Donders Graduate School for Cognitive Neuroscience
Master of Science Programme
MSc Thesis

Luminance contrast modulation of spatial frequency VEPs in 5-year-old children

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Abstract

Different components of visual perception such as spatial frequency (SF) detection, luminance contrast sensitivity and colour vision develop at different rates. At 5-6 years of age, High SF (HSF) sensitivity is nearly adult-like and luminance contrast is also nearing the end of its maturation around 5-7 years. Low SF (LSF) on the other hand still has a substantial development to undergo till the age of 12. Additionally, there is a shift in selective processing of SF from the N2 component of visual evoked potential (VEP) in 3-6 year olds to the earlier N80 component of VEP at ages 7-8. Adult literature has revealed a complex interaction between SF and luminance contrast. How this interaction takes form in children however is relatively unknown. The aim of this study is to investigate the interaction between spatial frequency and luminance contrast in 5-6 year olds when these different components of visual perception are at different developmental stages to gain more insight into how this interaction develops. VEP modulations of HSF/LSF gratings at high and low luminance contrast levels were measured with electroencephalography (EEG) in 22 children aged 5. Results show that the P1 peak shows an adult-like pattern in 5 year olds, with an increase in amplitude as contrast increases, irrespective of SF. The N80 peak however shows only partial resemblance to the adult VEPs, showing the same selective enhanced activity for HSF but not LSF, yet is still lacking the interaction with contrast. Contrarily the N2 peak closely resembles the interactions patterns found for the N80 peak in adults. Taken together, the argument can be made that the complex interaction between SF and Contrast is characteristic for the selective processing of HSF and LSF stimuli and that the interaction between spatial frequency and contrast depends on the maturity of the underlying systems.

Introduction

Vision is one of our most important senses and we rely heavily on it for our interactions with the world around us. Yet at birth this faculty is still very poorly developed as both the retina and the visual pathways are still immature. A new-born has roughly 1/30 of the visual acuity (the resolution of the visual system) of adults (Leat, Yadav, & Irving, 2009), little to no high spatial frequency detection, some luminance contrast sensitivity (Adams & Maurer, 1984) and virtually no colour vision (Crognale, Kelly, Weiss, & Teller, 1998). Only detection of the lowest spatial frequencies is relatively intact at birth (Adams & Courage, 2002). During infancy there is rapid development of all components of vision and this development continues on in childhood and during adolescence. A growing body of research has shown that different components of vision such as spatial frequency (SF) detection, luminance contrast sensitivity, colour vision, temporal motion detection, acuity - just to name a few - develop at different rates (Adams & Courage, 2002; Atkinson, 1992; Bradley, Arthur and Freeman, 1982; Crognale, 2002; Gwiazda, Bauer, Thorn, & Held, 1997; Pompe, Kranjc, & Brecelj, 2006; Van den Boomen, Jonkman, Jaspers-Vlamings, Cousijn, & Kemner, 2015). How these different developmental trajectories affect the interactions between these visual aspects in children is still largely unknown.

Of the afore mentioned components, SF is the most well studied, as it has clinical relevance (in assessing the performance of the visual system in a more complete way then just testing for visual acuity) and has the most prominent differential development rates between high spatial frequency (HSF) and low spatial frequency (LSF) sensitivity. Spatial frequency refers to the number of light/dark cycles per degree (c/deg) of visual angle on the retina. HSF provides information about fine local details whereas LSF is important for global information. The threshold for detecting different frequencies of light/dark cycles is in the literature also referred to as contrast sensitivity (Beazley, Illingworth, Jahn, & Greer, 1980). However, as to not create confusion with luminance contrast, the term spatial frequency is used in this paper. As stated earlier, LSF sensitivity is relatively well developed at birth whilst HSF sensitivity is not yet present. A cross-sectional and longitudinal visual evoked potential (VEP) study by Norcia, Tyler & Hamer (1990) showed that already in the earliest weeks of life there are differential developmental trajectories for the two frequency ranges. LSF sensitivity develops rapidly during the first 10 weeks and then asymptotes at half the adult level. HSF sensitivity, however, continues to develop even after 10 weeks and does not appear to level off within the measured age-range (1-45 weeks of age) (Norcia, Tyler, & Hamer, 1990). Beyond infancy this trend persists: several cross-sectional studies, using either preferential looking paradigms or two-alternative forced-choice procedures, showed that till the age of 4, HSF maturation dominates the development of SF detection, reaching near adult-like level between 4-6 years (Adams & Courage, 2002; Beazley et al., 1980; Gwiazda et al., 1997). Small improvements are still reported until 9-12 years of age (Leat et al., 2009). From the age of 4 onwards LSF shows gradual growth with somewhat rapid growth between 7-8 years to adult-like levels at 9 years of age (Adams & Courage, 2002; Beazley et al., 1980; Bradley, Arthur and Freeman, 1982; Gwiazda et al., 1997).

Van den Boomen et al. (2015) investigated the neural mechanisms underlying the selective processing of SF from childhood into adolescence using visual evoked potentials (VEP) measured with electroencephalography (EEG). They found that across age groups LSF gratings evoked larger P1 (positive peak around 100ms after stimulus onset) peak amplitudes with faster latencies (Van den Boomen et al., 2015). This is consistent with adult data and a cross-sectional child VEP study by Mahajan and McArthur (2012) but the reverse (HSF P1 amplitude> LSF P1 amplitude) has also been found in children VEP studies (Boeschoten, Kenemans, Engeland, & Kemner, 2007). For the N2 (negative peak around 200ms after stimulus onset) Van den Boomen et al. (2015) found that at ages 3- 8 N2 shows a large selective response, with larger peaks with faster latencies for LSF compared to HSF stimuli. Over time there is an overall decrease in N2 amplitude and importantly a loss of selectivity, with almost no differences between the LSF and HSF amplitudes at 14-15 years of age (Van den Boomen et al., 2015). Contrarily, they found the opposite for the N80 peak. In adults a negative N80 peak (around 80ms after stimulus onset) is found exclusively for HSF, and not for LSF (Ellemberg, Hammarrenger, Lepore, Roy, & Guillemot, 2001). In children, this selective pattern is first found at 7-8 years, with no N80 peak found in earlier age groups (Van den Boomen et al., 2015). Boeschoten et al. (2007) found the same N80 selectivity in healthy 9-10 year olds but not in children with pervasive developmental disorder of the same age. The increase in differential response for N80 and the decrease in selectivity in N2 seems to indicate a shift in selective SF processing from V2 and more lateral areas to earlier V1 areas (Van den Boomen et al., 2015).

