Development, maturation, and aging of chromatic visual pathways: VEP results

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It has been argued that the development and aging of the different achromatic and chromatic visual pathways may proceed independently. We review here the evidence for such independent changes with particular emphasis on electrophysiological results. Changes in chromatic and achromatic visual processing throughout the life span were studied using visual evoked potentials (VEPs). VEPs were recorded in response to the presentation of patterns designed to preferentially stimulate achromatic and S-(L+M) and (L-M) chromatic mechanisms. Recordings were made in subjects aged 1 week to 90+ years.

Longitudinal measurements were obtained from several infants and cross-sectional measurements were obtained from infants and older subjects. Responses to achromatic reversing patterns at low spatial frequencies appeared early and changed rapidly. Latencies of the achromatic reversal response decreased to mature values within the first 12-15 weeks of life. Responses to chromatic pattern onsets, however, appeared later (L-M: 4 weeks; S: 6-8 weeks) and changed continuously throughout the first year of life. Chromatic waveforms from 1 year to puberty appeared inverted relative to the adult waveform. The waveforms did not appear adultlike until about 12-14 years of age.

The latencies of the major negative component of the adult response reached a minimum around 17-18 years of age. Throughout the remainder of the life span, VEP latencies steadily increased and amplitudes slightly decreased. Latencies of responses to chromatic pattern onsets increased more rapidly than latencies to moderate contrast achromatic pattern reversals.

Keywords: color, development, visual evoked potential, visual evoked response, chromatic visual evoked potential, aging, visual pathways

Introduction

There has been much research interest in the development, maturation, and aging of the chromatic visual pathways. Here we attempt to review research in this area with a particular emphasis on information obtained in our lab employing the visual evoked potential as a measure of response. Numerous other studies have contributed to this area of research and have provided the foundation upon which we worked (e.g., Allen, Banks, & Norcia, 1993; Kelly, Borchert, & Teller, 1997; Morrone, Burr, & Fiorentini, 1990; Regan & Spekreijse, 1974; Rudduck & Harding, 1994; also reviewed by Regan, 1989).

Research in adults has demonstrated that low spatial frequency isoluminant patterns presented in an onset-offset mode are optimal for producing robust, reliable responses from chromatic pathways (e.g., Berninger, Arden, Hogg, & Frumkes, 1989; Murray, Parry, Carden, & Kulikowski, 1987; Rabin, Switkes, Crognale, Schneck, & Adams, 1994). Previous research has demonstrated that the latency of the large major negative wave in this response is quite reliable even in the face of unavoidable local departures from isoluminance and large intentional luminance contribution (Porciatti & Sartucci, 1999; Rabin et al., 1994). Of particular importance is the ability to generate large and reliable responses from color mechanisms with short-wavelength cone input (S-(L+M) pathways). The robust nature of the chromatic responses have allowed researchers to apply the visual evoked response (VEP) technique as a sensitive and objective measure of neural integrity in the clinic (Crognale et al., 1993) where color vision mechanisms, and particularly the S cone pathways, have frequently been shown to be especially vulnerable to insult from disease, trauma, and toxins (Crognale et al., 1993).

The major goals for the work summarized here follow: 1) To understand the developmental time course of the chromatic responses. The appearance of the waveforms in young adults is known and preliminary work in infants showed that their responses might be quite different. However it is not known how the waveforms change shape during development to finally appear as they do in the adult. 2) To better understand the development of the B/Y response that has often been neglected in studies of color vision. 3) To understand the relative time course of development of the B/Y (S-(L+M)), R/G (L-M), and achromatic (L+M+S) mechanisms. 4) To try to develop a normative set of waveforms over the life span to use in the clinical setting. Success in the clinic with young adults motivated our efforts to extend this research to children, adolescents, and the aging population. To achieve these goals, we applied the visual evoked potential to measure neural responses to

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achromatic and isoluminant pattern onset stimuli over the life span from 1 week of age to 90+ years.

Methods

General

The experiments reported here were conducted at four different institutions and used subjects of many different ages; thus, the experimental procedures varied somewhat. The interested reader is referred to the original published studies for a more complete description of the procedures (Crognale, Kelly, Chang, Weiss, & Teller, 1997; Crognale, Kelly, Weiss, & Teller, 1998; Crognale, Page, & Fuhrel, 2001; Madrid & Crognale, 2000; Rabin et al., 1994).

Subjects

We tested subjects ranging from 1 week to 93 years of age. Infants and children were recruited from the Seattle area. Initial adult subjects were recruited in Berkeley while those in the aging studies were recruited in the Reno areas. A total of 3 infants were tested longitudinally and 14 others were tested cross-sectionally. Only the longitudinal data are presented here. We tested 38 subjects ranging in age from 1 to 26 years for the maturation study. A total of 20 subjects were tested in the aging study, ranging in age from 21 to 93 years.

Stimuli

We utilized the extension of the MacLeod-Boynton cone-based color space (Derrington, Krauskopf, & Lennie, 1984) and the Smith-Pokorny (Smith & Pokorny, 1975) cone fundamentals to specify the stimuli. This color space and our application have been described in detail previously. Modulation of colors along specific directions in this color space produces selective activation of different chromatic mechanisms or cone classes. Patterns composed of colors modulated along an LM axis preferentially modulate the L and M cones in opposition and thus the red/green color opponent cells of the parvocellular pathway. The S axis preferentially modulates the S cones and thus the S-(L+M) color pathway. Modulation along the luminance axis modulates all three cones simultaneously and thus preferentially modulates the achromatic/luminance pathways. Use of a standard set of isoluminance values was justified by previous studies demonstrating that infant and adult isoluminance values are similar (Bieber, Volbrecht, & Werner, 1995) and by studies showing that the amplitudes and latencies of the major negative components of the chromatic onset responses are robust to large intentional luminance mismatches (Rabin et al., 1994; Porciatti & Sartucci, 1999). For infant data presented here, cone contrasts along the different axes were M axis: L=8.7%, M=17%; S axis: S=81%; and luminance axis: L, M, S= 90%. In the maturation study, the cone contrasts along the axes were LM axis: L=9%, M=18%; S axis: S=83%; and luminance axis: L, M, = 90%. In the aging study, the cone contrasts were LM axis: L= 8.7%, M= 17%; S axis: S=81%; and luminance axis: L, M, S=90%. The waveforms presented here were recorded in response to 0.5 cpd horizontal gratings subtending 21 deg. In some cases, we also recorded responses to large (160 arc min) reversing achromatic checks to compare with results from previous studies and to make sure that we were getting responses from infants at the earliest ages. Patterns were presented in an onset-offset mode (200 ms-on/800 ms-off). Patterns were generated by a personal computer (either a Macintosh or a PC with a Cambridge Research graphics board) and presented on a CRT display. The time and space-averaged luminances and chromaticities of the stimuli were kept constant across conditions in each study. The luminances and CIE chromaticity coordinates of the stimuli for the different studies were infants: 51.5 cd/m^2, 0.340, 0.360; maturation: 56 cd/m^2, 0.333, 0.333; and aging: 42.2 cd/m^2, 0.290, 0.304.

