



Development of spatial and temporal vision during childhood

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Received 24 February 1998; received in revised form 4 September 1998

Abstract

Using the method of limits, we measured the development of spatial and temporal vision beginning at 4 years of age. Participants were adults, and children aged 4, 5, 6, and 7 years ($n = 24$ per age). Spatial vision was assessed with vertical sine-wave gratings, and temporal vision was assessed with an unpatterned luminance field sinusoidally modulated over time. Under these testing conditions, spatial contrast sensitivity at every frequency increased by at least 0.5 log units between 4 and 7 years of age, at which point it was adult-like. Grating acuity reached adult values at 6 years of age. Temporal vision was more mature: at 4 years of age temporal contrast sensitivity at higher temporal frequencies (20 and 30 Hz) and critical flicker fusion frequency were already adult-like. Sensitivity at lower temporal frequencies (5 and 10 Hz) increased by 0.25 log units after the age of 4 to reach adult levels at age 7. The results suggest that temporal vision matures more rapidly than spatial vision during childhood. Thus, spatial and temporal vision are likely mediated by different underlying neural mechanisms that mature at different rates. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Children; Development; Spatial contrast sensitivity; Grating acuity; Temporal contrast sensitivity; Critical flicker fusion frequency

Both spatial and temporal contrast sensitivity are immature during infancy (e.g. Atkinson, Braddick & Moar, 1977; Banks & Salapatek, 1978; Swanson & Birch, 1990; Hartmann & Banks, 1992). However, little is known about their relative rates of development after infancy and about the age at which mature levels of visual performance are attained. Investigating their differential development could provide insights into the factors limiting spatial versus temporal vision and into differential rates of neural development.

Even at visible spatial frequencies, a 3-month-old child's contrast sensitivity is reduced by over 1.0 log units relative to that of the adult (Atkinson et al., 1977; Banks & Salapatek, 1978, 1981; Peterzell, Werner & Kaplan, 1995; Gwiazda, Bauer, Thorn & Held, 1997). At 4 years of age, spatial contrast sensitivity is still approximately 0.5 log units lower than that of adults (Beazley, Illingworth, Jahn & Greer, 1980; Atkinson, French & Braddick, 1981; Bradley & Freeman, 1982; Scharre, Cotter, Stein-Block & Kelly, 1990; Richman &

Lyons, 1994; Gwiazda et al., 1997). However, studies of older children report quite disparate findings. Whereas one study reported that spatial contrast sensitivity was still immature in a group of 8–15 year olds (Arundale, 1978), other studies either found adult levels of performance in children anywhere from 6 to 10 years of age (Mayer, 1977; Derefeldt, Lennerstrand & Lundh, 1979; Bradley & Freeman, 1982; Mantylarvi, Autere, Silvennoinen & Myohanen, 1989) or did not determine the age at which performance becomes adult-like (Beazley et al., 1980; Abramov, Hainline, Turkel, Lemerise, Smith, Gordon & Petry, 1984; Tytla, Mauher, Lewis & Brent, 1988; Scharre et al., 1990; Gwiazda et al., 1997). In addition to the disparity in results, it is difficult to draw conclusions from these studies because either there were too few participants at each age (i.e. fewer than eight—Mayer, 1977; Bradley & Freeman, 1982; Abramov et al., 1984; Tytla et al., 1988; Mantylarvi et al., 1989), and/or the data were pooled over a wide range of ages (e.g. 6–10 years—Arundale, 1978; Derefeldt et al., 1979; Beazley et al., 1980; Abramov et al., 1984; Tytla et al., 1988; Mantylarvi et al., 1989; Gwiazda et al., 1997).

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Like spatial contrast sensitivity, temporal contrast sensitivity is also immature during infancy (Swanson & Birch, 1990; Teller, Lindsey, Mar, Succop & Mahal, 1992; Hartmann & Banks, 1992; Rasengane, Allen & Manny, 1997). Contrast sensitivities for temporal frequencies ranging from 1 to 20 Hz are about 1.0 log unit lower than those of adults for 2-month-olds (Teller et al., 1992; Rasengane et al., 1997), 4-month-olds (Swanson & Birch, 1990; Rasengane et al., 1997), and even 8-month-olds (Swanson & Birch, 1990). Unfortunately, no conclusions can be drawn about the development of temporal contrast sensitivity beyond early infancy since 8 months is the oldest age at which temporal contrast sensitivity has been reported.