Besides spatial frequency, luminance contrast is another important component of vision. In new-borns, luminance contrast is the furthest developed out of all of the component contributing to vision. In a preferential looking paradigm, new-borns (1-5 days) showed a preference for a checkerboard with 11% luminance contrast compared to no checkers, but showed no difference in looking behaviour for the 5% contrast, indicating that new-borns are not yet able to detect these low luminance contrasts. Two months later this 5% luminance level is already detectable (Adams & Maurer, 1984). To put this perspective, adults can still detect stimuli with <1% luminance contrast. The luminance detection threshold decreases steadily and appears to reach adult-like levels between 5-7 years of age, although there is not much data on the developmental trajectory (Thibault, Brosseau-Lachaine, Faubert, & Vital-Durand, 2007). When adding an experimental task opposed to passive viewing, such as identifying the orientation of the gap-opening of C-optotypes under different luminance contrast, adult-like performance was found at the age of 12 (Bertone, Hanck, Guy, & Cornish, 2010).

Electroencephalographic (EEG) data puts the maturation of the luminance system earlier than the abovementioned behavioural tasks, as Gordon & McColloch (1999) found no significant differences between the signal-to-noise (SNR) level of 5 year olds, 8 year olds and adults for low (LC), medium and high (HC) luminance contrast levels (SNR reflecting the ability to see the luminance gratings. Critically they were not able to measure sufficient trials in the youngest age groups (5 years of age) and thus used the best trial of each contrast level of each group to analyse. Since inter-trial variability in EEG data is high (Faisal, Selen, & Wolpert, 2008), this choice of analysis strategy could have obscured developmental changes that were nonetheless already present. To our knowledge the Gordon & McColloch study is one of the only EEG studies to investigate the developmental trajectory of luminance contrast sensitivity beyond infancy, leaving a

large gap between how the brain develops from a still immature sensitivity at the end of infancy to adult-like sensitivity at 5-7 years old.

For both SF and luminance contrast the age at which the system as a whole reaches maturity is often disputed and varies across studies. For SF the reports range from 6 to 12 years. These differential findings can possibly be explained by statistical and sample differences, as most studies had small sample sizes or large age-spans that make it difficult to pinpoint an exact age, as well as experimental and non-neural factors, such as attention, motivation and general understanding of the experimental tasks (Gwiazda et al., 1997; Leat et al., 2009). Additionally, the criteria children use to determine their response could vary from those used by adults (children tend to guess more) which can be especially problematic for the often used yes/no stair-case design (Leat et al., 2009).

The discrepancies in the age of maturation between the behavioural data and the electrophysiological data can be explained by the range of perception they investigate. The behavioural data is almost exclusively about sensitivity functions, the most extreme end of perception of just barely detectable stimuli, whereas the VEP/EEG studies look at a more standard easily detectable range of stimuli. Just because the detection threshold is at an adult-like level does not necessarily mean that the underlying system of normative processing has also reached maturity.

Spatial frequency and luminance properties of an object or scene never occur in isolation, but are an interaction of the two aspects, e.g. the detection of a spatial frequency at a certain contrast level. In adults a modulatory effect of luminance contrast on the detection and VEP characteristics of SF has been reported. Van Ellemberg et al. (2001) recorded VEPs in adults of 6 SFs at 9 contrast levels. The P1 is observed at low contrast (4%) and increases in amplitude with increasing contrast independently of SF, and saturates at medium contrast levels (16%). N80 (in the literature also called N1) appears for HSF stimuli and is absent for LSF stimuli. With increasing SF N80 emerges at progressively lower contrasts (for the highest SF an N80 can already be found at 8% contrast, whereas at medium SF N80 only appears at 64% contrast and higher), increases in amplitude with increasing contrast and does not appear to saturate (Ellemberg et al., 2001). Ellemberg et al. (2001) did not investigate the effect of SF and contrast on latency. Other studies do indicate some latency changes, with an increase in P1 latency as luminance contrast or SF decreases (Bobak, Bodis-Wollner, & Guillory, 1987; Tobimatsu, Kurita-Tashima, Nakayama-Hiromatsu, Akazawa, & Kato, 1993). Schechter et al. (2005) found longer latencies for N2 (labelled N1) in low contrast compared to high contrast and chromatic conditions, but no statistics were reported.

These studies demonstrate a clear interaction between contrast and SF in adults. As far as we know this interaction has not been systematically studied in children. Looking at the interaction between contrast and SF in children can give new insight in how the interaction manifests at different ages during development when the three components, contrast sensitivity, and HSF & LSF detection abilities, are at different levels of maturity. At 5-6 years of age HSF is behaviourally near adult-like with luminance contrast also nearing the end of its maturation around 5-7 years whilst LSF still has a substantial development to undergo. Additionally there is a shift in selective processing of SF from N2 in 3-6 year olds to N80 processing in 7-8. One could imagine that due to these maturation differences a different interaction pattern may emerge compared to the

interaction pattern in adults, with different weights that vary across childhood and adolescence. On the other hand, the interaction could also be an independent feature of the visual system with its own developmental trajectory and maturation age. The aim of this study is to investigate the interaction between spatial frequency and luminance contrast in 5-6 year olds when the different components are at different developmental stages to gain more insight in how this interaction occurs. The VEPs evoked by different combinations of HSF/LSF and high and low luminance contrast were measured using EEG. The 3 peaks associated with visual processing , N80, P1 and N2 were investigated to see to what degree they present adult-like interaction patterns with respect to their amplitudes and latencies.