Recording

Because the experiments spanned several institutions and age ranges, the recording conditions and equipment varied somewhat from study to study. The recording procedures that were ideal in earlier studies in adults did not always work well in small children (e.g., earlobe clips for the ground and reference electrodes used in adults were favored toys of young children who usually pulled them off). Preliminary tests were run to determine if different electrode placements or recording apparatus resulted in significant differences in waveform shape. Results from these preliminary tests revealed that the shape of the chromatic waveform response was robust across our recording conditions in young adults. In general, VEP waveforms were recorded using Grass electrodes and amplifiers and a National Instruments data acquisition board input to either a PC or a Macintosh computer.

Results and Discussion

Before introducing the developmental data, we will review responses in the normal young adult. Figure 1 shows typical VEP responses from a young adult to the different stimuli. The top trace shows the response to a clinical standard, a reversing black and white checkerboard pattern. This response is simple in shape, and consistent across observers. The major component is a positive peak at about 100 ms that has been termed the P100 response. The second trace shows the well-known achromatic onset response with the typical triphasic positive-negative-positive complex responses most often termed C1 CII and CIII. The response to achromatic

onset at low spatial frequencies is generally small in amplitude, complicated, and varies between individuals. Consequently, responses to achromatic onset stimuli will not be reviewed here. The poor response to low spatial frequency achromatic onsets has been noted previously (reviewed in Rabin et al., 1994, and Porciatti & Sartucci, 1999) and is probably in part a reflection of the bandpass tuning of the achromatic mechanisms. It is likely that there are numerous underlying mechanisms contributing to this complex waveform.

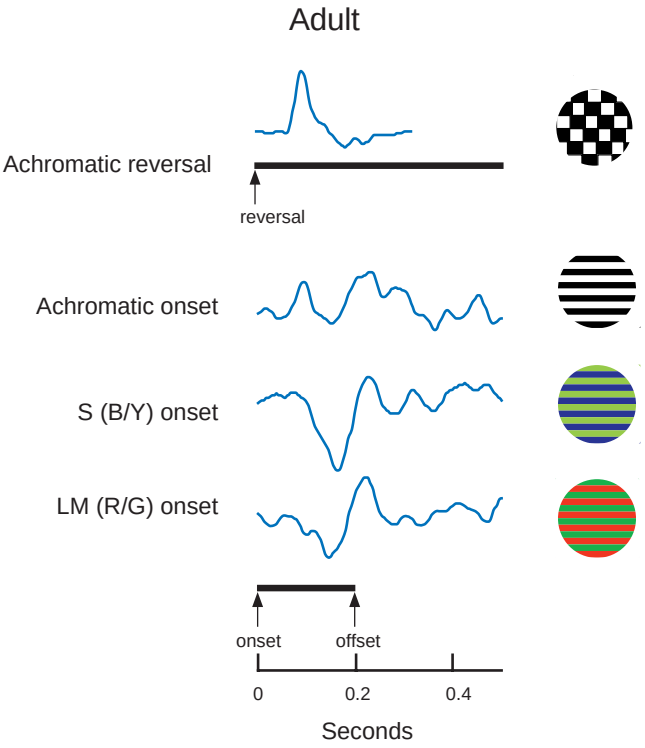

Figure 1. VEP waveforms obtained from a young adult in response to achromatic and chromatic stimuli. Stimulus appearance is simulated in the circular patterns on the right.

The bottom two traces show the isoluminant chromatic response generated using stimuli designed to preferentially modulate the S-(L+M) pathway (S) and the L-M pathway (LM). These waveforms are simpler than the achromatic onset response in that they are largely biphasic or monophasic with the major component being a large negative wave that appears to be similar to the CII component of the achromatic onset. The chromatic waveforms lack a significant P100 component. Unlike the achromatic onset response, the chromatic onset waveforms in adults are similar across individuals and for low spatial frequencies patterns are much larger than responses to achromatic onset stimuli even when the latter are at maximum contrast. The major difference between the LM and S axis waveforms is that the latency for the S axis response lags behind that of the LM response (e.g., Crognale et al., 2001; Porciatti & Sartucci, 1999).

It has been argued that the major negative wave of the chromatic response is largely generated by the parvo (and konio) pathway, whereas the positive peak at 100 ms or CI is generated by the luminance/magno pathway (e.g., Berninger et al., 1989; Murray et al., 1987; Porciatti & Sartucci, 1999; Rabin et al., 1994). That both of these components are apparent in the response to achromatic onsets is consistent with this suggestion. Further support for this position can be seen in the results from source-localization experiments by Ossenbloch and others (e.g., Ossenblok & Spekreijse, 1991).

Strong evidence that the present stimulus conditions preferentially modulate different chromatic and achromatic pathways has been given previously and include studies of chromatic adaptation, transient tritanopia, and color anomalous individuals (e.g., Crognale et al., 1993; Rabin et al., 1994).

Infant Responses

To characterize the development of the response to chromatic stimuli, we tested 3 infants in a longitudinal manner. They were as young as 1 week (see Figure 2) to the end of the first year. We also tested the parents of 2 of the infants. The longitudinal design allowed us to see the change in waveform shapes over very short intervals. In addition, we tested 14 infants in a cross-sectional manner and an obligate red-green color deficient infant as a control.

Figure 2. One of the setups for testing infants. Infant Sam is shown at 1 week of age.

Figure 3 shows waveforms obtained longitudinally for 2 of our subjects using achromatic reversing patterns. The most striking thing about these data is the smooth and orderly progression of the components to shorter latencies as the infant develops. These changes are easy to see by eye. The systematic changes in the waveform shapes for the reversals are essentially complete within the first several months. The latency of the main positive component of the reversal response shifts rapidly from about 300 ms to 96 ms and appears as it does in the adult (waveforms at top) by about 2-3 months of age. These latency data and data collected from our cross-sectional population agree nicely with results published from other

