The development of spatial frequency discrimination

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We compared thresholds for discriminating spatial frequency for children aged 5, 7, and 9 years, and adults at two baseline spatial frequencies (1 and 3 cpd). In Experiment 1, the minimum change from baseline necessary to detect a change in spatial frequency from either baseline decreased with age from 34% in 5-year-olds to 11% in 7-year-olds, 8% in 9-year-olds, and 6% in adults. The data were best fit by an exponential function reflecting the rapid improvement in thresholds between 5 and 7 years of age and more gradual improvement thereafter (r^2 = 0.50, $p < 0.0001$). In Experiment 2, 5-year-olds' thresholds were higher than those of adults, even when memory demands were eliminated by presenting the two spatial frequencies side by side for an unlimited time. The pattern of development for sensitivity to spatial frequency (this study) resembles those for the development of sensitivity to orientation (T. L. Lewis, S. E. Chong, & D. Maurer, 2009) and contrast (D. Ellemberg, T. L. Lewis, C. H. Lui, & D. Maurer, 1999). The similar patterns are consistent with theories of common underlying mechanisms in primary visual cortex (A. Vincent & D. Regan, 1995; W. Zhu, M. Shelley, & R. Shapley, 2008) and suggest that those mechanisms continue to develop throughout childhood.

Keywords: visual development, spatial frequency discrimination, children, adults

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Introduction

Spatial frequency, one of the basic building blocks of vision, appears to be processed by separate channels, each of which is tuned to a narrow band of spatial frequencies. Evidence from spatial frequency adaptation (Blakemore & Campbell, 1969; Pantle & Sekuler, 1968; Williams, Wilson, & Cowan, 1982), masking (De Valois & Switkes, 1983; Wilson, McFarlane, & Philips, 1983), subthreshold summation (Sachs, Nachmias, & Robson, 1971; Wilson & Bergen, 1979), spatial frequency aftereffects (Blakemore & Sutton, 1969), and discrimination studies (Regan & Beverly, 1983; Watson & Robson, 1981) suggest the existence of 6–8 channels. Electrophysiological evidence from cats and monkeys indicates that the channels probably arise at the level of V1 simple cells, which are tuned to different narrow bands of spatial frequency (Born & Tootell, 1991; Bradley, Skottun, Ohzawa, Sclar, & Freeman, 1987; Bredfeldt & Ringach, 2002; De Valois, Albrecht, & Thorell, 1982; Everson et al., 1998; Hubel & Wiesel, 1968; Mazer, Vinje, McDermott, Schiller, & Gallant, 2002; Silverman, Grosof, De Valois, & Elfar, 1989). Imaging studies in humans confirm the role of V1 in the processing of spatial frequency but also point to a network including higher visual areas, namely V2, V3, occipito-temporal areas, and occipito-parietal areas (Baumann, Endestad, Magnussen, & Greenlee, 2008; Greenlee, Magnussen, & Reinvang, 2000; Gulyas & Roland, 1995).

Adults are very sensitive to changes in spatial frequency. Thresholds to discriminate between two spatial frequencies with central vision range from a 2% to 10% change from the reference spatial frequency (Bennett & Cortese, 1996; Bennett, Sekuler, McIntosh, & Della-Maggiore, 2001; Burbeck & Regan, 1983; Campbell, Nachmias, & Jukes, 1970; Greenlee & Thomas, 1993; Heeley, Timney, Paterson, & Thompson, 1989; Hirsch & Hylton, 1982; Lin & Wilson, 1996; Mayer & Kim, 1986; O'Donnell et al., 2002; Regan, 1985; Yo, Wilson, Mets, & Ritacco, 1989). Differences in thresholds reported across studies may have arisen from differences in the reference spatial frequency (Hirsch et al., 1982; Wilson & Gelb, 1984), in memory demands (Bennett et al., 2001; Ben-Yehudah & Ahissar, 2004), and/or in stimulus characteristics such as contrast (Campbell et al., 1970) and stimulus size (Hirsch & Hylton, 1982). For example, adults' thresholds for discriminating spatial frequency improve with increasing contrast as contrast increases to three times the detection threshold, after which increases in contrast have no effect (Campbell et al., 1970).

