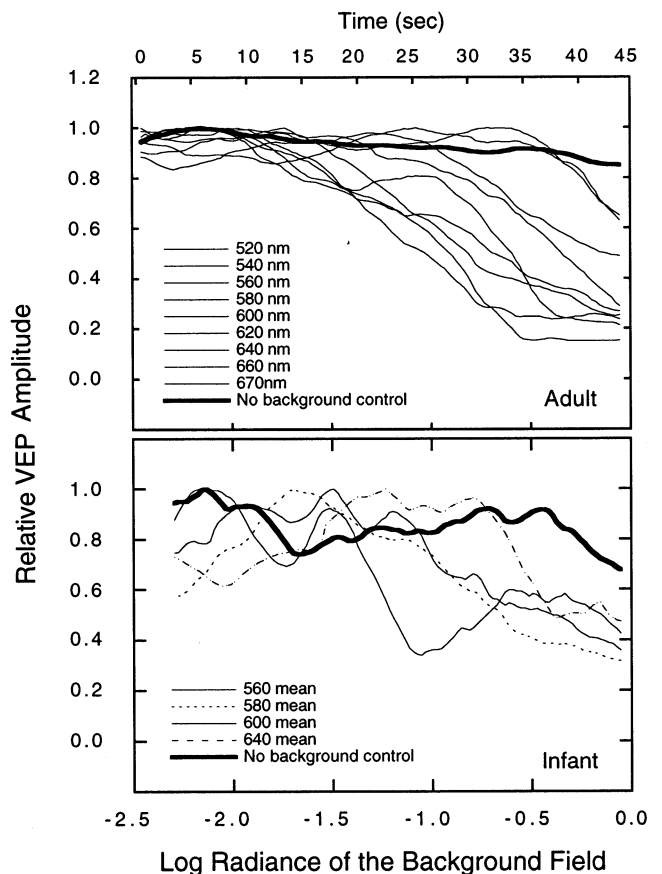


Fig. 3. Relative VEP amplitude is plotted as a function of the log radiance of the background field. Thin lines show mean response functions obtained from an adult (upper panel) and an infant (lower panel) for different background lights during one testing session. The bold curve represents the mean response to L-cone modulation alone (no background).

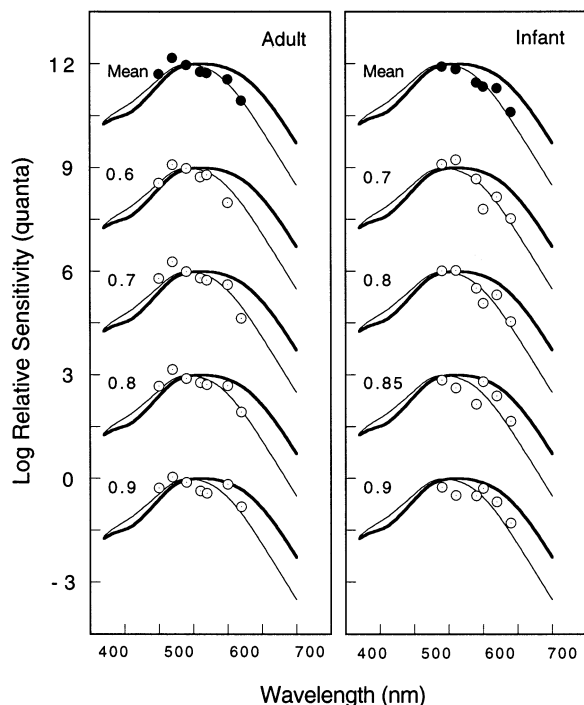


Fig. 4. Relative log sensitivity is plotted as a function of wavelength. The left and right panels show action spectra obtained from an adult and an infant, respectively, under conditions of M-cone isolation. Open circles represent action spectra determined from individual criterion reductions of the mean VEP response functions shown in Fig. 1. Filled circles show the mean action spectra calculated by averaging the four action spectra based on different criterion reductions (indicated by the values to the left of each action spectrum) in the VEP response.