Methods

Participants

The study included a total of 24 healthy children aged 5 (M_{age}= 67months SD=3.2) recruited through the Radboud Baby & Child Center's database. Two participants were excluded due to poor data quality. All participants had normal vision. All parents gave written informed consent before participation and the study was approved by the local ethics committee of the Radboud University Nijmegen, in accordance with the Declaration of Helsinki.

Procedure

When the children arrived the proceedings of the whole experiment were explained to them and their parent(s). They were allowed to explore or draw a little to get used to the situation. The experiment started with two behavioural letter reading tasks to assess the reading ability of the children as part of a larger ongoing study. After the letter tasks the EEG session followed. The EEG task consisted of 3 grating blocks. Additionally, 2 prospective memory blocks were performed as part of a larger study. During the grating blocks, gratings with different contrasts and spatial frequencies were presented to the participants on the computer under passive viewing conditions. As an active distractor task a display with two side-by-side cartoon objects was pseudo-randomly presented on roughly one out of six trials (no more than 2 distractor stimuli in a row, and a maximum of 10 gratings between 2 distractors). A total of 87 distractor stimuli were presented for a total of 450 passive grating stimuli. The two cartoon objects could either be the same or different. The participants were instructed to press the left button on the button box when the objects were the same and the right button if they were different from each other. The order of the distractor displays was fixed. No responses were required for the gratings. An additional oddball distractor task was added for some children if they had difficulties concentrating on the screen. For 5% of the trials the fixation cross was red instead of black. The distracted children were instructed to verbally report if they saw a red cross. To furthermore ensure that the children would pay attention, they played a few rounds of Whack-A-Mole in between the blocks. The EEG session lasted roughly 20-30 minutes. Finally, two subtests of the Dutch version of the Wechsler Preschool and Primary Scale of Intelligence for Children (WPPSI-III-NL), the Block Design and Information test, were done to assess the IQ. Not all children completed the intelligence tests, as they were either too tired or too distracted after such a relatively long sit. The parents were given 4 questionnaires to complete at home. Overall the experiment lasted 1.5 hours.

EEG stimuli

The stimuli consisted of horizontal sinusoidal gratings with a 2x2 design: 2 spatial frequencies (L: 0.75, H: 6.0 c/deg) each presented at 2 luminance contrast levels (L: 10%, H: 100%) see Figure 1A. All gratings were presented on a grey background, of which the luminance was calculated to be in the middle of the absolute black and white values of the monitor in order to ensure optimal contrast of the stimuli with the background (Black: 0.165 cd/m^2 White: 105 cd/$m^{2)}$. A separate stimulus condition with iso-luminant red-green colour gratings was also included to investigate chromatic VEPs at age 5. Previous research has shown that the EEG signal can be affected if the colours are not iso-luminant on the participant's eye. When a half green- half red circle is presented with a objectively real, matched luminance value, the green can often be perceived as brighter than the red colour, even though they are in fact equally bright. To prevent this effect and ensure visual iso-luminance an adapted version of the minimally distinct border (MDB) paradigm (Brill, 2016) was presented before the start of the grating task. Here 10 red-green MDB circles were presented with different green values, keeping the red value constant. The participants were instructed to choose the circle where they felt the colours looked equally bright.

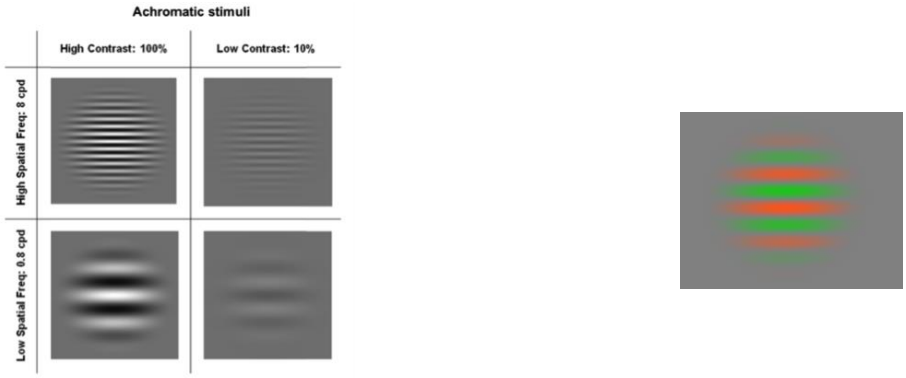

Figure 1. A) 2x2 stimulus conditions. Left to right, top to bottom: HSFxHC, HSFxLC, LSFxHC, LSFxLC .B) red-green chromatic grating.

The gratings were displayed on a 24 inch BenQ-monitor with a resolution of 1920x1080 and a 60 Hz refresh rate. Children sat at 57 cm from screen ensuring the stimuli were 7.0 degrees of visual angle in size. The gratings were presented for 500 ms with a jittered inter-stimulus interval that was varied from 700-900 ms to allow the EEG signal to return to baseline before presenting the next stimulus. Ninety trials per condition were presented resulting in 450 trials divided over 3 blocks. The EEG experiment was video recorded to later check if the child attended to the stimulus or not.

EEG Recording

EEG was recorded using a 32-active electrode Easycap with BrainAmp AC EEG amplifier using a time-constant of 10 s at a sampling rate of 1000 Hz. The forehead electrode was used as ground and FCz as reference electrode. Electrodes F3, Fz and F4 were removed from the cap and were used to monitor horizontal & vertical eye movements, with F3 & F4 being placed on the temples on each side for horizontal eye movement, and Fz on the left cheek to record vertical eye movement. Electrode Fp1 served as references for the horizontal eye movement. A standard scrubbing procedure was done after the cap was placed on the participant's head to ensure that the impedance was below 20kΩ before testing. The EEG was recorded using BrainVision Recorder 2.1.