Despite the abundance of studies on spatial frequency discrimination in adults, little is known about the development of spatial frequency discrimination during childhood. One study used masking to test for the presence and width

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of tuning in 6- and 12-week-old human infants (Banks, Stephens, & Hartmann, 1985). At 12 weeks, but not at 6 weeks, infants were able to detect the presence of a grating presented in noise when the noise mask and grating differed in spatial frequency by at least 2 octaves. This bandwidth of masking in 12 week olds is similar to the 1.3 octave bandwidth in adults. This study provided the first evidence of the presence of multiple, narrowband spatial frequency channels in infants.

To our knowledge, there are no published studies on the development of spatial frequency discrimination after infancy. The purpose of the present study was to provide the first measurement of the development of spatial frequency discrimination during childhood and to determine the age at which it becomes adult-like. We chose to start testing at 5 years of age because we have found this to be the youngest age at which children produce reliable psychophysical thresholds using traditional two-alternative forced-choice psychophysical procedures (Ahmed, Lewis, Ellemberg, & Maurer, 2005; Ellemberg et al., 2004; Ellemberg, Lewis, Liu, & Maurer, 1999; Ellemberg et al., 2003; Lewis, Kingdon, Ellemberg, & Maurer, 2007). In addition, we tested 7- and 9-year-olds in order to compare the development of spatial frequency discrimination to existing developmental data on other low-level visual abilities (i.e., orientation discrimination and temporal and spatial contrast sensitivities). Adults were tested for comparison.

In Experiment 1, participants were presented sequentially with a pair of horizontally oriented high contrast luminance-modulated sine-wave gratings and made a temporal forced-choice decision as to whether the lower spatial frequency (thicker stripes) appeared in interval 1 or 2. Each participant completed two runs, one at each of two reference spatial frequencies (1 and 3 cpd). These reference frequencies were chosen because they have been shown to activate distinct spatial frequency channels in adults (Ellemberg, Hess, & Allen, 2006). To evaluate the possibility that poor memory for the grating in interval 1 led to higher thresholds in the youngest children tested in Experiment 1, in Experiment 2 we used the same temporal two-alternative forced-choice paradigm in one condition and a spatial two-alternative forced-choice paradigm in the other condition. Specifically, participants were shown a pair of horizontally oriented, high contrast, luminance-modulated Gabors, presented either sequentially for a short duration or simultaneously for unlimited time. If spatial frequency discrimination is worse for the temporal forced-choice paradigm (sequential presentation) than for the spatial forced-choice paradigm (simultaneous presentation) in children but not adults, the findings would provide evidence for the contribution of memory limitations to worse performance in children. If there are residual differences between children and adults for the spatial forced-choice paradigm, the findings would also provide evidence for immaturities in spatial frequency discrimination.

Experiment 1

Methods

Participants

The final sample consisted of four groups of 20 participants each: 5-year-olds (±3 months, 8 males), 7-year-olds (±3 months, 11 males), 9-year-olds (±3 months, 11 males), and adults (mean age = 18.9, range = 17–20 years, 9 males). All participants had normal or corrected-to-normal vision with no history of eye problems and all met our criteria on a visual screening examination. Specifically, the three oldest groups had a linear letter acuity (Lighthouse Visual Acuity Chart) of at least 20/20 in each eye with a maximum of −2 diopters of optical correction (to rule out myopia greater than 2 diopters, which would reduce vision at our testing distance of 50 cm), worse acuity with a +3 diopter add (to rule out hypermetropia greater than 3 diopters), fusion at near on the Worth four dot test, and stereo acuity of at least 40 arcsec on the Titmus test. The 5-year-olds met the same criteria except that their acuity was tested with the Cambridge Crowding cards (catalogue # 4116022) and the criterion for a pass was reduced to 20/25. We used a more liberal criterion for the 5-year-olds because letter acuity is still immature at 5 years of age (reviewed in Maurer & Lewis, 2001). An additional eight 5-year-olds, two 7-year-olds, one 9-year-old, and five adults were excluded from the final sample: four 5-year-olds for not passing the criterion phase of the task (see Procedure section); one 5-year-old who demonstrated atypical behavioral development; three 5-year-olds, two 7-year-olds, one 9-year-old, and four adults for not passing visual screening; and one adult because of experimental error.

Apparatus and stimuli

The stimuli were created using VPixx 2.3 software running on an Apple Macintosh G4 computer and a Dell Trinitron monitor, 39° wide by 31° high (40 cm wide by 30 cm high) when viewed from 50 cm. The monitor had a pixel resolution of 1024 × 768 (1 pixel = 0.038°) and a frame refresh rate of 85 Hz.