Data on the limits to spatial and temporal vision—namely, grating acuity and critical flicker fusion frequency—suggest that they develop at different rates. When measured by preferential looking, grating acuity is approximately 1 c deg⁻¹ in the newborn, or about 40-fold less than in the adult (e.g. Miranda, 1970; Dobson, Kohl, Stern, Samek & Preston, 1986; van Hof-van Duin & Mohn, 1986). Although grating acuity improves quite rapidly during early infancy, even at 6 months it is still about 8-fold less than that of adults (e.g. van Hof-van Duin & Mohn, 1986). From that age on, grating acuity develops gradually (Mayer & Dobson, 1982; Lewis & Maurer, 1986; van Hof-van Duin & Mohn, 1986), and does not attain adult levels (40 c deg⁻¹) until 4 years of age (Mayer & Dobson, 1982). In contrast, critical flicker fusion frequency, appears to be quite mature during early infancy (Regal, 1981). When measured by preferential looking, critical flicker fusion frequency is approximately 41 hertz (Hz) at 1 month, and rapidly improves to an adult value (51 Hz) by 3 months old (Regal, 1981). These measurements suggest that critical flicker fusion frequency matures much more quickly than does grating acuity.

The currently available data suggest that there are different developmental patterns for spatial and temporal vision and for lower and higher frequencies. Specifically, critical flicker fusion frequency appears to become adult-like (around 3 months) before sensitivity to lower temporal frequencies (sometime after 8 months), grating acuity (around age 4 years), or sensitivity to lower spatial frequencies (after age 6). However, the comparisons are problematic because of variations across studies in parameters that are likely to affect sensitivity, such as the size and luminance of the stimuli. Moreover, no study has mapped the development of temporal contrast sensitivity until asymptote is reached. The purpose of our study was to chart the development of spatial and temporal vision tested under similar conditions in the same subjects, beginning at age 4 (the youngest age at which children could perform the task reliably) and continuing until the age at which performance is adult-like on all measures. By

starting at age 4, we hoped to document the final development of most parts of the spatial and temporal contrast sensitivity functions while acknowledging that some parts (i.e. critical flicker fusion frequency and perhaps grating acuity) were likely to be adult-like even at the youngest age tested. A secondary purpose of the study was to evaluate the implications of different rates of development for the development of underlying neural mechanisms.

Using the method of limits, we tested spatial and temporal vision under similar experimental conditions at five ages between 4 years and adulthood. In order to establish monocular norms for later comparison to children treated for visual deficits, all data were collected monocularly. We found that, under our testing conditions, spatial and temporal vision develop at different rates. We suggest that these differences between spatial and temporal vision result mainly from the manner in which the developing retina processes spatial versus temporal information.

1. Methods

1.1. Subjects

The participants included five groups of 24 subjects, 4-year-olds (± 1 month), 5-year-olds (± 2 months), 6-year-olds (± 2 months), 7-year-olds (± 3 months), and adults (mean age = 19.8 years, range = 18–26 years), all of whom were untrained observers. None of the participants had a history of eye problems, and all met our criteria on a visual screening exam. Specifically, the four oldest age groups had Snellen acuity of at least 20/20 in each eye without optical correction, worse Snellen acuity with a +3 dioptre add (to rule out hypermetropia of greater than 3 dioptres), stereoacuity of at least 40 arc s on the Titmus test, and fusion at near on the Worth four dot test. The 4-year-olds met the same criteria except that they were tested with the Sheridan–Gardner test of single-letter acuity instead of the Snellen chart. An additional 35 participants were excluded from the final sample because they failed to meet the criteria on the visual screening exam (two 4-year-olds, five 5-year-olds, five 6-year-olds, eight 7-year-olds, and three adults) or because they asked to discontinue testing before completing the tasks (nine 4-year-olds, two 5-year-olds, one 7-year-old).

1.2. Apparatus

The sine-wave gratings were generated on an oscilloscope CRT screen by varying the *z*-axis intensity with a wave form generator. The oscilloscope was a Tektronix (model 5103N) with a green phosphor. The temporal contrast sensitivity apparatus consisted of a spatially

unpatterned light source, the luminance of which was varied over time with a sinusoidal function generator.