### 3.2. Action spectra calculation

Action spectra were derived by calculating the reciprocal number of quanta from the superimposed monochromatic background field needed to reduce the amplitude of the VEP response by a criterion voltage. VEP responses modulated by univariant mechanisms (e.g. one receptor class), should produce action spectra with the same shape for any criterion. Field action spectra need not reflect univariant mechanisms, however, if the field acts on a post-receptoral site receiving signals other than those from the receptor class modulated by the test. It should be noted, however, that over the range of intensities that we used in calculating action spectra, there were no obvious violations of univariance. This was confirmed for all subjects in that the action spectra obtained using 3–4 different criterion amplitude reductions were nearly identical. This is illustrated for an adult (left panel) and an infant subject (right panel) in Fig. 4. Log relative sensitivity is plotted as a function of wavelength. Action spectra have been normalized using a least-squares criterion, to the [21] M- and L-cone fundamentals. Action spectra have been arbitrarily separated by 3 log units along the ordinate for clarity. The

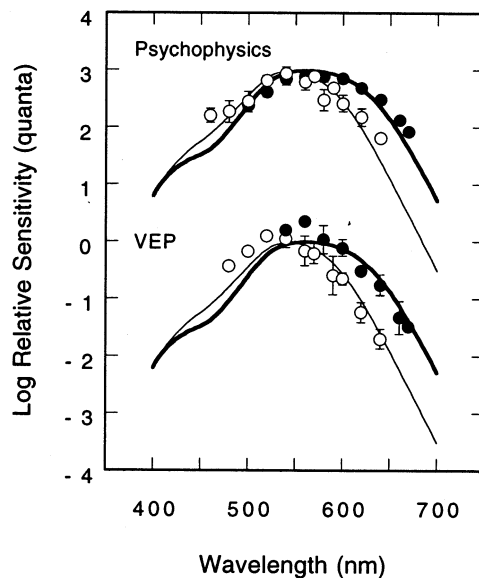


Fig. 5. Relative log sensitivity is plotted as a function of wavelength. Psychophysical and VEP-derived action spectra are shown in the upper and lower region of this figure, respectively, for two adults under conditions of M- and L-cone isolation. All data sets have been normalized to the M- (open circles) and L-cone (filled circles) spectral sensitivity curves using a least-squares criterion. Error bars denote S.D.

top function (filled circles) represents the mean of the lower four functions. These action spectra were calculated from the mean amplitude versus radiance functions shown in Fig. 1 that were obtained under conditions of M-cone isolation. The lower four action spectra in Fig. 4 (open circles) are derived from different criterion reductions in amplitude. There is reasonable agreement between the action spectra obtained for each criterion as would be expected if a single mechanism is being isolated. Therefore, the mean of 3–4 criteria was used to calculate action spectra for each subject in order to average out some of the noise in the VEP records. Moreover, the data of four observers (one adult, three infants) were analyzed using two additional fitting algorithms and no difference in the shapes of the derived action spectra<sup>1</sup> were found.

<sup>1</sup> One method involved fitting a Weibull function to each mean VEP response vs. radiance (RVR) curve. There was no theoretical motivation for this; the function, however, provided a reasonable fit to the data. The mean of 3–4 criterion levels ( $\alpha$ -values) was used to determine threshold. The second procedure involved normalizing all VEP–RVR curves obtained for each background wavelength along the abscissa and calculating a mean RVR curve. Assuming that a single receptor mechanism underlies each curve, the mean of all RVR curves should provide a good estimate of the shape of each individual RVR curve obtained under a given receptor-isolation condition. The mean RVR curve was then fit to the unnormalized VEP response curves and 3–4 criterion reductions in amplitude were determined from the template curves spaced differentially along the abscissa. There were no observable differences in the shape of the action spectra derived from either of these fitting methods.

### 3.2.1. Adult action spectra

Psychophysical and VEP-derived action spectra were obtained from two trichromatic adults. Fig. 5 shows their mean sensitivity data obtained under conditions of M-cone (open circles) and L-cone (filled circles) isolation plotted as a function of wavelength. Action spectra plotted in the upper (psychophysically) and lower (VEP technique) regions of the figure have been arbitrarily separated by 3 log units along the ordinate for clarity. Data obtained under M- and L-cone isolation were fit using a least-squares criterion to the Smith and Pokorny M- and L-cone spectral sensitivity functions, respectively. All remaining action spectra were fit in the same way unless otherwise stated.

There is good agreement between the data obtained using both psychophysics and the VEP and the respective M- and L-cone sensitivities, over most of the spectrum. The action spectra obtained psychophysically tend to be slightly broader than those obtained with the VEP. One possibility to account for this is that the sites determining each measure are different. Another possibility is that the experimental technique associated with each measure resulted in some differential adaptation or habituation that distorted the spectral sensitivities. We did not, however, pursue these hypotheses as such differences were secondary with respect to the goals of the present work.