The stimuli consisted of static high contrast luminance-modulated sine-wave gratings of spatial frequencies ranging from 1 to 6 cpd (see below) presented in a 10° (9 cm) square aperture on a gray background. The phase of the sine wave was jittered randomly to prevent judgments based solely on the luminance at the edges of the gratings. The reference spatial frequencies of the gratings were 1 and 3 cpd, and the corresponding comparison spatial frequencies ranged from 1.01 to 2 cpd and 3.01 to 6 cpd, respectively. The amplitude of the luminance modulation (Michelson contrast or depth modulation) was defined as

$$\text{Amplitude modulation} = (L_{max} - L_{min})/(L_{max} + L_{min}), \quad (1)$$

where L_{max} and L_{min} are the maximum and minimum mean local luminance values. The space-average luminance of the background was maintained at 13 cd/m^2 and the contrast of the stimuli was maintained at 89 ± 2%. Maximum luminance within each grating was 43.8 cd/m^2 and the minimum was 2.5 cd/m^2.

Procedure

The experimental procedures were explained and informed consent was obtained from participants and/or from their parents. All experimental protocols were approved by the McMaster Research Ethics Board.

Participants were seated 50 cm from the computer monitor with the chin resting in a chin rest so as to maintain a constant distance. They were tested binocularly in a room illuminated by only the computer monitor and were adapted to the lighting conditions for 5 min prior to the test. Parents of participants were permitted to remain in the testing room provided they sat out of their child's sight and remained silent during testing.

A temporal forced-choice procedure was used to obtain spatial frequency discrimination thresholds. Participants were instructed to fixate on a central 1° black circle that appeared at the beginning of each trial. Each trial consisted of two 1-s sequential presentations of sine-wave gratings separated by an interstimulus interval of 0.5 s during which a gray screen was displayed. The task on each trial was to indicate whether interval 1 or 2 contained the grating of lower spatial frequency (thicker stripes). The stimulus with the lower spatial frequency (always the reference spatial frequency) appeared equally often in each of the two intervals. The experimenter said: "In this game, a black dot will appear and you have to look right at the black dot. Then, the black dot will disappear and you will see one square filled with stripes followed by another square filled with stripes. Square one will disappear before you see the second square. [Point to square 1] This first square is square one. [Point to square 2] This second square is square two. It is your job to tell me which stripes are fatter, those in square one or those in square two." The experimenter sat facing the participant, at the side of the monitor and behind its front edge, in order to continuously monitor the participant's eyes while remaining blind to the stimulus on the monitor. The experimenter initiated each trial by pressing a key only when the participant's eyes were focused on the center of the screen. The experimenter also entered the responses by means of a keyboard.

Participants each completed two runs, one at each of the reference spatial frequencies: 1 and 3 cpd. Order was counter-balanced across participants within each age group. The procedure began with a demonstration, criterion trials, and a practice run with the same reference spatial frequency (1 or 3 cpd) that was to be tested first.

Demonstration and criterion trials. The demonstration consisted of four trials with the maximum spatial frequency comparisons (1 versus 2 cpd or 3 versus 6 cpd). Two trials had the lower spatial frequency (thicker stripes) in the first interval, and the other two trials had the higher spatial frequency (thinner stripes) in the first interval. For each demonstration trial, the experimenter was aware of the stimuli and pointed out the fatter stripes. After the demonstration trials, the procedure continued with criterion blocks of 4 trials with the maximum comparison but the participant was expected to indicate whether the fatter stripes were in interval 1 or 2. No feedback was provided unless an error was made, after which the remaining trials in that block were used as demonstration trials and the criterion test resumed in the following block. Participants met criterion by getting all four trials in a block correct and had three chances to do so; four 5-year-olds failed to meet this criterion and were replaced in the final sample; the remaining participants usually passed within the first block. The experimenter was unable to see the stimuli during the criterion trials and all subsequent phases of the experimenter.

Practice run. Thresholds were calculated using a maximum-likelihood threshold estimation procedure (ML-PEST) in which the spatial frequency difference on the first trial was set at a one octave difference from the reference spatial frequency (where an octave is a halving or doubling of a value) and the value on each subsequent trial was the best estimate of the subject's threshold based on the history of the run (Harvey, 1997). Threshold was defined as the minimum change of spatial frequency required to identify accurately the interval with the thicker stripes. Specifically, threshold measurement stopped at the value corresponding to 82% correct responses with a confidence interval of 95% that the estimate of threshold was accurate within ±0.1 log units. There was no prespecified maximum number of trials.