1.3. Stimuli

The stimuli used to assess spatial vision consisted of vertically-oriented sinusoidal gratings, 13° wide and 10° high when viewed from a distance of 57 cm. Spatial contrast sensitivity was measured at the eight following spatial frequencies: 0.33, 0.5, 1, 2, 3, 5, 10, and 20 c deg⁻¹. Acuity was assessed with a contrast level of 52%. The stimuli used to assess temporal vision consisted of unpatterned luminance fields that were sinusoidally modulated over time and 5° in diameter when viewed from a distance of 57 cm. Temporal contrast sensitivity was measured for the four following temporal frequencies: 5, 10, 20, and 30 Hz. Critical flicker fusion frequency was assessed at a contrast level of 65%.

The space- and time-average luminances of the test stimuli were 9 cd m⁻². The contrast of the patterns was defined as the difference between maximum and minimum luminance divided by their sum. A Minolta LS-100 photometer verified that the peak and the trough luminances of the stimuli varied linearly with changes in contrast up to 52 and 65% for spatial and temporal contrast stimuli, respectively. Consequently, grating acuity and critical flicker fusion frequency were measured at 52 and 65% contrast, respectively.

1.4. Procedure

All participants were tested monocularly in a dimly illuminated room. Half of the participants in each group were tested with the left eye, whilst the remaining half were tested with the right eye. The eye not being tested was patched with 3 M Micropore™ tape. The procedures were explained and informed consent was obtained from the parents of the children and from the adults who participated. Parents of children sat in the testing room out of their child's sight and were asked to remain silent during testing.

Both spatial and temporal thresholds were measured with the method of limits. For the tests of spatial contrast sensitivity, participants sat 57 cm from the oscilloscope for spatial frequencies ranging from 0.33 to 10 c deg⁻¹ and were moved back to twice that distance to view the 20 c deg⁻¹ grating. Participants were asked to indicate when the stimulus just appeared as contrast was increased from subthreshold values—ascending threshold, and to indicate when the stimulus first disappeared as contrast was reduced from suprathreshold levels—descending threshold. Specifically, both adults and children were instructed to say 'there' as soon as the stripes *appeared* and to say 'gone' as soon as the stripes *disappeared*. No feedback was given during the

test but children were praised periodically for their good efforts (e.g. 'that's great; you're doing a good job'). Three ascending and three descending thresholds were recorded for each spatial frequency, with the ascending thresholds measured first. The frequencies were tested in a random order. The procedure for testing grating acuity was the same except that participants were moved back to a viewing distance of 342 cm and they were asked to indicate when the stimulus first disappeared as spatial frequency was increased from suprathreshold values, or just reappeared as spatial frequency was decreased from subthreshold values.

Temporal contrast sensitivity was assessed from a viewing distance of 57 cm. Unlike spatial contrast sensitivity, only ascending thresholds were used because afterimages cause unpatterned flicker to persist after the flicker has stopped. Three ascending thresholds were taken for each temporal frequency. The frequencies were tested in a random order. Critical flicker fusion frequency was also assessed at a viewing distance of 57 cm, but both ascending and descending thresholds were measured, in accordance with the classical literature (De Lange, 1952, 1954). Participants were asked to indicate the point at which the light ceased to flicker as temporal frequency was increased from visible flicker levels, and then to indicate the point at which flicker reappeared as temporal frequency was decreased from nonvisible flicker values. Specifically, the participants were instructed to say 'there' as soon as flicker *appeared*, and to say 'gone' as soon as flicker *disappeared*. Three ascending and three descending thresholds were recorded, with the ascending thresholds measured first.

Half of the participants in each age group first received the tests for acuity and spatial contrast sensitivity, with acuity always measured first. The remaining participants first received the tests for critical flicker fusion frequency and temporal contrast sensitivity, with critical flicker fusion frequency always measured first. We counterbalanced tests of spatial and temporal vision and randomized the order of spatial and temporal frequencies to control for any effects of fatigue and/or practice.

A practice run was given before each of the four tasks. No feedback was given during practice, but children were praised periodically. At the end of the practice run, participants were asked if they understood the task and if so, testing began. The procedure lasted about 55 min, including a rest period of 5 min after every 15 min of testing. Participants were told that additional breaks would be given at their request, but only a few children made such a request.