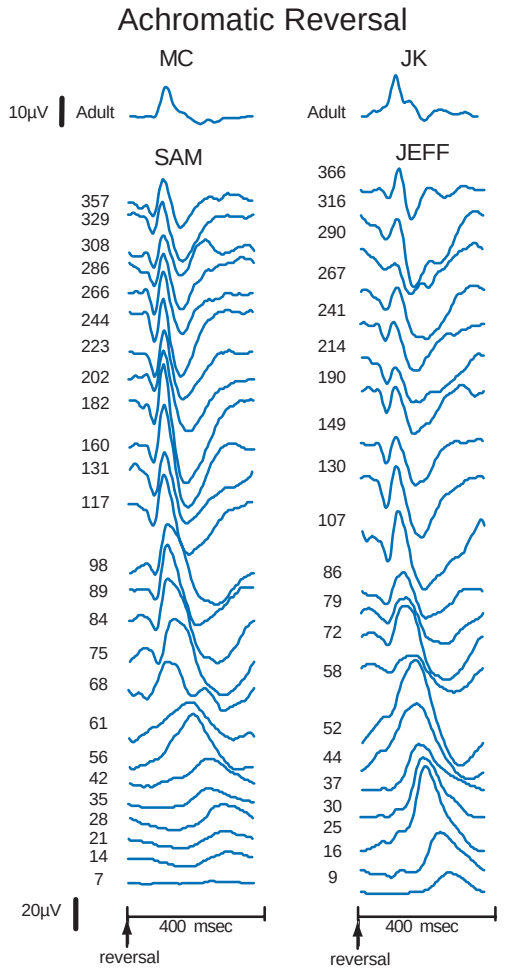

Figure 3. Longitudinal series of responses from 2 infants to achromatic reversing checks (163 min, 1.4 Hz). The ages in days are indicated. Responses from parents (M.C. and J.K.) of the infants are shown above (modified from Crognale et al., 1997).

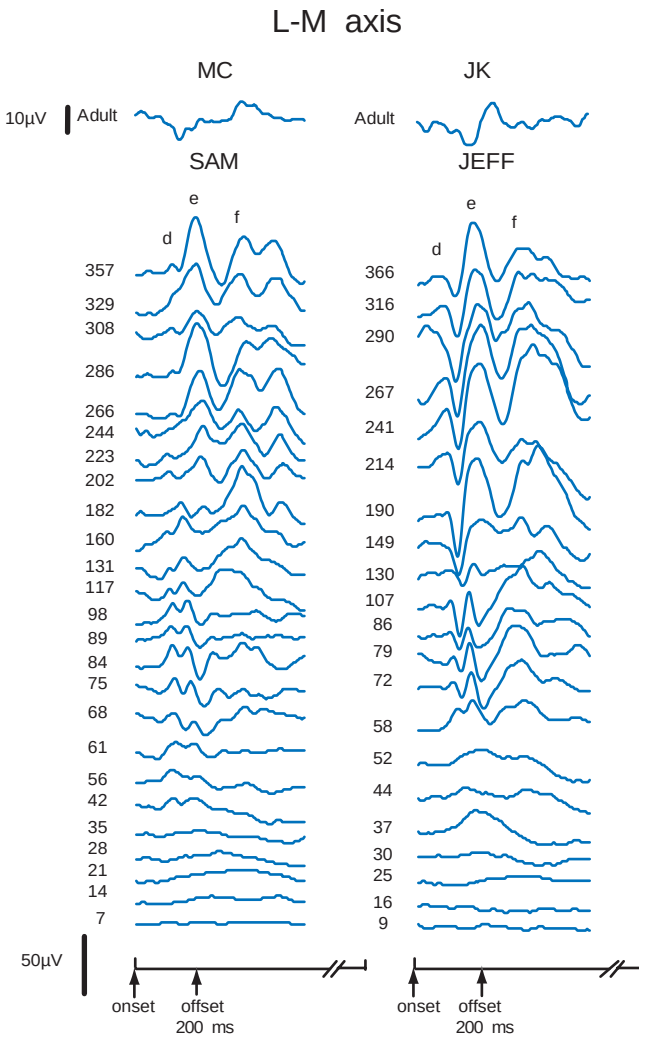

Figure 4. Responses to isoluminant L-M stimuli. Other conventions as in Figure 3 (modified from Crognale et al., 1998).

labs using achromatic reversal stimuli (e.g., McCulloch, Orbach, & Skarf, 1999; Moskowitz & Sokol, 1983).

The pattern of changes in the LM stimulus waveforms shown in Figure 4 is quite different than that of the achromatic reversal. In particular, the responses do not become reliable until a month or so after birth. The changes in the major components are systematic but more complex than those seen with achromatic reversals. The component peaks shift in latency and appear and disappear throughout the first year. For example, multiple early positive peaks at about 150 ms appear in the response around 1.5 months, do not shift much in latency, eventually disappear by about 4 months of age, and are absent from the adult waveforms. In addition, there are other large components that do not appear until much later in development, about 4-6 months of age. The early waveforms lack the characteristic prominent P100 peak seen early on in the achromatic waveforms.

Most importantly, the LM waveforms are not yet adultlike at 1 year of age. The waveforms display a positive-negative complex rather than the adult negative-positive shape.

Examination of the responses to S axis stimuli shown in Figure 5 reveals a similar story. The S axis responses do not begin to be reproducible until about 6 weeks of age. The major positive and negative components shift continuously in latency but do so at different rates so that they get closer together later in development.

Like the LM waves early in development, there are small positive components at about 140-180 ms that disappear in the later waveforms. Also like the LM waveforms, the S axis responses become quite large and the early waveforms lack the prominent P100 peak seen in the achromatic responses. The S axis waveforms at 1 year of age also do not yet appear as they do in the adult and are still changing.

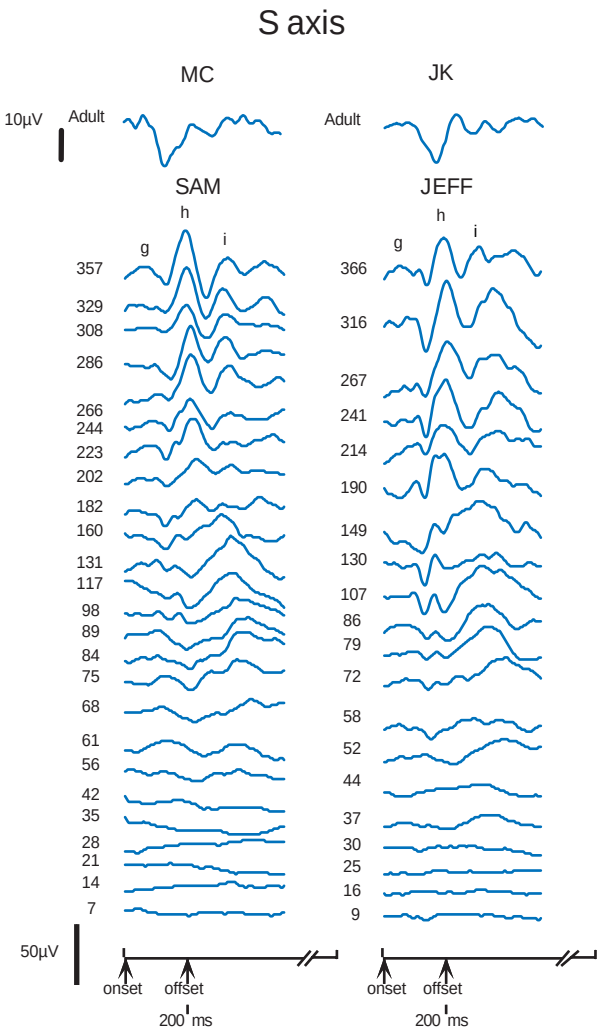

Figure 5. Responses to isoluminant S stimuli. Other conventions as in Figure 3 (modified from Crognale et al., 1998).