Participants completed one full practice staircase for the condition they were being tested on first. Computer-generated positive and negative feedbacks were provided during the practice phase. Positive feedback after correct responses consisted of a 15° by 15° cartoon happy face in the center of the screen accompanied by audio encouragement pre-recorded from various male and female voices. Negative feedback after incorrect responses consisted of a 15° by 15° cartoon sad face in the center of the screen accompanied by a low-pitched tone (duration of feedback = 0.2 s).

Test of thresholds. The test of threshold was identical to the practice run. Demonstration and test phases were then repeated for the second reference spatial frequency. The mean number of trials per staircase was 56 (range = 37–121) for 5-year-olds, 56 (range = 38–91) for 7-year-olds, 61 (range = 38–123) for 9-year-olds, and 69 (range = 41–156) for adults. Participants were given as many breaks as necessary, and all participants completed the testing protocol in a single session that lasted no longer than 1 h.

Data analysis

Thresholds were converted to Weber fractions using the following formula:

$$\frac{\Delta f}{f}, \tag{2}$$

where Δf is the minimum difference in spatial frequency required to discriminate stripe width accurately, and f is the reference spatial frequency. The Weber fractions were subsequently subjected to an outlier removal procedure outlined by Kirk (1990). Specifically, each Weber fraction was converted to a Z score using the mean and standard deviation for that age and reference spatial frequency. Z scores greater than +2.5 or less than −2.5 were treated as outliers and were replaced with the original group mean (i.e., the mean threshold for the condition before removal of the outliers). Three data points were replaced: one from an adult tested with a reference spatial frequency of 1 cpd, one from a 9-year-old tested with a reference spatial frequency of 1 cpd, and one from a 7-year-old tested with a reference spatial frequency of 3 cpd. (Note that analyses completed on the original data set, without the removal of outliers, did not differ from the pattern of results when the analyses were completed with outliers removed.) The data were log transformed before analyses because a Levene's test indicated non-homogeneity of variance in the original data set ($ps < 0.00001$). After the log transformation, homogeneity of variance was improved but remained imperfect ($ps < 0.0001$). Partial eta squared (η_ρ^2) values were used for estimates of effect size when examining more than two groups. The figures show the original untransformed data.

Results

As shown in Figure 1, spatial frequency discrimination thresholds decreased with age. A mixed ANOVA with one between-subjects factor (age) and one within-subjects factor (reference spatial frequency) revealed a significant main effect of age, with thresholds decreasing as age increased, $F(3,76) = 57.79$, $p < 0.0001$, partial eta squared $\eta_\rho^2 = 0.70$, power = 1.0. There was no main effect of reference spatial frequency, $F(1,76) = 1.66$, $p > 0.20$, and no significant interaction between age and reference spatial frequency, $F(3,76) = 0.72$, $p > 0.55$. Tukey post-hoc tests revealed a significant difference in sensitivity between 5-year-olds and the older observers ($ps < 0.0001$) and between 7-year-olds and adults ($p < 0.0001$), but not between 7-year-olds and 9-year-olds ($p > 0.11$). Nine-year-olds did not differ significantly from adults ($p > 0.21$). Compared to adults, the minimum change necessary to discriminate spatial frequency, when averaged across the two reference spatial frequencies, was 5.7 times (0.29 log units) higher in 5-year-olds, 1.9 times higher in 7-year-olds, and 1.4 times higher in 9-year-olds. Curve fitting indicated that thresholds decreased exponentially with age, $R^2 = 0.50$, $y = 1996 * \exp(-0.856x) + 6.505$. The best-fitting exponential function collapsed across spatial frequency is shown as the smooth black curve in Figure 1.