EEG Pre-processing

The raw data was band-pass filtered between 0.1-30.0 Hz. The EEG timeseries were segmented into epochs of -100ms pre- to 480 ms post-stimulus onset. Based on the video recordings, 23-30% of epochs were rejected because the child was not looking at the screen (the child had to look that the screen for the entire duration of the stimulus presentation for the trial to be included in the analysis). There was no difference in epoch rejection between stimulus conditions ($F(4,105)=0.417$; $p=.79$). Eye movement and eye blinks were corrected with the Gratton et al. (1983) correction as implemented in BrainVision analyser 2.1. The data was baseline corrected with a -100 to 0 ms pre-stimulus window. Remaining artifacts were semi-manually removed defined by voltage change of more than 50uV per sampling point, a voltage difference of less then 150uV per 100ms, or amplitude above -150 or 150 uV or lowest amplitude difference of 1uV per 100ms. After pre-processing on average 68% of the trials remained (58-63 trials remaining per condition). There was no difference in the amount of artifacts rejection between conditions ($F(4,109)=0.79$; $p=.53$). The participants whom had less than 40 trials remaining per stimulus condition after pre-processing were excluded from further analysis, resulting in 2 participants being excluded for the analysis. For one participant the second gratings block was done twice as the participant had to use the bathroom in-between, resulting in 545 trials before pre-processing. All pre-processing was done in BrainVision Analyser 2.1.

Statistical analysis

VEPs were averaged per participant per conditions for the 3 electrodes of interest O1, Oz and O2. Peak detection was done semi-automatically by means of visual inspection of the automatically detected peaks. The selected peaks were double-checked by a second experimenter. N80 was defined as the lowest point between 50 ms to 110 ms, P1 as the highest point between 80 ms and 140 ms and N2 as the lowest point between 100 ms and 250 ms. The timeframes selected for the peaks are a bit wider than commonly used in children VEP studies, as we expect variance in the latencies due to the different stimulus conditions. If no peaks were found this was considered a missing value. Amplitudes and latencies were exported to SPSS for further analysis. Based on previous research Oz was chosen for further analyses, as activity is maximal in this electrode location. A 3x2x2 factor repeated measures ANOVA (2 SF (high/low) x 2 Contrast (10%/100%) x 3 Electrodes (O1, O2, Oz)) was performed to confirm this decision. Two 2x2 repeated measures ANOVA with SF (0.75 c/deg/6.0 c/deg) and Contrast (10%/100%) as within subject factors were performed for each peak, one for amplitude and another for latency. The number of measurements varied slightly between peak analyses due to the distribution of the missing values. Due to the narrow age range, only 10 months difference between the oldest and the youngest participant, age was not corrected for in the ANOVAs. To see whether there were still some developmental changes in this age range separate analyses were performed using bivariate correlations, correlating amplitude and latency of each peak, for all conditions, with age in months. A grand average waveform of the chromatic condition was obtained and the peaks were correlated with age to investigate possible age effects. No comparative analysis was done of the chromatic versus the achromatic conditions. Outliers were replaced similar to Quee et al. (2011) where values exceeding 2 S.D. from the mean group condition were replaced by the mean of the group condition. In total, 4.15% of data was replaced.

Results

The 3x2x2 ANOVA confirmed Oz to be best suited for further analysis. For the P1 peak a significant effect of electrode location was found (amplitude (F(2,24)=6.39, p<.05)) with Oz having higher overall amplitudes while the pattern of activity remained the same across all 3 electrodes. No differences between electrode sites were found for N2 (amplitude *(*F(2,20)=0.67, p=.521)), latency(F(2,20)=2.86, p=.081)). For N80 significant effects of electrode location were found (F(2,24)=7.43, p<.05) due to both differences in amplitudes, and patterns. These differences can be attributed to the high levels of noise, and as Oz has the least noise among the 3, this site was still deemed best suited for further analysis. The statistics for electrodes O1 and O2 are listed in Appendix A1. The grand average waveforms are plotted in Figure 2A.

N80

N80 peaks were not sufficiently reliably detectable in all participants. Instead we analysed the mean activity in a 20 ms time window around the grand average N80 peak of each condition (HSF/HC: 72-92ms, HSF/LC: 86-106ms, LSF/HC: 72-92ms, LSF/LC: 34-54ms). The 2x2 repeated measures ANOVA revealed an effect of SF on the mean activity (F(1,21)=26.33, p<.001), with a greater negative response for HSF gratings compared to a positive evoked activity for LSF (Fig 3.). There was no effect of Contrast (F(1,21)=0.06, n.s) nor an interaction effect (F(1,21)=0.77, n.s). As mean activity was measured no latency-analysis was possible.

P1

Amplitude. For P1 there is a significant effect of Contrast (F(1,18)=57.24, p<.001) where high contrast evokes a stronger response compared to low contrast, irrespective of SF (F(1,18)=1.94, n.s) (Fig. 4A). There is no significant interaction between SF and Contrast *(*F(1,18)=0.01, n.s).

Latency. For the P1 latency there are significant effects of SF (F(1,18)=25.78 , p<.001), Contrast (F(1,18)=170.03, p<.001) and an interaction effect of SF*Contrast (F(1,18)=9.21 p<.05). The low contrast gratings had longer latencies compared to the high contrast ones, while within one contrast level the HSF gratings had longer latencies than the LSF ones (Fig. 4B).

N2

Amplitude. There are significant effects of SF (F(1,17)= 51.75, p<.001), Contrast (F(1,17)= 25.94, p<.001) and an interaction effect of both factors (F(1,17)= 15.85, p=.001). The highest amplitude is evoked by the HSF stimuli at high contrast, followed by the same HSF at low contrast. The LSF evoke lower amplitudes than both the HSF, with the LSF at low contrast even showing a positive average amplitude (Fig. 5A).