Although the waveform changes in the chromatic series are complex at any given age, the waveforms themselves are quite reproducible as shown by test-retest data for both chromatic and achromatic waveforms. For the achromatic stimuli, waveforms are reproducible by our earliest recording (1 week). For the LM stimuli, waveforms are consistent by about 6 weeks of age. For S axis waveforms, the responses appear to be reliable just after 6 weeks of age. Suttle, Anderson, and Harding (1997) provide convincing evidence that the S responses appear between 4-8 weeks of age but suggest that they appear before the LM responses. One possible explanation for this discrepancy is that Suttle et al. used a lower spatial frequency (0.2 cpd) than we did in our studies (0.5 cpd). In adults, it is known that the spatial tuning function for S stimuli is shifted to lower frequencies relative to that of the LM pathway. Though small, such differences in stimulus spatial frequency may be enough to bias one system over the other. Another explanation may simply be inaccuracies introduced by small sample sizes in both studies because 1 of the 5 infants in the Suttle et al. study showed LM responses developing before S responses. Nonetheless, the conclusion of Suttle et al. that S and LM pathways develop at a similar *rate* is not seriously challenged by the results presented here.

It is reassuring that not only are the main features of the waves constant but also the more subtle fluctuations are reproducible and therefore might be meaningful. In addition, we have found that although the relative contribution of different components differs across infant subjects, the latencies of the major components appear to be in reasonable agreement across subjects at a given age.

Figure 6 plots the amplitudes and latencies of the responses as a function of age on a log scale for 3 infants studied longitudinally. The smooth and systematic shift in the latencies of the achromatic reversal responses is shown in the upper left panel. The adult latency of the P100 response is reached early in the first year of life. The amplitudes of the chromatic responses increase over the first few months and then decrease during the remainder of the first year.

The middle and lower panels quantify the waveform changes for the chromatic responses. The latencies of some of the major components indicated in Figures 4 and 5 are plotted on the left. There are apparent discontinuities in the latency changes with age. However, these abrupt changes occur because the waveform shape changes are complex and some peaks appear to be replaced by others during development. Nonetheless, gradual decreases in latency and prolonged developmental changes are apparent.

To help verify that the stimuli that were effective in isolating the different pathway responses in adults were also effective in infants, we recorded responses from a child who was classified as obligate deuteranomalous because the mother of this child was deuteranomalous (Crognale et al., 1998). The responses from this infant for stimuli modulated along luminance and S axes were extremely similar to those of age-matched infants with presumably normal color vision (see Figure 7) (the status of normal color vision for this subject has subsequently been verified at age 4). However, for stimuli modulated along the LM axis, the major components of the responses were clearly diminished. Interestingly, the small, early, positive components at about 100 ms were preserved in the deutan infant responses suggesting that these components may not be generated by the LM chromatic pathways, and perhaps they were a result of luminance contribution as has been observed in adults.

These results demonstrate that the chromatic VEP is useful for detection of congenital color vision deficits in infants and extend our previous work showing that the VEP recorded in response to stimuli modulated in different directions in color space can reliably detect and classify both congenital and acquired color deficits (Crognale et al., 1993).

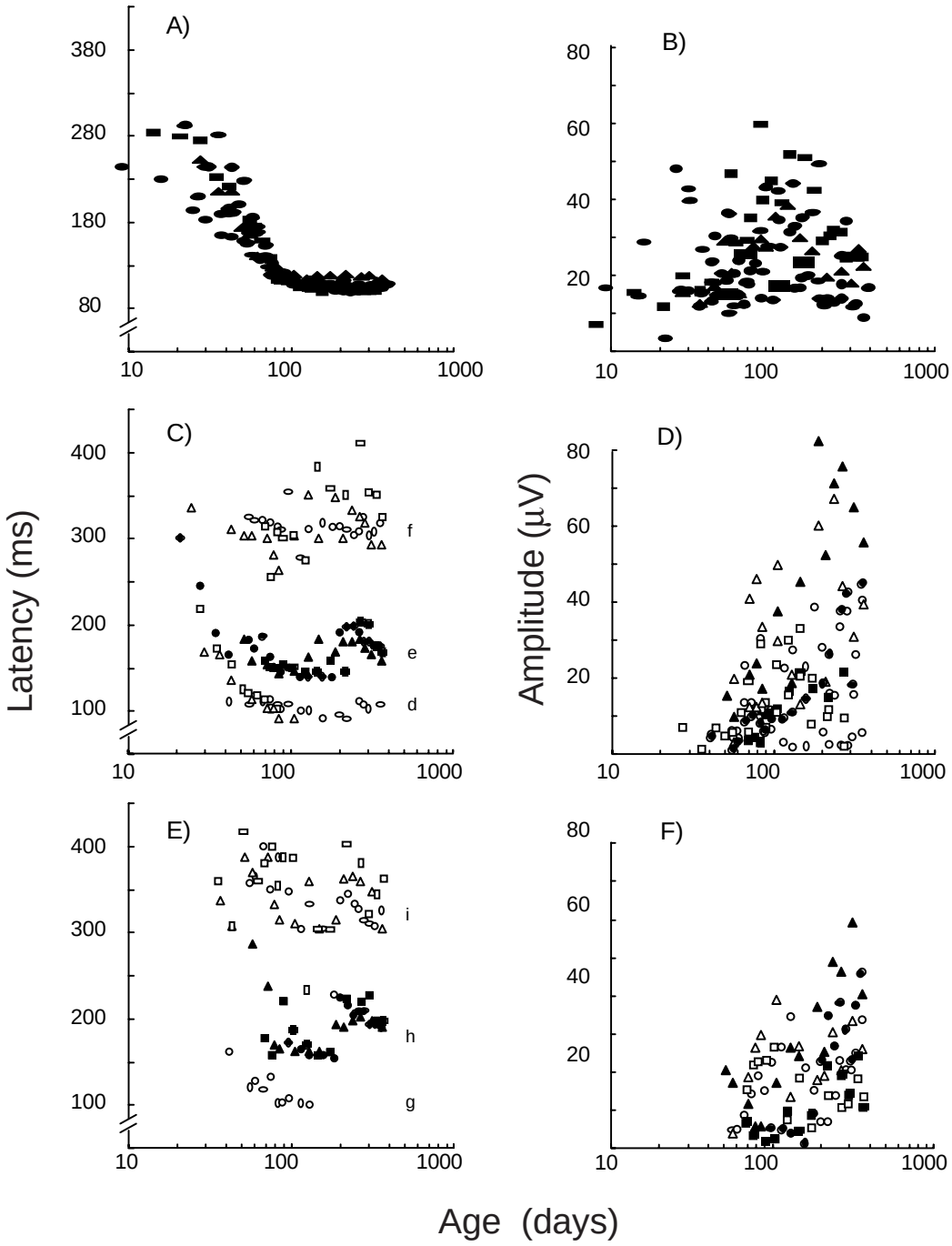

Figure 6. Latencies (left) and amplitudes (right) for 3 longitudinal subjects. Panels A and B plot data for the major positive component of the achromatic reversal response in Figure 3. Panels C and D plot the data for major components of the LM chromatic waveforms for the 3 infants. The components are labeled d, e, and f and correspond to the major peaks indicated in Figure 4. Panels E and F show the data for the S cone axis and the major component peaks of Figure 5 are labeled g, h, and i.