### 3.2.2. Infant action spectra

Mean amplitude versus radiance functions (from 4–9 wavelengths) were obtained from seven infants. For five of these infants, action spectra were determined under both M- and L-cone receptor-isolation. The action spectra obtained from these five infants are shown in Fig. 6. Relative log sensitivity is plotted as a function of wavelength. Individual data sets have been arbitrarily separated by 3 log units along the ordinate, for clarity.

The infant data are more variable than the adult data, as expected from the more variable infant behavior during data collection and also because more records were obtained at each wavelength from the adult observers than from the infant observers. For most infants (except for infant AP, M cone condition), however, there is reasonable agreement between the action spectra obtained under M- and L-cone isolation to the respective M- and L-cone fundamentals. More important is the obvious separation between the two functions obtained for each infant.

The mean action spectra obtained under conditions of M- (open circle) and L-cone (filled circles) isolation for all seven infants are shown in the top portion of Fig. 7. Also shown (lower) are the mean VEP-derived action spectra obtained from the adult subjects. The systematic differences between the spectral sensitivities measured under the two isolating conditions demonstrate that at least two different mechanisms are operat-

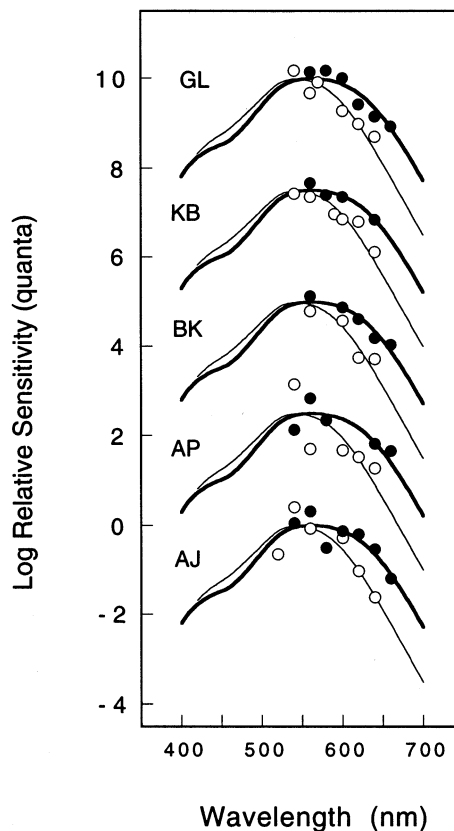


Fig. 6. Relative log sensitivity is plotted as a function of wavelength for five infants from whom action spectra were obtained under both M- (open circles) and L-cone isolation (filled circles). Each M- and L-cone isolation data set has been normalized to the M- and L-cone sensitivity functions (smooth curves), respectively, using a least-squares criterion.

ing in this part of the spectrum. Moreover, for both the adults and infants the agreement between the mean action spectra and the corresponding receptor sensitivities is excellent.

### 3.3. Statistical analysis

Additional analyses of the data were performed to reinforce the interpretation that the responses obtained under M- and L-cone isolation are indeed measures of the M- and L-cones, respectively. The sum of the squared errors (SSE) were calculated for each individual data set when fit to both the log M- and L-receptor templates. Action spectra were fit using a least-squares criterion to the rod, M- and L-cone spectral sensitivities and the SSE between each was calculated. In all cases the SSE was smallest when the action spectra were fit by their respective sensitivity functions (e.g. SSEs were smaller when the action spectra obtained under M-cone isolation were fit to the M-cone rather than the L-cone sensitivity function). The proportional reduction in error for each data set when normalized to the respective versus the counter-respective cone fundamental was, on

average, 66% which is significant at  $P = 0.05$  ( $df = 1.4$ ; conservative estimate; [14]).

When the action spectra obtained under M-cone isolation were fit to the M-cone spectral sensitivity function, on average, the sum of squared errors was reduced by a factor of 3 over the fit to the L-cone spectral sensitivity function, and a factor of 5 with respect to the rods. The same was true for the L-cone isolation data with respect to the L-cone spectral sensitivity and rods. The average reductions in squared error in this case were a factor of 5 with respect to the M-cone fits and a factor of 16 with respect to the rod fits. If one assumes that the probability that each of the three template curves is equally likely to yield the smallest squared error when fit to a given data set, then the probability that all 12 data sets are fit best by the appropriate templates is  $3^{-12}$ .