Latency. For the N2 latency there is a significant effect of SF (F(1,17)= 11.51, p<.05) and a significant interaction effect of SF*Contrast (F(1,17)=48.67, p<.001). This interaction results in HSF having shorter latencies than the LSF in the low contrast gratings, but longer latencies than the LSF in the high contrast gratings (Fig. 5B). Contrast has only a marginally significant effect on the N2 latency (F(1,17)=3.11, p=.096)

Age

To investigate whether participant age - despite the narrow ten-month age range – affected peak amplitudes and/or latencies, age was correlated with the peak amplitude and latency for all peaks. Out of all of the tested correlations only several (marginally) significant correlations were found. For N2, HSF/LC amplitude becomes more negative with age ($r(20)=-.44$, $p=.051$), meaning the VEP becomes stronger; N2 LSF/HC decreases in latency with age ($r(22)=-.41$, $p=.059$), and N80 LSF/LC becomes more positive with age ($r(22)=.46$, $p<.05$), indicating a less pronounced peak with age. All correlations are weak to moderate.

Chromatic gratings

The grand average of the red-green colour grating is plotted in Figure 2B. No correlation effects were found of age and peak amplitudes or latencies.

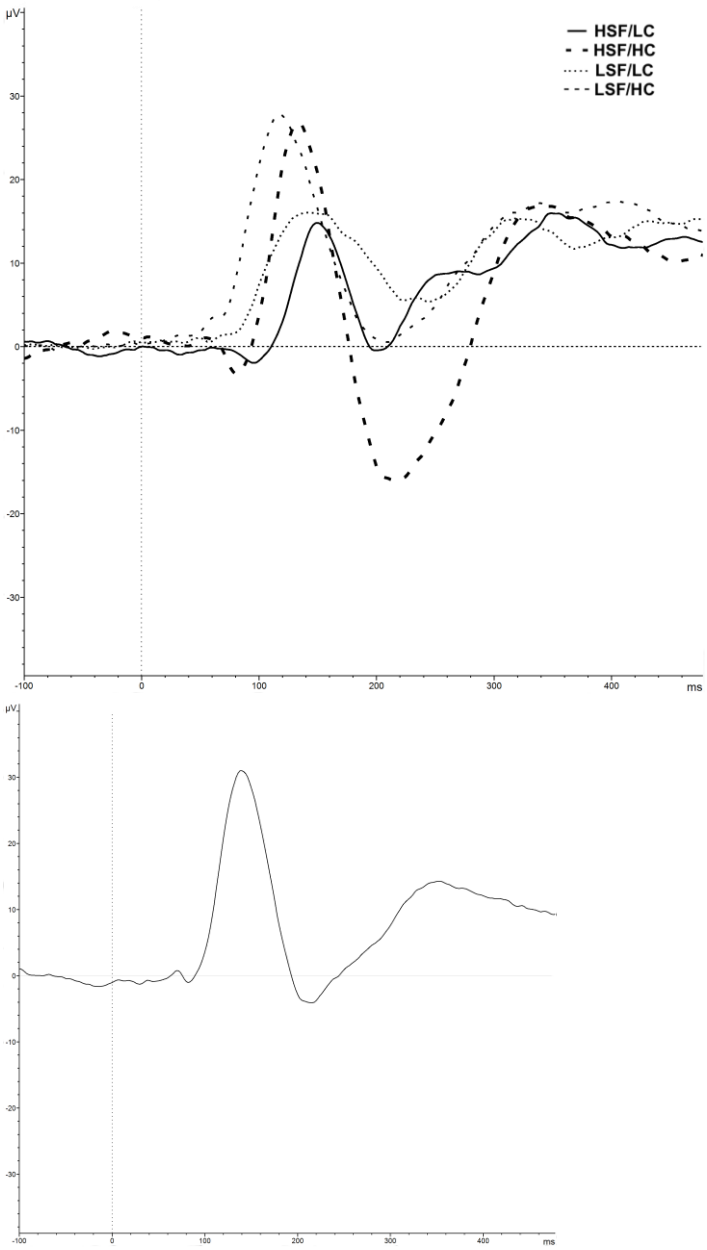

Figure 2. A) Grand average waveforms plotted for each stimulus condition and B) Grand average waveform for the chromatic red-green grating

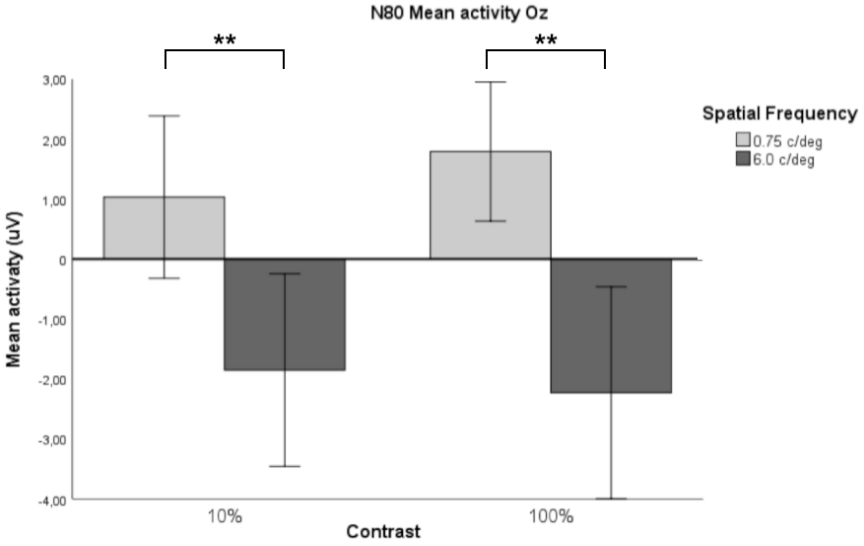

Figure 3. Mean activity of N80 under the different SF x Contrast conditions. Significance denoted as **= p<.001 and *= p<.05.