In sum, the major differences in the longitudinal development of the achromatic and chromatic waveforms at low spatial frequencies are 1) the chromatic waveforms develop later and are more complex than the achromatic reversal waveforms, and 2) the latencies of the major fast components of the achromatic responses are mature by about 3 months whereas the chromatic waveforms are still changing substantially at 12 months of age. The complex changes seen in the chromatic waveforms during development suggest caution when interpreting chromatic results from steady state or sweep techniques in a developmental context. Because these techniques measure amplitudes at a fixed temporal frequency, one might expect complex effects on response amplitudes due to the changes in the individual components of the response as the infant develops.

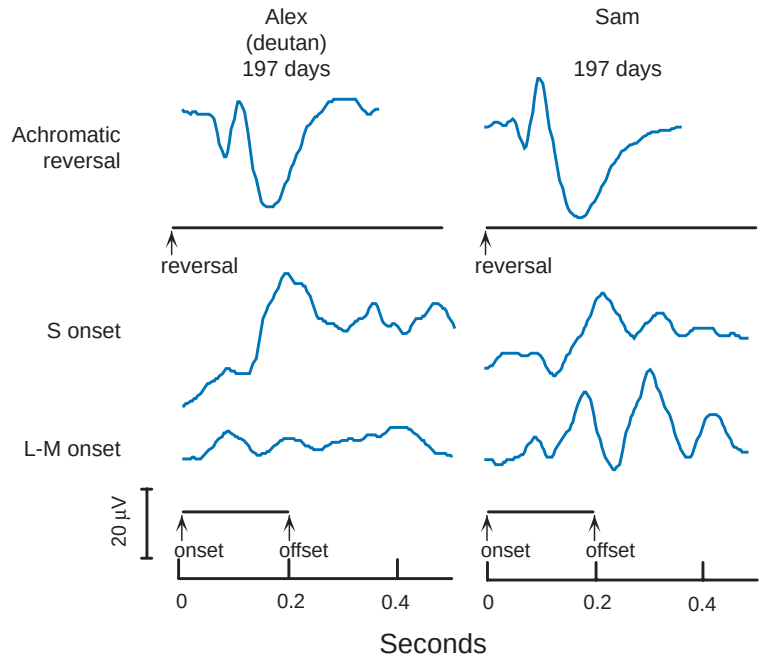

Figure 7. Responses obtained from an obligate deutan infant (Alex, left) and those of an age-matched infant with normal color vision (Sam, right) (Figure modified from Crognale et al., 1998).

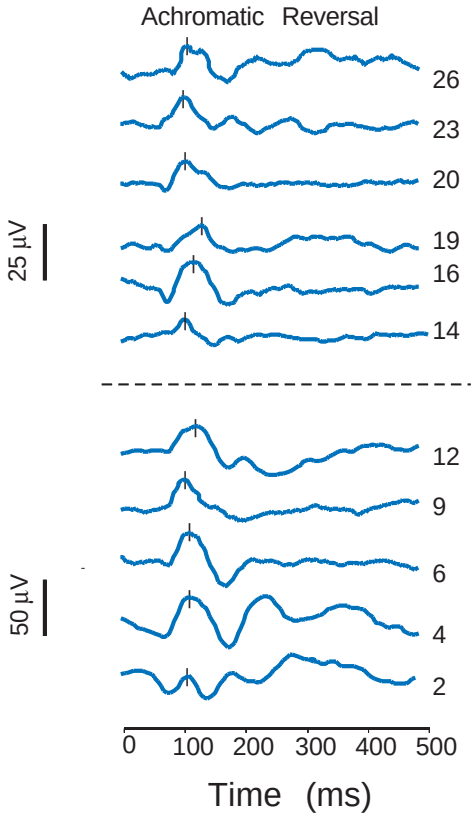

Figure 8. Representative VEP responses to achromatic reversing stimuli. The ages in years of the subjects are indicated. Vertical hatchmarks indicate location of the peak of the P100 response. Note the change in scale between the younger and older subjects.

Adolescent Responses

The result that the infant responses were not yet adultlike at the end of the first year led to an examination of the responses of subjects aged 1-18 years. Figure 8 shows representative achromatic reversal responses from 2 years to adulthood. Consistent with previous reports using low spatial frequency stimuli, the waveform shapes change very little with maturation. The amplitudes, however, decrease with age. It has been proposed that the sources of the reduction in amplitude may be gross changes in skull morphology and thickness as well as skin conductance. In contrast though, the latency of the positive response, the P100 component (vertical hatch marks), remains relatively fixed over this period. These results are thus in agreement with conclusions drawn by others (reviewed by Zemon et al., 1995) that skull thickness or morphology cannot account for decreases in amplitude with age.

Figure 9 shows representative responses to the LM chromatic onset stimuli. In contrast to the achromatic reversal responses, the waveforms change shape in a systematic way. It appears that the major negative wave gradually moves forward in time while the positive peak does not and eventually the positive negative complex turns into the typical negative positive complex seen in the adult. There is a point about at puberty where the responses may appear to cancel. The adult waveforms are not attained until after puberty.

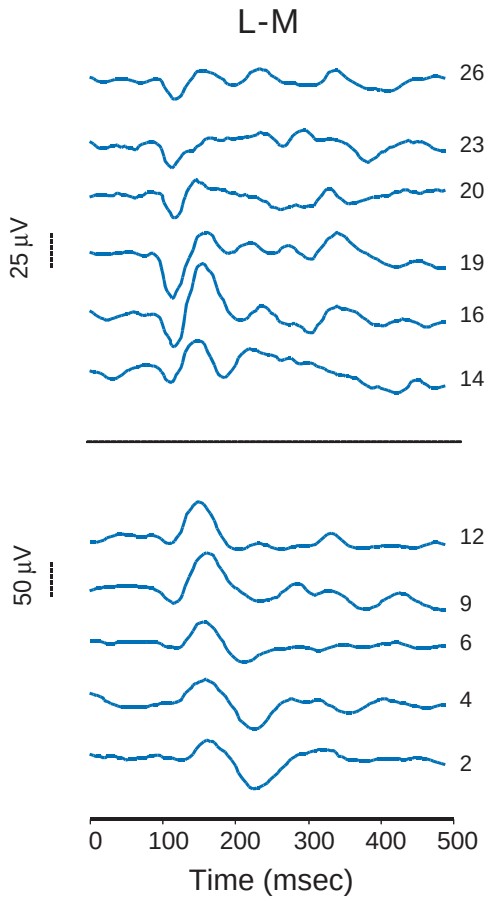

Figure 9. Representative VEP responses to LM onset stimuli. Other details as in Figure 8.