### 3.3.1. Residual analysis

Supplementary analyses of the signed residuals were also performed. When the log M-cone fundamental is fit to the log L-cone fundamental, the residuals for M–L and L–M follow the pattern shown by the solid curves in Fig. 8. Also shown in Fig. 8 are the patterns of residuals that result for each infant observer when his or her data obtained under M- (open circles) and L-cone isolation (filled circles) are fit to the counter-re-

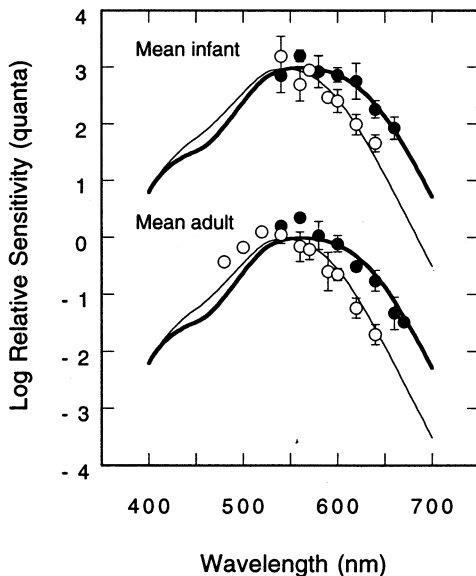


Fig. 7. Relative log sensitivity is plotted as a function of wavelength for the mean infant (upper portion of figure) and the mean adult VEP action spectra collected under both M- (open circles) and L-cone isolation (filled circles). Mean M- and L-cone isolation data sets have been normalized to the M- and L-cone sensitivity functions (smooth curves), respectively, using a least-squares criterion.

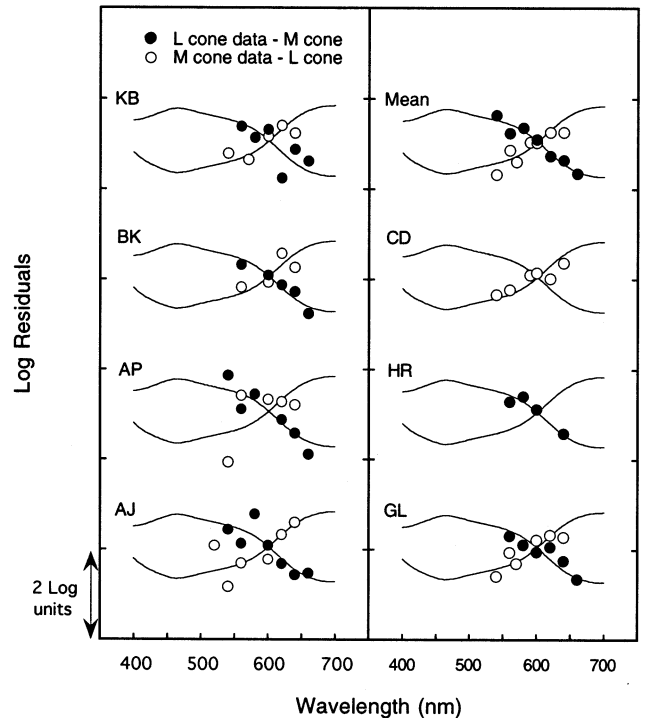


Fig. 8. The solid curves show the log difference (residual) between the [21] M-cone and the L-cone sensitivities (M-L and L-M) as a function of wavelength. Data points represent the residuals when the infant data obtained under L-cone isolation (filled circles) and M-cone isolation (open circles) are normalized by the method of least-squares to the M- and L-cone fundamentals, respectively.

spective cone fundamental (e.g. action spectrum obtained under M-cone isolation fit to the L-cone fundamental). The signed residuals are plotted as a function of wavelength for each infant tested, as well as the mean infant functions. Notice that for each subject the pattern of residuals is not random, but instead follows the specific pattern predicted if the data obtained are indeed measures of M- and L-cone spectral sensitivities. This tendency is confirmed by a goodness-of-fit test between the mean infant residuals and the M–L and L–M curves, (M-cone residuals:  $\chi^2 = 4.8$ ,  $df = 5$ , n.s.; L-cone residuals:  $\chi^2 = 1.96$ ,  $df = 6$ , n.s.). These data, thus, bolster the conclusion that the two different receptor mechanisms isolated are those of the M- and L-cones.

The preceding analysis was also used to compare the pattern of residuals formed by each data set (obtained under either M- or L-cone isolation) when fit to the rod spectral sensitivity function. In this case, the pattern of residuals of data obtained under M-cone isolation (fit to rods) corresponded to the pattern of residuals seen when the M-cones are fit to the rod spectral sensitivity curve. Similarly, data obtained under L-cone isolation (fit to rods) corresponded to the pattern of residuals between the L-cone curve and the rod spectral sensitivity curve, fit to each other.