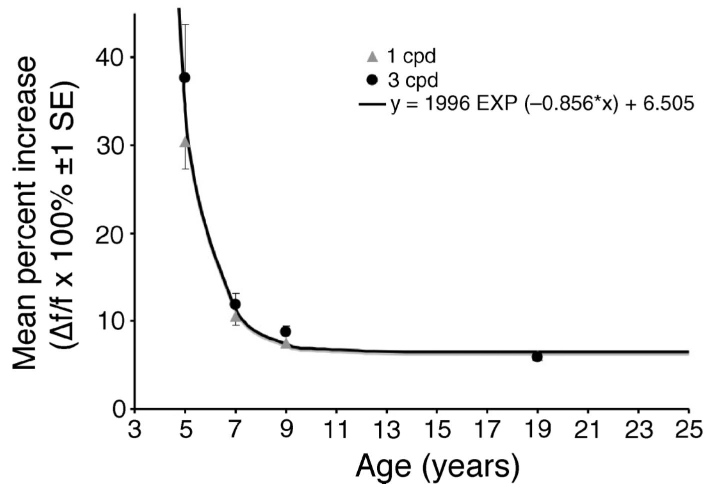

Figure 1. Mean percentage increase (±1 *SE*) for discriminating spatial frequency as a function of age. Data are from Experiment 1, which used a 2-alternative temporal forced-choice procedure. Gray triangles represent thresholds for discrimination from a reference of 1 cpd and black circles represent thresholds for discrimination from a reference of 3 cpd. Where not shown, error bars are smaller than the symbols. The best-fitting exponential function collapsed across spatial frequency is shown as the smooth black curve.

Discussion

In order to discriminate spatial frequency under the conditions tested here, adults required a 5.9% change from 1 cpd and 6.1% change from 3 cpd. Our values fall within the range of values obtained from previous studies that used similar methodologies with suprathreshold luminance-modulated sine-wave gratings. Specifically, thresholds for discriminating spatial frequency in adults range between 2% and 10% (Bennett & Cortese, 1996; Bennett et al., 2001; Campbell et al., 1970; Heeley et al., 1989; Hirsch & Hylton, 1982; Lin & Wilson, 1996; Mayer & Kim, 1986; Yo et al., 1989). As in the current study, previous studies that measured discrimination thresholds in adults found that sensitivity with baseline spatial frequencies of 1 and 3 cpd is similar when expressed as a Weber fraction (Campbell et al., 1970; Hirsch & Hylton, 1982; Yo et al., 1989).

When averaged across the two baseline spatial frequencies, thresholds were 5.7 times (0.29 log units) worse in 5-year-olds and 1.9 times (0.13 log units) worse in 7-year-olds than in adults. Although the 9-year-olds did not differ significantly from adults, the variability was still high (see Figure 1) and the mean values were still 1.4 times (0.07 log units) worse than those of adults. Together, these results are well described by an exponential development trajectory where the most rapid development is seen between 5 and 7 years of age, and more gradual development is seen thereafter.

One possible explanation for the poor spatial frequency discrimination observed in 5-year-olds is that the simple cells in primary visual cortex, on which spatial frequency discrimination depends (Hubel & Wiesel, 1968), are still immature. Support for this explanation comes from studies of the development of other basic visual abilities that implicate mainly cells in the primary visual cortex. Specifically, as in the current study, thresholds obtained for spatial and temporal contrast sensitivities (Ellemberg et al., 1999) and sensitivity to orientation (Lewis, Chong, & Maurer, 2009) are very immature at 5 years of age, are still two times worse than adults by age 7, and continue to show gradual improvement after the age of 7.

A second possibility is that 5-year-olds' performance is worse than that of older age groups because their poorer memory affects their performance with a temporal forced-choice procedure. Specifically, in the procedure used in Experiment 1, the participants had to remember the spatial frequency in interval 1 in order to compare it to the subsequent spatial frequency in interval 2. Although the interstimulus interval was very short (0.5 s), it is possible that there are improvements after age 5 in short-term memory for spatial frequency. We evaluated that possibility in Experiment 2. We tested new groups of 5-year-olds and adults both with the design used in Experiment 1 and with simultaneously presented gratings that removed the memory component. Because there was no effect of the reference spatial frequency in Experiment 1, we used only 1 cpd as the reference spatial frequency in Experiment 2. To rule out the possibility that edge cues could be used to solve the task when the comparison gratings were presented simultaneously, we used Gabors rather than using the sine-wave gratings within a square aperture of Experiment 1.

Experiment 2

Methods

Participants

The participants were new groups of twenty 5-year-olds (±3 months, 12 males) and 20 adults (mean age = 19, range = 18.2–20.8 years, 8 males) similar to those described in Experiment 1. An additional two adults were excluded from the final sample: one adult for not passing visual screening and one adult because of experimental error.