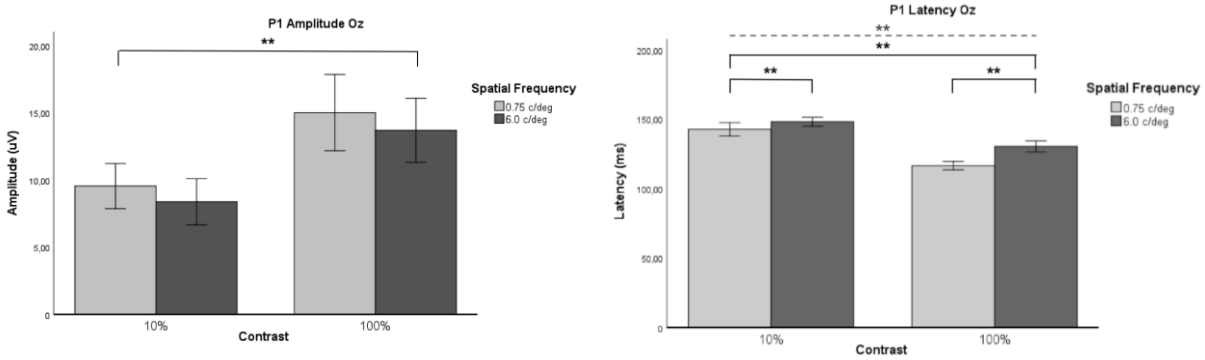

Figure 4. A) amplitude of P1 peak and B) latency of P1 peak under the different SF x Contrast conditions. Significance denoted as **= p<.001 and *= p<.05. Interaction effect denoted with dashed line.

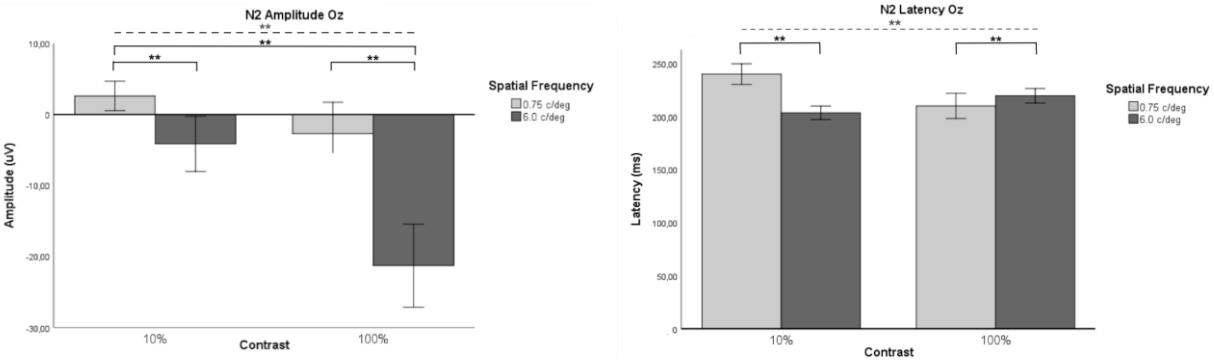

Figure 5. A) amplitude of N2 peak and B) latency of N2 peak under the different SF x Contrast conditions. Significance denoted as **= p<.001 and *= p<.05. Interaction effect denoted with dashed line.

Discussion

In the current study we investigated how luminance contrast and spatial frequency (SF) interact and modulate visual evoked potentials (VEP) in 5 year olds. We found adult-like patterns for some but not all peaks, reflecting that some of the underlying processes are already mature while others are still developing. The results show that the P1 peak the interaction patterns are already adult-like, whereas the interaction in the N80 peak is still immature. The N2 peak curiously shows an interaction pattern that closely resembles that of the N80 peak in adults. These findings will now be discussed in more detail.

The first positive VEP peak P1 in particular showed an adult-like pattern, with an increase in amplitude as contrast increases irrespective of SF, a finding reported in several adult contrast-SF interaction studies (Bobak et al., 1987; Ellemberg et al., 2001; Tobimatsu et al., 1993). The reduced latencies for both HSF and LSF in high contrast, with a greater reduction for LSF stimuli were found, are in agreement with Bobak et al. (1987). Although in line with adult findings, these findings seem to contradict child literature where strong effects of SF are often reported. Van den Boomen et al. (2015) and Mahajan et al. (2012) both found higher amplitudes elicited by low spatial frequency (LSF) stimuli over high spatial frequency (HSF) stimuli. This differential response remained stable over time even though the overall P1 amplitude decreased with age. One explanation for this apparent contradiction could be the dominating effect of contrast. The aforementioned studies showed that when looking at the effect of SF on the P1 in isolation, there is a clear differential effect of SF. However, when investigated in combination with contrast, the effect of low versus high contrast is so large that the differential effect of SF becomes too small to (statistically) detect. This shows that although P1 plays some role in selective processing of SF, it is predominately involved in the selective processing of luminance contrast and is already adult-like at 5 years old, as the underlying process of luminance contrast detection is very near the end of its developmental trajectory.