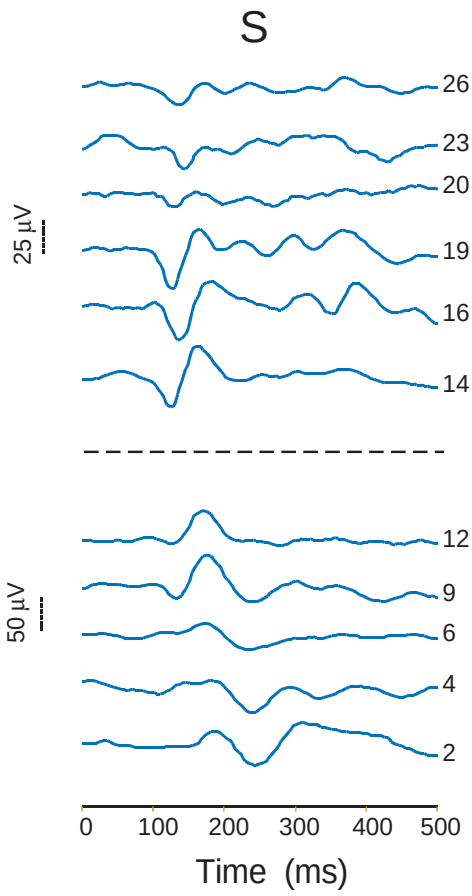

Figure 10. Representative VEP responses to S onset stimuli. Other details as in Figure 8.

The representative responses from the S stimuli (see Figure 10) are very similar to the responses from the LM stimuli. The waveforms show a gradual change from a positive-negative complex to a negative-positive wave. As with the LM responses, the cause of the changes in shape appears to be a decrease in the latency of the negative component of the waveform.

These chromatic results are similar to the results discussed by de Vries-Khoe and Spekreijse (1982) for maturation of achromatic onset responses. However, the long-term changes in the de Vries-Khoe and Spekreijse data were predominantly seen when using stimuli with high spatial frequency content. Also, the changes were more complex, resulting in triphasic adult waveforms, as mentioned earlier, and could not be modeled easily by a simple shift in latency. Data here suggest that some of the changes seen in the de Vries-Khoe and Spekreijse data may be due to changes in pathways that carry chromatic information at low spatial frequencies and achromatic information at high spatial frequencies as has been suggested for parvocellular pathways. Data presented here also support the results from Gordon and McCulloch (1999) and their claim that parvocellular pathways continue to show immaturities at least as late as 11 years of age.

The results from experiments presented here suggest that the neural pathways that process chromatic information are not mature until around puberty. This conclusion is further supported by the results of psychophysical studies that demonstrate continued improvement in color sensitivity until late childhood (Abramov et al., 1984; Hollants-Gilhuijs, Ruijter, & Spekreijse, 1998; Knoblauch et al., 1987; Knoblauch, Vital-Durand, & Barbur, 2001; Verriest, Van Laethem, & Uvijls, 1982). Furthermore, the source of this late maturation is likely be in the cortex as suggested by source localization data (e.g., Ossenblok, Reits, & Spekreijse, 1992) and numerous studies indicating immature connections in cortex prior to puberty. It is probable that continued myelinization and development of lateral connections contribute to the complex changes seen in the VEP from birth through puberty.

Figure 11 plots the amplitudes of the responses obtained from 38 subjects, aged 2-26 years. Amplitudes were calculated as baseline to peak for the achromatic responses and baseline to the major trough for the chromatic responses. In general, the amplitudes appear to increase until about the age of 9 and then slowly decrease with increased age. There is large variability in the amplitude data as reported previously.

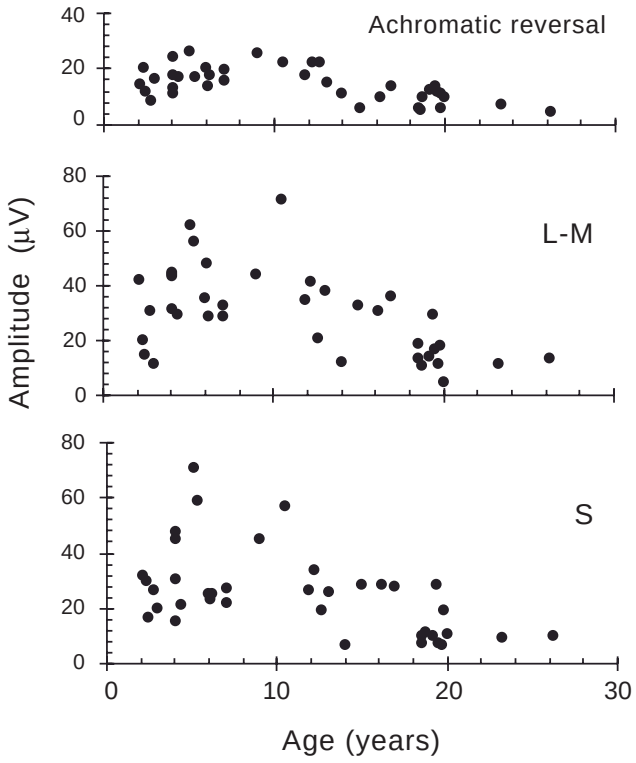

Figure 11. Amplitudes of the VEP in response to achromatic reversal and chromatic onset stimuli as a function of age (modified from Madrid & Crognale, 2000).