Stimuli

The stimuli were Gaussian-windowed ($\sigma = 2$) static horizontal sinusoidal gratings. The luminance profile of the Gabor stimulus is described by

$$L(x, y) = A \sin(2\pi f(x)) e^{-\frac{x^2+y^2}{2\sigma^2}}, \tag{3}$$

where A is the signal contrast (or amplitude modulation) set at 89 ± 2%, and f is the spatial frequency ranging from 1 to 2 cpd. The Gabor stimuli were rendered in a 15° circular aperture on a gray background and phase was jittered randomly. The resulting blurred edges of varying phase prevented participants from making judgments based on a direct comparison of the adjacent edges of the stimuli in the spatial condition. The space-average luminance of the background was maintained at 45.4 cd/m^2 and the contrast of the stimuli was maintained at 89 ± 2%. Maximum (L_{max}) luminance within each grating was 97.6 cd/m^2 and the minimum (L_{min}) was 5.6 cd/m^2. The reference spatial frequency for the gratings was 1 cpd, and the corresponding comparison spatial frequency ranged from 1.01 to 2 cpd.

Procedure

For the temporal forced-choice condition, the procedure was identical to that in Experiment 1. For the spatial forced-choice condition, participants were instructed to fixate on a central 1° black circle that appeared at the beginning of each trial. The fixation circle was replaced by the simultaneous presentation of the reference and test Gabor stimuli positioned with their centers 8° to the right and left of center. The task on each trial was to indicate whether the Gabor on the right or left was of lower spatial frequency (thicker stripes). The stimuli remained on the screen until the participant provided a response with no pre-specified time limit. A picture of a rabbit was placed on the right side of the monitor and a picture of a lion on the left side of the monitor to aid the 5-year-olds in distinguishing right and left. The pictures of the lion and rabbit were illuminated from the back to improve visibility. The stimulus with the lower spatial frequency (always the reference spatial frequency) appeared equally often on the right and left sides of the display. The experimenter said: "In this game, a black dot will appear and you have to look right at the black dot. Then the black dot will disappear and you will see two circles filled with stripes. [Point to circle on right] This circle is closer to the rabbit on the right. [Point to circle on left] This circle is closer to the lion on the left. It is your job to tell me which stripes are fatter, those that are closer to the rabbit or those that are closer to the lion".

The procedure was identical to that in the first experiment except that each participant contributed two thresholds obtained using two different paradigms rather than at two different baseline spatial frequencies. Order was counter-balanced across participants within each age group. The procedure began with a demonstration, criterion trials, and a practice run of the same test paradigm (temporal or spatial) that was to be tested first. The practice run was stopped at n = 30 trials, because pilot data from 5-year-olds indicated that 5-year-olds had difficulty completing an entire practice run combined with two test conditions. Demonstration and test phases were then repeated for the second test paradigm.

Data analysis

The data were subjected to an outlier removal procedure identical to the one used in Experiment 1. Five data points were replaced: one simultaneous and one sequential threshold from one adult, two simultaneous thresholds from two 5-year-olds, and one sequential threshold from a third 5-year-old. Subsequent analyses were conducted using this revised data set. (Analyses completed on the original data set, without the removal of outliers, did not differ from the pattern of results observed when the analyses were completed with outliers removed.) The data were log transformed before analyses, a transformation that eliminated non-homogeneity of variance ($p > 0.08$). The figures show the original non-transformed data.

Results

The results are shown in Figure 2. A repeated-measures ANOVA with one within-subjects factor (condition) and

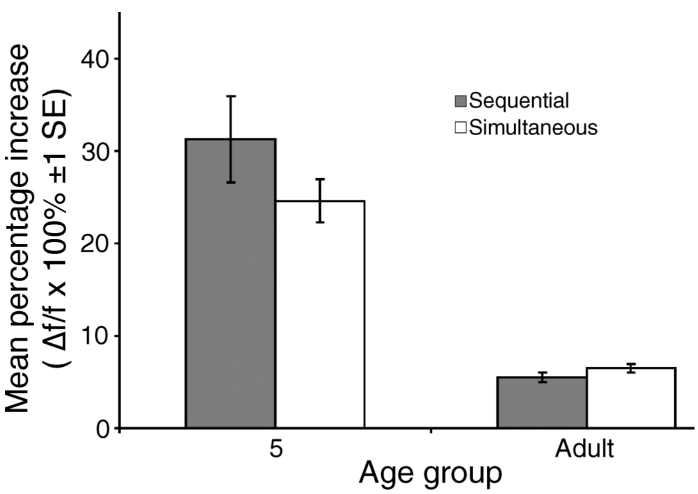

Figure 2. Mean percentage increase (±1 *SE*) for discriminating spatial frequency in 5-year-olds and adults. Data are from Experiment 2, which compared a temporal 2-alternative forced-choice procedure (sequential condition represented by gray bars) to a spatial 2-alternative forced-choice procedure (simultaneous condition represented by white bars). The error bars represent within-subject error.