For each participant, the threshold for each condition was taken as the geometric mean of the recorded contrast thresholds. We combined the data for left and right eyes across participants of the same age to calculate the thresholds for each condition because four

ANOVAs (one for each task) showed that, at none of the five ages, did thresholds for any stimulus condition differ for participants who had the left eye tested versus those who had the right eye tested. For analyses, the thresholds were log transformed, and all the figures are plotted in log coordinates. However, for clarity, the labels on the axes have been anti-logged. The spatial and temporal contrast sensitivity at each frequency are plotted as the reciprocal of the geometric mean for the 24 participants at each age.

2. Results

2.1. Spatial vision

The mean spatial contrast sensitivity functions of the five age groups are plotted in Fig. 1. All the curves peak at around 3–5 c deg⁻¹. The adult and the 7-year-old curves overlap greatly, as do the curves for the 4- and 5-year-olds. When compared to adult contrast sensitivity, the 4- and 5-year-olds' contrast sensitivity was lower on average by a factor of two.

A five (age) × eight (spatial frequency) ANOVA yielded a significant main effect of age, $F_{4, 115} = 41.40$ ($P < 0.001$), a significant main effect of spatial frequency, $F_{7, 805} = 1983.44$ ($P < 0.001$), and a significant interaction of age and spatial frequency, $F_{28, 805} = 3.04$ ($P < 0.001$). A Tukey HSD post-hoc statistical analysis on the main effect of age indicated no significant difference in contrast sensitivity between the 4- and 5-year-

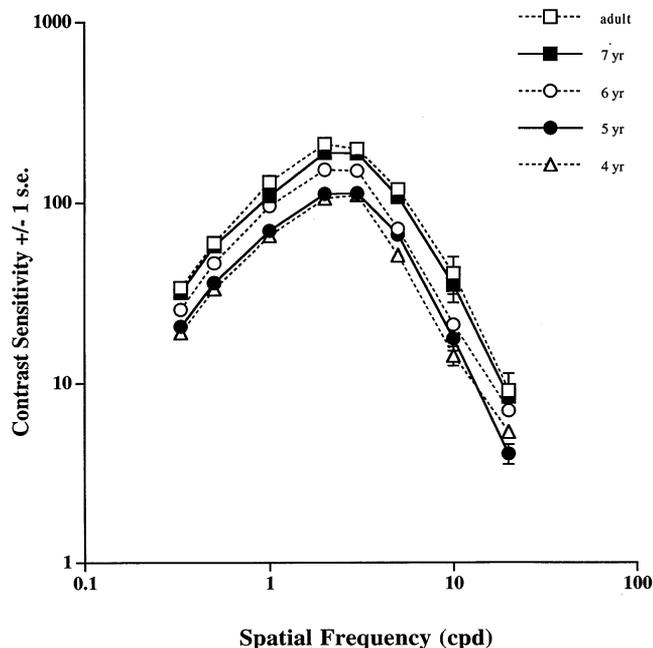


Fig. 1. Mean contrast sensitivity (± 1 S.E.) as a function of spatial frequency for adults and four groups of children. When not shown, standard error bars are smaller than the data points.

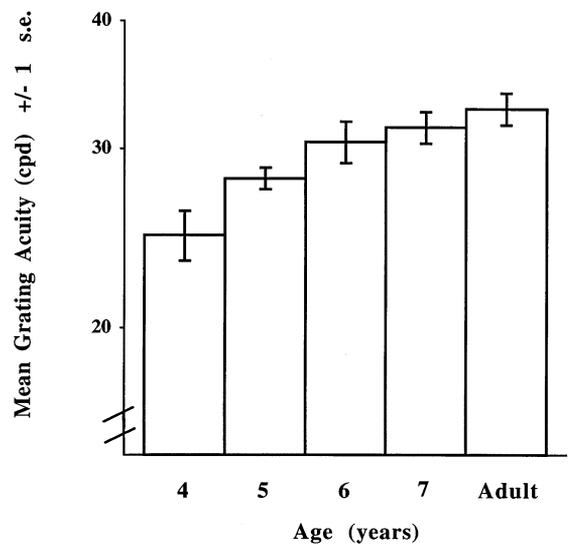


Fig. 2. Mean grating acuity (± 1 S.E.) for adults and four groups of children.

olds or between the adults and 7-year-olds ($P_s > 0.10$). The contrast sensitivity of 5-year-olds was significantly lower than that of 6-year-olds ($P < 0.001$), whose sensitivity was significantly lower than that of 7-year-olds ($P < 0.005$).