#### 4. Discussion

Action spectra obtained from infants under conditions of M- and L-cone isolation correspond closely to the Smith and Pokorny M- and L-cone fundamentals, respectively. These results confirm the functioning of M- and L-cones inferred from the response functions in 8-week-olds and strengthen our previous interpretation that M- and L-cones are functional as early as 4-weeks after birth [1]. One potential criticism of the present results however, may be that sensitivity data were not obtained at wavelengths shorter than 540 nm. One might argue that measurement of only the long wavelength limb of the isolated mechanisms is, in and of itself, not enough to conclude that these data reflect M- and L-cones. For example, it might be suggested that the data obtained under M-cone isolation fit just as well to the L-cone function if the proper vertical shift of the data is applied. The analysis of residuals, however, refutes this hypothesis. Given the nature of infant testing, particularly at this age, it would not have been feasible to collect data under both receptor-isolation conditions across the entire spectrum from individual observers. In fact, it was not entirely clear at the start of this study if it would be possible to collect data in response to both isolation conditions from individual infants. While it is true that additional points at shorter wavelengths would strengthen the argument that these data are indeed mediated by the responses of individual cone classes, it seems not to be necessary, given the quality of the present fits to the M- and L-cone sensitivities.

Given the shorter outer segments of infant cones, one might be surprised that the infant data resemble so closely those of the adults. One would have expected the infant spectral bandwidths to be narrower. It should be noted that the expected magnitude of such effects is small ( $\approx 0.1$ – $0.18$  log units at the long wavelength spectral extreme in relation to the precision of our data). In addition, the least-squares fitting procedure which adjusts the curve to minimize the errors at all wavelengths may de-emphasize such effects. Normalization at the peak wavelength would better highlight them.

Fig. 9 summarizes the results of the present study and data from previous VEP studies from our laboratory. Relative log sensitivity is plotted as a function of wavelength. Data obtained from Volbrecht and Werner [10], shown by the triangles, have been normalized to the S-cone sensitivity function of Vos and Walraven [15] corrected for the ocular media density of an average infant. The data obtained by Werner [8], shown by the squares, have been normalized to a rod template based on CIE  $V'_{\lambda}$  corrected similarly for ocular media density as above. Note that several points at the long-wave extreme were excluded from this function where

rod isolation was not obtained. Data obtained in the present experiments under conditions of M- (open circles) and L-cone isolation (filled circles) have been normalized to M- and L-cone templates, also, corrected for ocular media as above.

#### 5. Conclusion

The present data provide unequivocal evidence for the functioning of M- and L-cone photoreceptors as early as 8 weeks of age. The similarity of responses previously measured at 4 and 8 weeks [1] suggests that both M- and L-cones are functional as early as 4 weeks, though the signals appear to be of lower amplitude. Taken together with earlier studies that conclusively identified rod [8,7] and S-cone responses [10], it can be concluded that all photoreceptor classes of the adult human retina are functioning within a month of birth.

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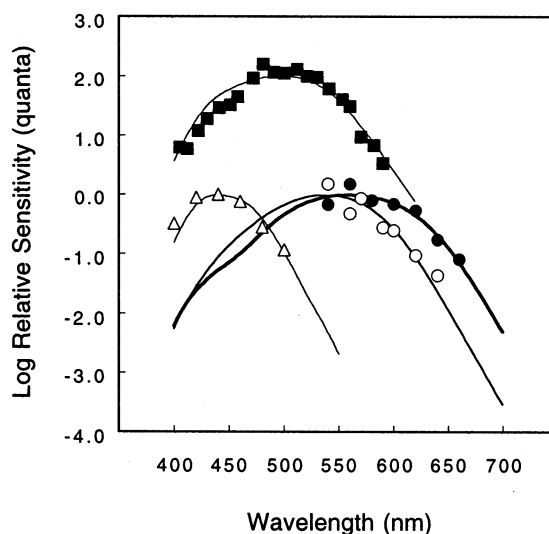


Fig. 9. Relative log sensitivity is plotted as a function of wavelength. Rod spectral sensitivity data (squares) from one 4-month-old infant [8] have been normalized to the CIE  $V'_{\lambda}$  function. Average data from seven infants at 4–5 weeks for S-cones [10] and the average M- and L-cone action spectra from the present study are shown as the triangles, open and filled circles, respectively. Data have been normalized by a least-squares criterion to the rod, S-, M- and L-cone templates corrected for the ocular media density of an average infant [8].

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