two between-subjects factors (order and age) revealed a main effect of age, $F(1,36) = 113.89$, $p < 0.0001$, partial eta squared $\eta_\rho^2 = 0.76$, power = 1.0, and an interaction of condition and order, $F(1,36) = 10.46$, $p < 0.003$, partial eta squared $\eta_\rho^2 = 0.23$, power = 0.88. There was no main effect of order, $F(1,36) = 3.46$, $p > 0.07$, or condition, $F(1,36) = 0.32$, $p > 0.58$, no significant interactions of age with either order, $F(1,36) = 1.40$, $p > 0.25$, or condition, $F(1,36) = 3.47$, $p > 0.07$, and no significant 3-way interaction among order, condition, and age, $F(1,36) = 0.58$, $p > 0.45$. Regardless of order or condition, 5-year-olds' thresholds were significantly worse than those of adults.

Further inspection of the two-way interaction between condition and order revealed that participants had better thresholds in the second condition, regardless of whether it was simultaneous or sequential (order 1: $t_{19} = 2.1$, $p < 0.04$; order 2: $t_{19} = -2.3$, $p < 0.03$).

Discussion

Similar to the results of Experiment 1, adults' spatial frequency discrimination thresholds were 5.5% for the sequential condition and 6.5% for the simultaneous testing condition. Again, the values compare closely to those obtained from studies that used similar methodologies with suprathreshold luminance-modulated sine-wave gratings (Bennett & Cortese, 1996; Bennett et al., 2001; Campbell et al., 1970; Heeley et al., 1989; Hirsch & Hylton, 1982; Lin & Wilson, 1996; Mayer & Kim, 1986; Yo et al., 1989). However, our results are contrary to those reported in a study by Ben-Yehudah and Ahissar (2004) in which the mean threshold of normal adults was, paradoxically, 1.7 times better when the spatial frequency discrimination task was sequential rather than simultaneous. However, unlike the current study, Ben-Yehudah and Ahissar (2004) used extremely short presentation times in both the sequential and simultaneous conditions. It is possible that the faster processing demand created the paradoxically worse performance in the simultaneous condition. As the results from Experiment 2 demonstrate, when that faster processing demand is eliminated by unlimited viewing time, adults' sensitivity to simultaneously presented spatial frequencies is as good as their sensitivity to ones that are presented sequentially, at least with the parameters tested here.

As in Experiment 1, 5-year-olds' thresholds for spatial frequency discrimination were significantly worse than those of adults. Specifically, 5-year-olds were 5.7 times (0.76 log units) worse than adults at discriminating spatial frequency for the sequential condition and 3.8 times (0.58 log units) worse than adults for the simultaneous condition, with no significant difference in the size of the immaturity for the two conditions. The significant interaction of order with condition indicated that both adults and 5-year-olds did better on the condition tested second, likely as the result of practice with the task. Nevertheless, 5-year-olds' mean threshold in the second condition was still 4.0 times (0.60 log units) worse than that of adults, even for the simultaneous condition, the one that reduced the memory demand. Overall, reducing the memory demands by presenting the stimuli simultaneously for an unlimited time did not improve the accuracy of 5-year-olds over that found in the sequential condition.

Non-visual factors such as attentional, motivational, and criterion differences between 5-year-olds and adults may have contributed to the observed threshold differences. However, it is unlikely that they account for the full difference. By 5 years of age, children can perform as well as adults on psychophysical tasks that use methods that have similar performance demands to the ones used in the present study. For example, a study testing sensitivity to direction of local motion that used a two-alternative forced-choice procedure to measure thresholds found that 5-year-olds were nearly adult-like for luminance-defined stripes moving at 1.5 or 6 deg/s (Ellemberg et al., 2003). Another study using a two-alternative forced-choice procedure to measure sensitivity to direction of global motion in random dot kinematograms found that children were mature by age 3 (Parrish, Giaschi, Boden, & Dougherty, 2005). Although age of maturity will vary with the parameters of the stimuli and the visual decision required, these studies indicate that children can show adult-like visual thresholds by age 5. Thus, it is unlikely that non-visual factors account entirely for the immaturities observed in the present study.