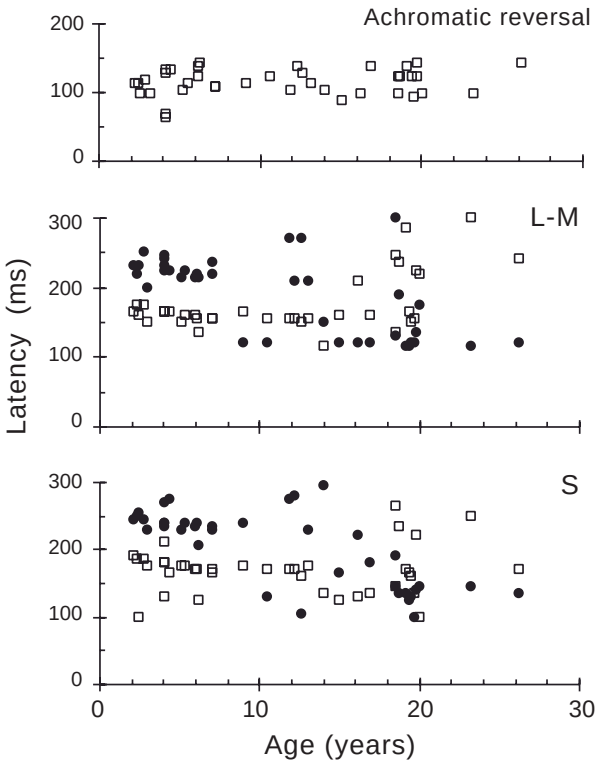

Figure 12. Latencies of the VEP in response to achromatic reversal and chromatic onset stimuli as a function of age (modified from Madrid & Crognale, 2000).

The latency data for these subjects are shown in Figure 12. The latencies of the major positive (open squares) component of the achromatic reversal response are shown in the top panel. There is little change with age. The latencies of the major negative (filled circles) and positive components (open squares) are plotted in the middle and bottom panels for the LM and S axis stimuli, respectively. The apparent inversion in the shape of the waveform around 14-16 years of age is easily seen as a discontinuity where the positive and negative components swap latencies.

Aging Responses

The fact that the chromatic waveforms do not appear adult-like until past puberty raised the possibility that the waveforms continue to change shape throughout life This possibility arises because almost all of our previous adult data were collected on young adults (aged 18-30 years). In addition, we had particular interest in this question because we had been advocating the use of the onset chromatic VEP as a measure of neural integrity in the clinic. Major changes in the shape of the waveform with age would undermine our efforts to develop a normative database for chromatic onset VEP responses in the aging population. To the contrary, a simple, monotonic relationship between latency and age would not pose serious problems to the development of clinical standards.

Fiorentini, Porciatti, Morrone, and Burr (1996) showed that for both chromatic and achromatic reversal stimuli, the phase of the fundamental response and thus the apparent latency of the response increase throughout adulthood during aging. Chromatic onset waveforms, however, have not been reported in the aging population. Therefore, we measured chromatic onset responses in the aging population to characterize maturational changes of the waveforms (Crognale et al., 1998).

Figure 13 shows representative responses to achromatic reversing stimuli from subjects aged 20-89 years. In general, the response amplitudes decrease with age, but we did not find any appreciable increase in latency of the response with our stimuli.

The finding of stable latencies with age is surprising because they seem to contradict the report by Fiorentini et al. (1996). There are a number of possible explanations for the apparent discrepancy. We believe that the most plausible explanation is that our data were collected with high-contrast achromatic patterns whereas those of Fiorentini et al. were collected with stimuli that were reduced in contrast to match their achromatic stimuli (on a 10-times threshold basis). It is likely that our achromatic data were collected on a higher and possibly more saturating portion of the contrast versus latency function than those of Fiorentini et al., and thus less sensitive to aging effects.

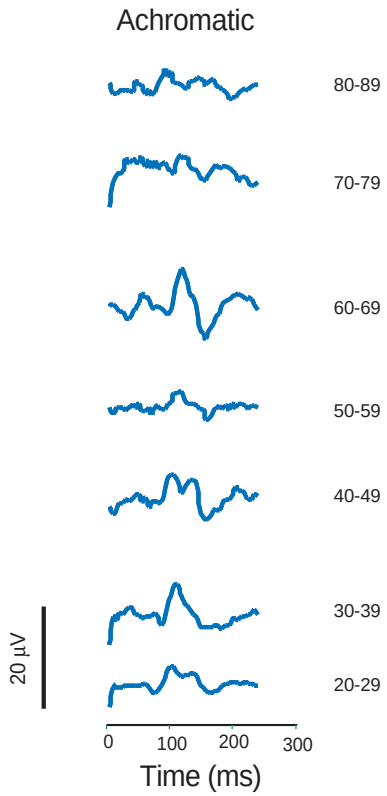

Figure 13. Representative VEP responses to achromatic reversing stimuli in adults. The ages in years of the subjects are indicated.

Another possible source of the discrepancy is that Fiorentini et al. (1996) did not use achromatic stimuli but rather used yellow-black stimuli for their "luminance" condition. Such patterns obviously also modulate the S-(L+M) chromatic pathways. This point is often ignored in studies of chromatic versus luminance processing, and the use of yellow-black patterns to measure luminance responses is common in the literature.

The VEPs recorded in response to LM stimuli are shown in Figure 14. The major finding of interest to us was that the shapes of the waveforms do not change appreciably with age. What may also be apparent in the sample waveforms is that the latency of the major negative component of the waveform increases with age (Crognale et al., 2001). This increase is fairly linear with age with a magnitude of about 9 ms per decade. This agrees well with an increase of approximately 7 ms per decade found for reversing chromatic patterns by Fiorentini et al. In addition to the increases in latency, there were decreases in amplitude, although the relatively large variability in amplitude data hides a significant decrease in the sample waveforms of the figure.

As mentioned above, we were particularly interested in characterizing the changes with age in shape of the waveforms in response to S axis stimuli. This interest is partially because the responses in this pathway have not been characterized to the extent that responses to LM or red/green stimuli have and partially because the S axis responses have clinical utility.

Figure 15 shows the responses to S axis stimuli. The responses observed in older adults are robust and similar in shape to those seen in young adults.

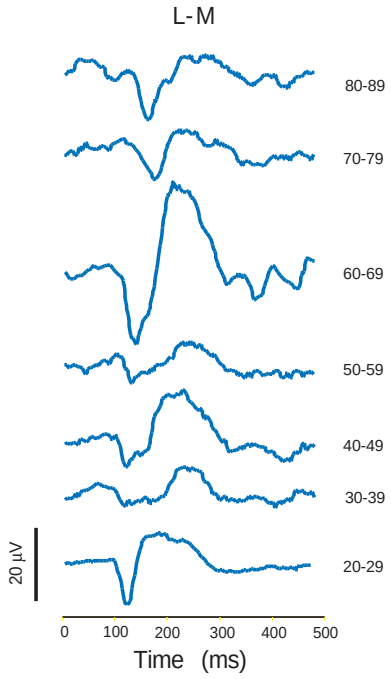

Figure 14. Representative VEP responses to LM stimuli in adults. Other details as in Figure 13.