The statistical analysis failed to identify the source of the interaction. The Dunnett post-hoc analysis revealed that, compared to adults, sensitivity was significantly lower at each of the eight spatial frequencies for the 4-, 5-, and 6-year-olds ($P_s < 0.01$). There was no significant difference between the 7-year-olds and the adults at any spatial frequency ($P_s > 0.05$). Although the post-hoc tests failed to identify the source of the interaction, Fig. 1 indicates that the difference in sensitivity between the adult group and each of the other groups tended to be greater at higher than at lower spatial frequencies. Finally, the significant main effect of spatial frequency does not come as a surprise since the curves have the quadratic shape typical of contrast sensitivity functions.

The results for acuity are summarized in Fig. 2. A one-way ANOVA revealed a significant main effect of age, $F_{4, 115} = 13.35$ ($P < 0.001$). Dunnett post-hoc tests revealed that acuity was significantly lower than that of adults at 4 and 5 years of age ($P_s < 0.05$), but not at 6 and 7 years of age ($P_s > 0.05$).

2.2. Temporal vision

The temporal contrast sensitivity functions for the five age groups appear in Fig. 3. There is great overlap among the functions for the five age groups. A five (age) × eight (temporal frequency) ANOVA yielded a significant main effect of age, $F_{4, 115} = 4.16$ ($P < 0.001$), a significant main effect of temporal frequency, $F_{3, 345} = 2549.01$ ($P < 0.001$), and a significant interac-

tion between age and temporal frequency, $F_{12, 345} = 3.26$ ($P < 0.001$). Post-hoc Dunnett tests on the interaction showed no significant difference in contrast sensitivity between the 7-year-olds and the adults at any of the temporal frequencies ($P_s > 0.05$). Adult contrast sensitivity was significantly greater than that of the 4-, 5-, and 6-year-olds at 5 and 10 Hz ($P_s < 0.01$), and also significantly greater than that of the 6-year-olds at 20 Hz ($P < 0.01$). However, at no age did children differ from adults at 30 Hz and the differences at lower frequencies, although significant, are quite small.

A Tukey HSD post-hoc statistical analysis on the main effect of age revealed no significant difference in sensitivity between the 4-, 5- and 6-year-olds ($P_s > 0.10$), all of whom had significantly lower sensitivity than the 7-year-olds and adults ($P_s < 0.001$). No significant difference in sensitivity between adults and 7-year-olds was found ($P > 0.10$). Finally, the significant main effect of temporal frequency was expected since the curves have the quadratic shape typical of temporal contrast sensitivity functions.

Fig. 4 summarizes the results for critical flicker fusion frequency. A one-way ANOVA revealed no significant difference in the visual performance of the five age groups, $F_{4, 115} = 0.94$ ($P > 0.10$).

3. Discussion

Under the present testing conditions, the spatial contrast sensitivity of the 4- and 5-year-olds is lower than

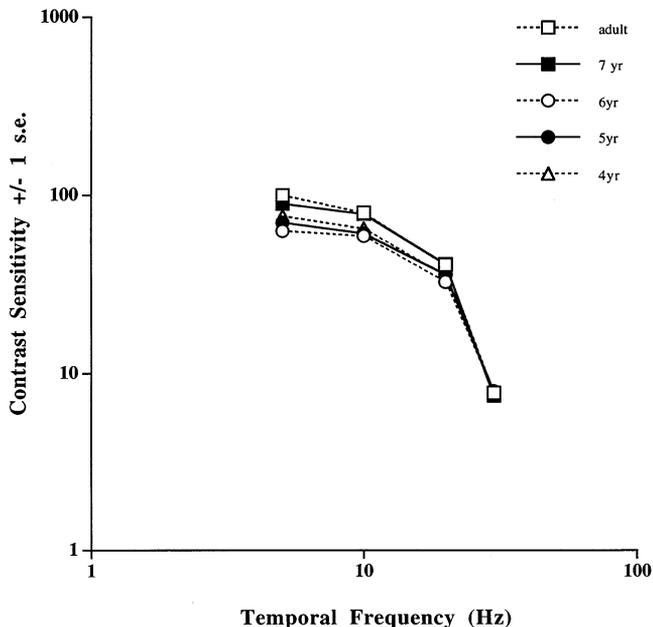


Fig. 3. Mean contrast sensitivity (± 1 S.E.) as a function of temporal frequency for adults and four groups of children. When not shown, standard error bars are smaller than the data points.