Where P1 closely resembles adult patterns in both amplitude and latency patterns, and in the lack of interaction between contrast and SF, N80 shows only partial resemblance to the adult VEPs. N80 mean activity shows the same selective enhanced activity for HSF but not LSF, yet is still lacking the interaction with contrast. As mentioned before, an intricate interaction is observed in adults where an increase in SF results in the N80 appearing at progressively lower contrasts, whilst increasing the contrast results in the N80 appearing at lower SF and an overall increase in amplitude. None of these interactions were found in the current study on 5 years olds. This makes sense when looking at where the N80, and the components that attribute to its signal, are in their developmental trajectory. LSF still has major development to undergo till the age of 12, and although N80 shows some differentiation between HSF and LSF at 5-6 years, this is still immature and continues to develop till 7-8 years of age. The lack of interaction effects could reflect this still immature differential response. This argument becomes more compelling when looking at N2. As stated earlier Van den Boomen et al. (2015) reported that in 3-6 year olds selective processing of HSF and LSF is predominantly seen in the N2 peak. This ability disappears over time, as at 7-8 years there is a shift in selective processing from N2 to N80 (Van den Boomen et al., 2015). Our results show interaction patterns for the N2 peak that closely resemble the interactions found for N80

in adults: enhanced amplitudes for high contrast and HSF, with high contrast evoking larger amplitude than low contrast stimuli, yet HSF/LC still evoking a greater response than LSF/HC. Though Ellemberg et al. looked more that the interaction of the full response function considering the fact that they measured more SFs and contrast levels, when looking at the specific data points corresponding to our stimuli values, the pattern of enhancement of N80 in adults is the same as we found for N2 in 5 year olds. Taken together the argument can be made that the complex interaction between SF and contrast is characteristic for the selective processing of HSF and LSF stimuli. The complex interaction is first present in N2 and shifts to N80 around 7-8 years as the underlying selective processing of HSF/LSF shifts to N80. At age 5, in our study, this shift is not yet complete.

That said alternative explanations for the lack of interaction effects found for N80 cannot be ruled out. One reason why no interaction effect has been found could be due to noise. As the N80 peak was not yet reliably detectable across our sample, mean activity was analysed instead. Even with this manipulation there was still considerable noise as evident when looking at the results from other 2 electrode locations O1 and O2). For both P1 and N2 the same pattern of results were found for all 3 occipital electrodes of interest (O1, Oz, O2), with the only difference being higher overall amplitudes for Oz, which is consistent with previous literature. For N80 however, different effects were found for different electrodes, with no effects found in O2, whilst O1 showed effects of both SF and contrast but no interaction effect. Although studies have shown an effect of SF on the spatial location of N80 processing, with HSF activating relatively primary visual areas and LSF activating more secondary visual areas in adults (Boeschoten, Kemner, Kenemans, & van Engeland, 2005), Van den Boomen at al. reported no such findings, suggesting that the differences between electrodes for N80 are more likely due to high levels of noise. An effect from P1 might also play a role, where a stronger P1 response could already effect the earlier N80 response, resulting in more positive N80 peak values. Similar carry-over effects of P1 on N2 have been reported where peak-to-peak analyses were used to correct for this(Mahajan & McArthur, 2012; Rokszin, Győri-Dani, Bácsi, Nyúl, & Csifcsák, 2018). This method could however not be applied to our N80 as the peaks were not reliable detectable throughout the sample. A second factor complicating the stated account is that no systematic investigation of SF in combination with contrast manipulation in adults is available for N2. N2 is thought to has lost its role in selective processing of SF in adults (Van den Boomen et al., 2015). Instead N2 is appears to have a more top-down role, especially in discrimination processes (Hopf, Vogel, Woodman, Heinze, & Luck, 2002; Vogel & Luck, 2000). Studies have shown an enhanced N2 response when the subjects were asked to make a discrimination between two stimuli compared to when they just had to report a detection of a stimulus. The enhanced effect was found when subjects discriminated on the bases of colour, form, velocity, and visual-spatial variations. This process is closely linked to attentional effects (Hopf et al., 2002; Vogel & Luck, 2000). Given that the N2 appears to be involved more top-down processes later in life, one can image that the adult VEP pattern would have different from the one we found in 5 years olds, where the modulation effect of SF and contrast might play a much smaller role, though more research is needed to make such assumptions.

In general the chromatic VEP waveform is consistent with reports from the developmental trajectory of colour vision. For the chromatic gratings the grand waveform shows a small beginning of an N80 peak, however, the response is dominated by a large P1 peak. These results are consistent with longitudinal and cross-sectional work by Crognale (Crognale, 2002; Crognale et al., 1998; Madrid & Crognale, 2000) as well as others (Pompe et al., 2006; Tobimatsu, Tomoda, & Kato, 1996) who have reported a reversal from a predominantly positive P1 response peak to a mostly negative C1 response peak (roughly similar to N80) as the colour system matures from childhood into adolescence. This transition from a positive to a negative peak start at around 6 years and lasts till 14-15 years varying slightly for the different colour channels. Even though the developmental changes are less complex compared to achromatic stimuli, no effects of age were found (likely due to the narrow age range).

Differential processing of SF and luminance contrast are often linked to the parvocellular pathway and the magnocellular pathway, respectively. The parvocellular pathway favours processing colour contrast, HSF and low temporal frequency stimuli, whereas magnocellular processes stimuli with low-luminance contrast, LSF and high temporal frequencies. A body of work of human and primate research have linked the N80 peak with parvocellular processing and the P1 with magnocellular processing (Ellemberg et al., 2001; Foxe et al., 2008; Hammarrenger et al., 2003). From a developmental perspective our findings add to this that the P1-linked magnocellular pathway is near mature and adult-like in 5 years olds, while the N80-linked parvocellular pathway is lagging behind and still has to undergo further development. Infant studies into the development of both pathways show a similar trend, where magnocellular activity is present at birth and matures fast during the first year of life while parvocellular activity only appears later and shows slower developmental (Hammarrenger et al., 2003; Norcia et al., 1990). Our data suggests that this parvo- over magnocellular trend persists till at least 5 years of age.

There are a handful of studies that have attempted to connect the different developmental trajectories of the visual system to perception and behaviour. In face perception, children, aged 3-8, rely on HSF for both rapid categorization of emotions and explicit processing of facial expression, opposed to adults who only rely on HSF for processing the latter. Even for rapid fear processing children aged 3-8 rely more on detailed HSF than global feature LSF information (Vlamings, Jonkman, & Kemner, 2010). Rokszin et al. (2018) found similar HSF driven processing for the rapid classification of everyday photographs of objects in 7-8 year olds. This fits with the previous stated developmental account of earlier maturation of HSF and the parvocellular pathway over LSF and the magnocellular pathway. As HSF processing reaches maturity, it might become most efficient to use the fully developed HSF for the rapid categorization over the still immature LSF information (Vlamings et al., 2010).