General discussion

The results of Experiments 1 and 2 indicate that the spatial frequency discrimination of 5-year-olds is immature. In Experiment 1, there was an exponential developmental trend that showed rapid development between 5 and 7 years of age and gradual development between 7 years of age and adulthood. Sensitivity to orientation and to temporal and spatial contrast sensitivities show similar developmental patterns to those seen here for sensitivity to spatial frequency: significant immaturity at 5 years of age, marked improvement between 5 and 7 years of age, and gradual improvement between 7 years of age and adulthood on the order of a twofold reduction in the mean (Ellemberg et al., 1999; Lewis et al., 2009). Interestingly, Regan et al. (Regan & Beverly, 1985; Regan & Price, 1986; Vincent & Regan, 1995) have proposed a physiological explanation that could account for the similar patterns across these low-level visual tasks. They suggest that subpopulations of neurons in the primary visual cortex have a preferred orientation, a preferred spatial frequency, and a preferred contrast that vary independently from neuron to neuron but with different connectivities between subpopulations tuned to these properties that unconfound the three dimensions. If simple cells of V1 are responsible for transducing these three stimulus properties simultaneously, then their patterns of development would be expected to be similar.

Lower sensitivity in children to the spatial frequency signal could be caused by broader tuning of the V1 cortical neurons responsible for spatial frequency discrimination. However, single-cell recordings of neurons in the primary visual cortex in macaque infants as young as 1 week of age show adult-like tuning to spatial frequency, and no further changes between 1 and 16 weeks of age (Kiorpes & Movshon, 2004). Nevertheless, little is known about developmental changes in the spatial frequency tuning of neurons in the primary visual cortex of humans. Psychophysical measures of infants' contrast sensitivity function combined with either masking (Banks et al., 1985) or analyses of individual differences (Peterzell & Teller, 1996) indicate that the infant's visual system contains at least two spatial frequency channels. Between 4 and 8 months of age, the peak of the spatial frequency channel tuned to the coarsest spatial frequencies shifts to higher spatial frequencies but has still not reached the adult value of 1 c/deg by 8 months of age (Peterzell & Teller, 1996). No estimates of developmental changes after infancy in the exact tuning widths or numbers of individual spatial frequency channels are available.

Alternatively, or in addition, the poorer sensitivity in children could be explained by an immaturity in the ability to compare across different spatial frequency channels, an ability that depends on the selection of appropriate channels and the interactions between them. Immaturities in the ability to select appropriate channels may arise from greater internal noise in 5-year-olds than in adults, which would decrease the signal-to-noise ratio. Higher internal noise in children could be caused by higher levels of spontaneous firing and/or higher levels of spatial frequency-specific random firing. Furthermore, immaturities may also exist in the mechanism by which different channels interact with one another. A recent neuronal network model of the primary visual cortex demonstrates that spatial frequency selectivity in a particular neuron depends not only on feed-forward convergence of LGN cells onto V1 cells (Hubel & Wiesel, 1968) but also on non-linear cortical suppression (Zhu, Shelley, & Shapley, 2008). If this is the case, immaturities in the inhibitory mechanisms underlying spatial frequency tuning could contribute to the higher thresholds seen in children than in adults. Similar immaturities in the mechanisms underlying orientation discrimination could contribute to the observed immaturities in orientation discrimination and contrast sensitivity at 5 years of age (Ellemberg et al., 1999; Lewis et al., 2009). However, immaturities at the level of the retina and LGN likely also contribute to the immaturity in contrast sensitivity (reviewed in Ellemberg et al., 1999).

Regardless of the explanation, it is evident that spatial frequency discrimination is very immature at 5 years of age and shows significant improvement over the next 2 years and more gradual improvement thereafter. Further studies to elucidate the levels of internal noise and/or differences in the balance of excitatory and inhibitory influences in children compared to adults could elucidate the neural basis of the immaturity. This could be done by adding external noise to the stimulus in order to evaluate whether it elevates thresholds (as expected if the level of external noise exceeds the level of internal noise), by anatomical investigations of excitatory and inhibitory receptors, by using spatial frequency masking to investigate the breadth of tuning in children, and/or by varying the spatial frequency content of the area surrounding the stimulus. Such studies would help elucidate the reasons children are so slow to develop adult-like sensitivity to one of the building blocks of visual perception.

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