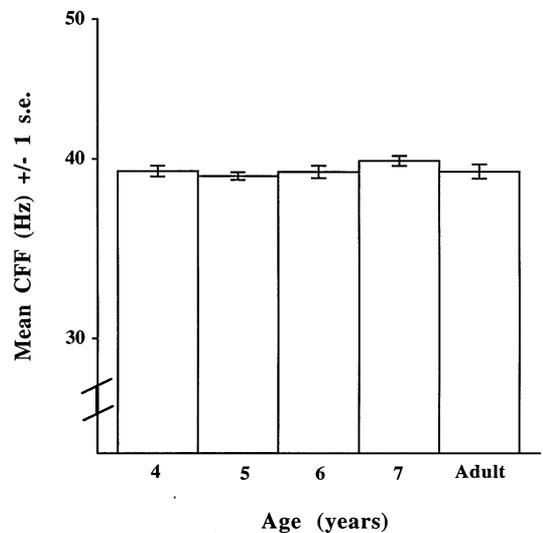


Fig. 4. Mean critical flicker fusion frequency (± 1 S.E.) for adults and four groups of children.

adult values by approximately a factor of 2 or 0.5 log units. These findings are similar to those reported previously for children of the same age (Beazley et al., 1980; Atkinson et al., 1981; Bradley & Freeman, 1982; Scharre et al., 1990; Richman & Lyons, 1994; Gwiazda et al., 1997). Between 5 and 6 years of age, there is a significant improvement in contrast sensitivity at each spatial frequency; yet sensitivity is still significantly lower than in adults. By age 7, spatial contrast sensitivity attains adult values for all spatial frequencies measured in this study. This finding is in close agreement with that of Bradley and Freeman (1982) who found that asymptotic levels were reached by 8 years of age (but see Arundale, 1978; Beazley et al., 1980; Scharre et al., 1990; Gwiazda et al., 1997).

Like spatial contrast sensitivity, only at age 7 is temporal contrast sensitivity mature at every frequency. Nonetheless, sensitivity to temporal contrast appears to develop at a different rate than sensitivity to spatial contrast. Firstly, temporal contrast sensitivity at higher temporal frequencies (30 Hz) was mature even at 4 years of age whereas spatial contrast sensitivity was immature at all frequencies until 7 years of age. Secondly, prior to 7 years of age, temporal contrast sensitivity at lower temporal frequencies (5 and 10 Hz) was reduced relative to adults by approximately a factor of 1.4 or 0.25 log units, whereas spatial contrast sensitivity, at all spatial frequencies tested, was reduced by approximately a factor of 2 or 0.5 log units.

Under these testing conditions, grating acuity does not mature until 6 years of age. The difference in age between our findings and those of Mayer and Dobson (1982) who found that grating acuity is adult-like by 4 years, may have been caused by differences between studies in the maximum contrast (52 vs. 84%) and in

the mean luminance of the gratings (9 vs. 16 cd m⁻²). An additional difference is that we tested participants monocularly using the method of limits, whilst Mayer and Dobson tested participants binocularly using a forced choice preferential looking paradigm with response feedback. Binocular tests tend to yield lower thresholds than monocular tests and a forced choice procedure with feedback may be more sensitive than the method of limits.

Critical flicker fusion frequency was adult-like in the 4-year-olds. Based on the literature this was expected, since critical flicker fusion frequency reaches adult values by 3 months of age (Regal, 1981).

Therefore, under these testing conditions, grating acuity and critical flicker fusion frequency mature earlier than sensitivity at lower spatial and temporal frequencies, with critical flicker fusion frequency reaching maturity much earlier than grating acuity. Moreover, during childhood, temporal contrast sensitivity appears to develop at a faster rate than does spatial contrast sensitivity.