Limitations

One limitation of the present study is that it could not explore the full complexity of the interaction between SF and contrast in young children due to the fact that only 2 contrasts and 2 spatial frequencies were investigated. The modulations of intermediate contrasts and frequencies and the development of the characteristic differences in saturation levels of the parvo- and magnocellular pathways are some of the questions

not answered in this study. Though tempting to add many additional contrasts and frequencies, one must first consider the limitations of children VEP research. Children's attention spans are limited and a high number of trials need to be recorded per condition in order to have sufficient trials remaining after artifact rejection, due to the higher rejection rates. Adding more conditions makes the experiment take a long time. With just 5 conditions our EEG session lasted 20-30 min. which was considered the maximum duration for the children already. To investigate the full range of the interaction between contrast and SF a different paradigm may need to be employed or alternatively older children with a greater attention span could be tested.

Another concern is whether or not iso-luminance was achieved for the red-green chromatic grating using the minimally distinct border paradigm. This method was chosen instead of the often used flicker fusion paradigm as it was deemed to be easier and less taxing on the children in an already relatively long experiment. The children were instructed to choose the circle where they felt the red and green looked equally bright. The children gave of a distinct impression that they did not understand what was asked of them even when the question was rephrased several times. As a result the children overwhelmingly choose the circle that was *the brightest* rather then the circle of *equal brightness*. Non-isoluminance is known to affect waveforms, yet how precisely it affects the waveform especially in children is not fully understood. Given that we only looked that overall shape of the chromatic response without going in to detail, the non-isoluminance might not be as problematic yet some caution in interpreting the chromatic results might still be warranted.

Future research

A full cross sectional design with a wider range of ages could further explore the conclusions drawn in this paper. In the current study the age group was too narrow to investigate age effects, as this was not our primary interest. A younger age group could be added to see the modulation of contrast and SF before HSF and luminance contrast reach maturity. It would also be interesting to see an older age group, 7-8 years, to investigate how the selective processing shifts from N2 to N80. This shift could also be studied as a shift in processing location, using fMRI of dense EEGs as N2 and N80 are thought to have different source locations, the former being more extrastriate and the latter primary visual areas.

Some effort can be made to reduce the difference in range investigated between the behavioural studies and the EEG studies (with behaviour using mostly extreme ranges of stimuli to detection thresholds while EEG uses a more normative range of stimuli) allowing for closer comparison. Thus the EEG studies should investigate not just the normal range of stimuli but include the extreme threshold cases as well. The other way around, by studying the normal range more closely in a behavioural manner subtle differences can be detected that then could be linked to the discrepancies found in the EEG signals. Bridging the gap between ranges used in behavioural and EEG could help solve the discrepancies in findings of when a subsystem of vision reaches maturity.

In conclusion the current study reveals that the interaction between spatial frequency and contrast in 5 year olds is already adult-like for P1, as the underlying system of contrast processing is nearly mature. The interaction patterns were found for N2 but not N80, as the selective processing of high spatial frequency over low spatial frequency is

still processed through N2 and will only later in development shift to N80. Taken together this shows that the interaction of spatial frequency and contrast depends on the maturity of the underlying systems. Research into different age groups, where the maturation levels of all aspects vary, would help generate a greater understanding of these interactive mechanisms.

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Appendix

A1

Table A.1
Results of 2x2 repeated measures ANOVA for all occipital electrodes

	Oz				O1				O2			
	df	***F***	***p***	***N***	***df***	***F***	***p***	***N***	***df***	***F***	***p***	***N***
N80 mean activity												
Spatial freq.	1.21	26.330**	0.000	22	1.21	13.987**	0.001	22	1.21	0.816	0.377	22
Contrast	1.21	0.063	0.805	22	1.21	4.708*	0.042	22	1.21	2.587	0.123	22
SF*LC	1.21	0.769	0.390	22	1.21	1.634	0.215	22	1.21	0.016	0.900	22
P1 Amplitude												
Spatial freq.	1.21	26.330**	0.000	22	1.21	13.987**	0.001	22	1.21	0.816	0.377	22
Contrast	1.21	0.063	0.805	22	1.21	4.708*	0.042	22	1.21	2.587	0.123	22
SF*LC	1.21	0.769	0.390	22	1.21	1.634	0.215	22	1.21	0.016	0.900	22
P1 Latency												
Spatial freq.	1.18	25.784**	0.000	19	1.13	3.397	0.088	14	1.16	7.9*	0.013	17
Contrast	1.18	170.039**	0.000	19	1.13	61.218**	0.000	14	1.16	98.005**	0.000	17
SF*LC	1.18	9.209*	0.007	19	1.13	4.551	0.053	14	1.16	7.059*	0.017	17
N2 Amplitude												
Spatial freq.	1.17	51.746**	0.000	18	1.12	76.593**	0.000	13	1.16	46.302**	0.000	17
Contrast	1.17	25.942**	0.000	18	1.12	19.708**	0.001	13	1.16	16.971**	0.001	17
SF*LC	1.17	15.846**	0.001	18	1.12	9.627*	0.009	13	1.16	31.003**	0.000	17
N2 Latency												
Spatial freq.	1.17	11.509*	0.003	18	1.12	0.032	0.860	13	1.16	7.300*	0.016	17
Contrast	1.17	3.110	0.096	18	1.12	0.279	0.607	13	1.16	1.548	0.231	17
SF*LC	1.17	48.668**	0.000	18	1.12	22.993**	0.000	13	1.16	22.425**	0.000	17

Note: Significant levels are denoted with * of p=<.001 and * for p=<.05