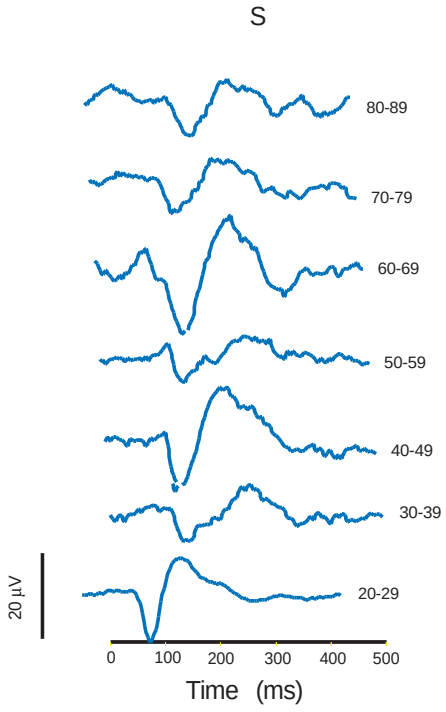

Figure 15. Representative VEP responses to S stimuli in adults. Other details as in Figure 13.

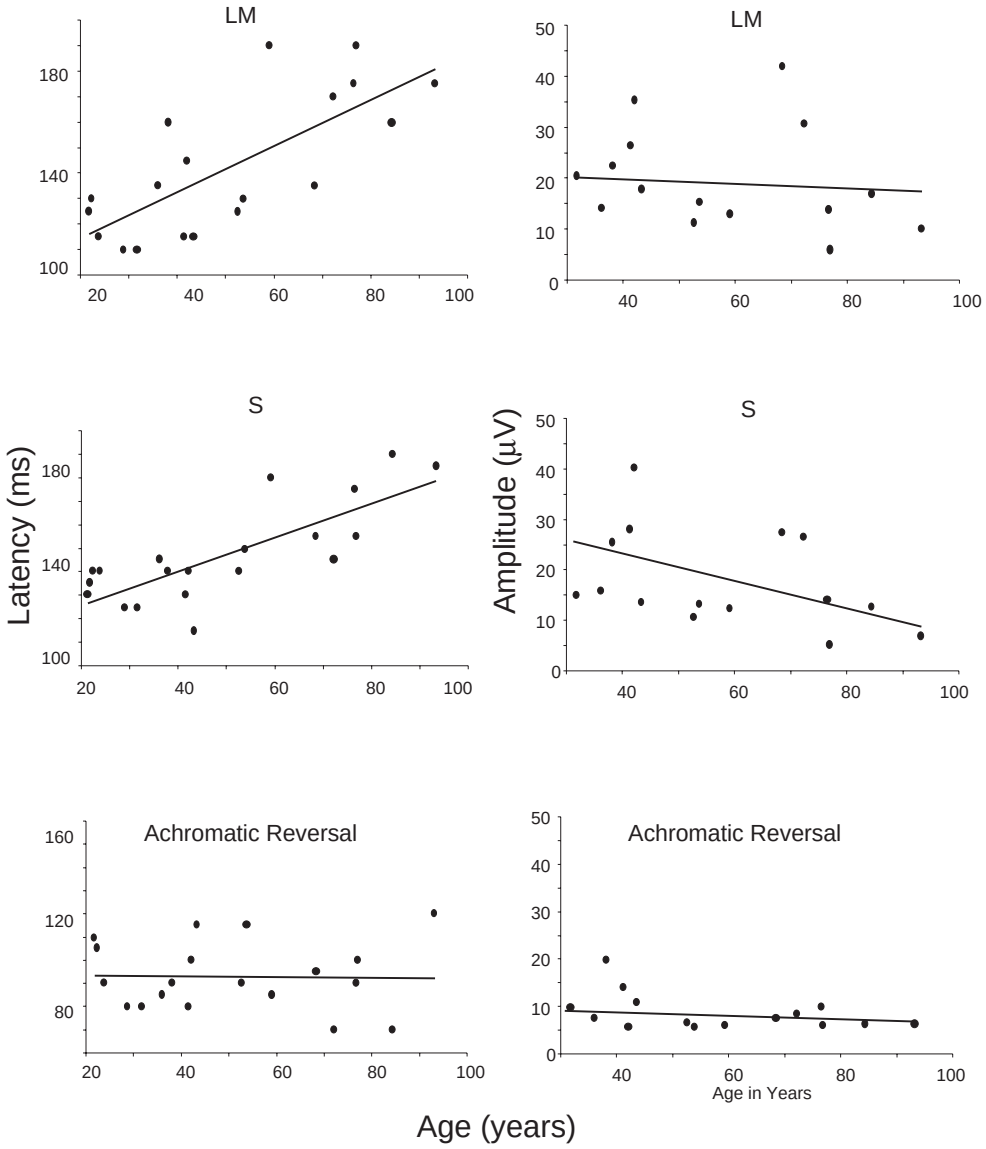

Figure 16. Latencies (left) and amplitudes(right) of the chromatic and achromatic VEP for the aging population. The latency data, though shifted between conditions, are on similar scales.

Changes in the S axis responses with increases in age appear to follow a pattern similar to those of the LM responses with slowly decreasing amplitudes and increasing latencies. The rate of increase in latency was similar to that observed in the LM responses at about 9 ms per decade. Importantly, the waveform shapes to not change substantially over the adult span. This consistency greatly simplifies the task of developing normative data for use in the clinic and may explain some of the variability in the data set of Porciatti and Sartucci (1999).

Figure 16 shows a plot of the amplitudes (right) and latencies (left) of the amplitudes of the responses for the aging population. As described above, latencies increase with age for the chromatic responses but not for the high-contrast achromatic responses. Again the amplitudes are much more variable than the latencies and show a trend toward decreased responses with age.

Summary

Our data demonstrate that the chromatic onset waveforms, although robust and reproducible, continue to change in shape from birth to about puberty. Over the first year, the changes are rapid, complex, and dramatic. In contrast, the achromatic reversal responses at low spatial frequencies are highly stable after about 2-3 months. This contrast suggests that development of underlying cortical pathways rather than changes in gross cortical or cranial morphology is the source of these changes. The appearance of reliable waveforms from LM stimuli during development lags behind appearance of the achromatic responses. With our stimulus conditions, reliable S responses develop shortly after the LM responses. Even at the end of 1 year, the chromatic responses do not resemble those from the adult.

From 1 year until around puberty, the latencies of the major negative component slowly decreases until the waveform changes from a positive-negative complex to the adult negative-positive complex. From puberty to around 18 years of age, the latencies reach a minimum for the life span. Throughout the remainder of the life span, the latency of the major negative component slowly increases and amplitudes slowly decrease. However, the overall shape of the chromatic response does not undergo further dramatic change. The stages of development are similar to those described previously for higher spatial frequency achromatic onset stimuli except that the chromatic waveforms are not as complex as the achromatic waves after the first year of age. The achromatic reversal responses on the other hand have a consistent shape from about 3 months on.

It is important to remember that the conclusion and data reviewed above were collected using a specific set of parameters chosen to optimize the chromatic VEP response. As such, the data represent a single slice through a multidimensional parameter space and may not be representative of other conditions. We are currently expanding our investigation in the contrast and spatial frequency dimensions to provide a more complete understanding of the development and maturation of the different visual pathways.

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