3.1. What factors underlie the observed developmental changes?

3.1.1. Non-neural factors

Non-visual factors such as differences in attention or criterion may have contributed to reductions in performance, but are not likely to account for the overall pattern of results: all tasks measured thresholds, yet the children's performance was more immature on some tasks than on others. To verify that differences in attention or criterion were unlikely to have affected the pattern of results, we carried out several additional analyses. First, an inspection of the standard error bars in Figs. 1–4 indicates little between subject variability in mean thresholds for each age group. Second, we used a five (age) × two (frequency) ANOVA to compare age differences in within subject variability, measured by the standard deviation of the ascending thresholds, at both the highest and lowest spatial and temporal frequencies. Not surprisingly, within subject variability was significantly greater in each group of children than in adults at both the highest spatial and temporal frequencies ($P_s < 0.05$). The higher variability in children might reflect less attentiveness or a more variable criterion. However, it is unlikely to have affected the pattern of results because children 4–6 years old showed reduced sensitivity at all spatial frequencies but only at the lower temporal frequencies. Moreover, although the within-subject variability of 7-year-olds was similar to that of younger children, their performance was adult-like. Finally, ANOVAs investigating possible age differences in response bias between ascending versus descending measures of threshold for spatial contrast sensitivity, acuity, and critical flicker fusion

frequency did not reveal any interaction between ascending versus descending thresholds and age ($P_s > 0.10$).

Poor optics also likely did not contribute to reductions in visual performance: participants were screened for refractive errors. Moreover, by 4 years of age (the youngest age tested), children typically no longer have the refractive and accommodative errors that are common during infancy (Banks, 1980; Hainline et al., 1992; Howland, 1993).

3.1.2. Neuronal influences on the development of spatial vision

Although a large amount of retinal maturation takes place between birth and early childhood, the 45-month-old's retina is yet to be mature (Yuodelis & Hendrickson, 1986). In the one 45-month-old retina studied by Yuodelis and Hendrickson (1986), the outer segment length of foveal cones was 30–50% shorter than in adults, and cone packing density was only half that of the adult fovea.

Spatial contrast sensitivity is likely to be affected by the reduction in the length of the cones' outer segments, because it would make the cones less efficient in producing isomerization for a given quantum and thus, less sensitive to a luminance pattern. As would be expected from this analysis, spatial contrast sensitivity is dependent on luminance (Pasternak & Merigan, 1981). This position is supported by the Wilson (1988, 1993) and Banks and Bennett (1988) models on the front-end limits (optical and receptor) of spatial vision during development. The Wilson (1988, 1993) model predicts that the 45-month-old's shorter cone outer segments should cause a reduction in contrast sensitivity of a factor of 1.1. Assuming that the data from the one 4-year-old retina provided by Yuodelis and Hendrickson (1986) lie within the normal range for that age group, the difference between the Wilson (1993) predictions for the reduction in contrast sensitivity at age 4 (reduction of a factor of 1.1) and our findings (a reduction of a factor of 2.0) could then be attributed to post-receptor immaturities. We cannot compare our results to those predicted by the Banks and Bennett (1988) model, because that model makes quantitative predictions about spatial vision only during early infancy.

Acuity is likely to be affected both by the reduction in cone packing density and by the reduction in length of the cone outer segments. Reduced cone packing density produces a reduction in spatial sampling, and hence in acuity. Acuity varies with luminance (Brown, Dobson & Mayer, 1987; Allen, Bennett & Banks, 1992) and as noted in the previous paragraph, reduced length of the cone outer segments reduces sensitivity to luminance. Based on the assumption that the optics are adult-like during infancy, Wilson's (1993) model pre-

dicts that the reduction in the photoreceptors' spatial sampling and in the outer segments' quantal catch should result in a 28% reduction in the 4-year-old's acuity. This estimate corresponds closely to the 29% reduction reported in this study.

Thus, it appears that retinal development plays a role in the spatial visual development we observed after 4 years of age. It is not as clear whether post-retinal changes in the geniculostriate pathway also contribute. On the one hand, some aspects of the geniculostriate pathway have already matured by 4 years of age, and hence would not contribute to the limitations we observed at that age. Retinal afferents to the lateral geniculate nucleus (LGN) differentiate to their adult form within the first few months of birth and LGN neurons reach their adult size by 2 years of age (Hickey, 1977; Brauer, Leuba, Garey & Winkelman, 1985). Cortical volume of the primary visual cortex is also adult-like shortly after birth (Huttenlocher & De Courten, 1987). On the other hand, there is evidence of changes in connectivity and responsivity within the geniculostriate pathway that extend past infancy. Within the primary visual cortex, there is an increase in synaptic density followed by about a 50% decrease that is not complete until 11 years of age (Huttenlocher, De Courten, Garey & Van Der Loos, 1982; Garey & De Courten, 1983; Huttenlocher, 1984). This pruning may be related to the reduction of cortical neurons' receptive fields and the fine tuning of their spatial frequency response profiles, both of which have been documented in developing monkeys (Blakemore, 1990). These cortical changes may contribute to the increase in acuity and spatial contrast sensitivity that occurs during childhood (until pruning reaches the Nyquist limit set by the retina). Studies of infant monkeys suggest, in turn, additional limitations from immaturities in the inputs to the cortex, viz., immaturities in the sensitivity of individual LGN neurons and the inputs to them from the retina (Blakemore & Vital-Durand, 1986; Blakemore, 1990; Movshon & Kiorpes, 1993). The role of the retina in limiting the functioning of the geniculostriate pathway, at least during early infancy, is also indicated by the finding that cortical spatial contrast sensitivity and acuity, as measured by visually evoked potentials, mature no faster than the contrast sensitivity and acuity measured by the electroretinogram (Fiorentini, Pirchio & Spinelli, 1983; Fiorentini, Pirchio & Sandini, 1984).

Thus, it appears that the development of spatial vision is limited by slow retinal development, with some possible additional limitations from immaturities in the geniculostriate pathway. Recently, Kiorpes and Movshon (1998) drew similar conclusions based on their psychophysical measurements of additive and

non-additive noise in the visual detection of the infant monkey.

3.1.3. *Neuronal influences on the development of temporal vision*

Whereas retinal immaturities including shorter cone outer segments and reduced cone packing density likely limit the spatial vision of the 4-year-old, the same does not appear to be true for temporal vision. Shorter cone outer segments reduce retinal illuminance, which is known to reduce sensitivity more at higher than lower temporal frequencies (De Lange, 1952, 1954; Kelly, 1971). Yet we found the opposite pattern in the 4-year-olds: reduced sensitivity at lower, but not at higher, temporal frequencies. Therefore, our results suggest that the temporal contrast sensitivity of 4-year-olds is not affected by reductions in receptor quantal catch. Cone packing density also appears not to limit temporal vision because adults' critical flicker fusion frequency tends to be somewhat higher in the retinal periphery than in the fovea (Tyler, 1981).

The retina's efficiency in resolving time-varying information also does not appear to limit children's temporal resolution because critical flicker fusion frequency, as measured by electroretinograms, is nearly adult-like by 2 months of age (Heck & Zetterstrom, 1958). Although these findings do not tell us what the visual system can resolve, they do indicate that the infant retina can signal temporal changes as rapidly as the adult retina, and therefore suggest that the limits on children's temporal vision are post-retinal. That conclusion is supported by the finding that temporal sensitivity evaluated from electroretinograms approaches adult values by 5 months of age, whereas temporal sensitivity evaluated from visual evoked potentials is still immature at that age (Fiorentini & Trimarchi, 1992). This comparison suggests that the limits to temporal vision during infancy may reside in the striate cortex or in its inputs from the LGN.

4. Conclusion

Under these testing conditions, spatial and temporal vision mature at different rates during childhood. The immature retina appears to limit the information it relays to higher visual centres about spatial vision but not the information it relays about temporal vision. However, the retinal immaturities may not account for all of the limitations measured in spatial vision. Therefore, consistent with evidence from non-human primates, it appears that post-retinal immaturities in the geniculostriate pathway account for the limitations measured in temporal vision and may contribute to the limitations measured in spatial vision.

Acknowledgements

This research was supported by the Medical Research Council of Canada (grant MT-11710) and by the National Institutes of Health (grant EY03475). Some of these data were presented at the annual meeting of the Association for Research in Vision and Ophthalmology, Ft. Lauderdale, May 1998. Requests for reprints should be sent to Terri L. Lewis, Department of Psychology, McMaster University, Hamilton Ontario, L8S 4K1. E-mail: lewistl@mcmaster.ca.

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