Tracking changes in spatial frequency sensitivity during natural image processing in school-age: an event-related potential study

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Abstract

Several studies have shown that behavioral and electrophysiological correlates of processing visual images containing low or high spatial frequency (LSF or HSF) information undergo development after early childhood. However, the maturation of spatial frequency sensitivity in school-age has been investigated using abstract stimuli only. The aim of the current study was to assess how LSF and HSF features affect the processing of everyday photographs at the behavioral and electrophysiological levels in children aged 7-15 years and adults. We presented grayscale images containing either animals or vehicles and their luminance-matched modified versions filtered at low or high spatial frequencies. Modulations of classification accuracy, reaction time and visual event-related potentials (posterior P1 and N1 components) were compared across five developmental groups and three image types. We found disproportionately worse response accuracies for LSF stimuli relative to HSF images in children aged 7-8 years, an effect that was accompanied by smaller LSF-evoked P1 amplitudes in this age period. At 7-8 years of age, P1 and N1 amplitudes were modulated by HSF and LSF stimuli (P1: HSF>LSF; N1: LSF>HSF), with a gradual shift towards the opposite pattern (P1: LSF>HSF; N1: HSF>LSF) with increasing age. Our results indicate that early cortical processing of both spatial frequency ranges undergo substantial development in school-age, with a relative delay of LSF analysis, and underline the utility of our paradigm in tracking the maturation of LSF vs. HSF sensitivity in this age group.

Keywords: school-age; vision; spatial frequencies; event-related potential; ERP

Introduction

When we look at a complex visual scene such as a street containing living beings and artificial objects, our visual system analyzes the image at different spatial scales simultaneously (Campbell & Robson, 1968). On a subcortical level, low- and high spatial frequencies (LSF and HSF) are coded by the magnocellular (M) and parvocellular (P) subcortical channels, respectively (Livingstone & Hubel, 1988). Whereas global characteristics of the visual input such as image layout and object shapes are primarily determined by LSF information and activity in the M system, HSF-sensitive parvocellular neurons convey information about local stimulus details and fine texture (Livingstone & Hubel, 1988; Schiller, Logothetis, & Charles, 1990). Functioning of these two channels not only determines visual processing in adults, but due their unique developmental patterns across infancy and childhood, they also shape how children perceive the world (Atkinson, 1992; Johnson, 2005; Leonard, Karminoff-Smith, & Johnson, 2010).

Visual perception during the first months of life is dominated by coarse LSF information (Adams & Courage, 2002; Braddick & Atkinson, 2011; Gwiazda, Bauer, Thorn, & Held, 1997; Hammarrenger et al., 2003). In this period infants perceive relatively few details, but this ability develops rapidly in the first years of life (Adams & Courage, 2002; Gwiazda et al., 1997). There is ample evidence that the maturation of both LSF and HSF processing continues after infancy, but at different speed. Several behavioral studies using abstract stimuli such as sinusoidal luminance-contrast gratings found that development of LSF sensitivity lags behind that of HSF between 8-12 years of age (Adams & Courage, 2002; Benedek, Benedek, Kéri, & Janáky, 2003; Benedek et al., 2010; Gwiazda et al., 1997). However, there is also evidence for the ongoing development of HSF processing at 12 years, since children's performance is still not adult-like at this age (van den Boomen & Peters, 2017). Finally, a study assessing the maturation patterns of HSF vs. LSF sensitivity using two

spatial frequencies reported similar trajectories for both stimulus types between 5 years and early adulthood (Patel, Maurer, & Lewis, 2010). Thus, it seems that both LSF and HSF processing are characterized by prolonged, but non-linear maturation, and at present it is difficult to know whether either LSF or HSF analysis is fully mature before adulthood, as this might depend on the SF range tested, stimulus contrasts and/or paradigms used. It is important to note, though, that none of the above studies used complex, meaningful stimuli such as photographs of everyday objects or scenes, nor applied a task that required participants to recognize and discriminate stimuli based on their semantic content. Studying the development of SF processing with paradigms sensitive to higher-level vision can have important implications not only for typical development, but also for certain neurodevelopmental disorders that are simultaneously characterized by altered SF sensitivity and disrupted processing of complex stimuli (Deruelle, Rondan, Gepner, & Tardif, 2004; Gori, Seitz, Ronconi, Franceschini, & Facoetti, 2016; Vlamings, Jonkman, van Daalen, van der Gaag, & Kemner, 2010). This is because processes linked to more elaborate visual analysis such as the detection of category-specific features might not be recruited to the same degree in experiments using relatively simple designs, and hence, the influence of disrupted SF sensitivity on vision in e.g. autism spectrum disorder or developmental dyslexia might be different for sinusoidal luminance-gratings relative to emotional facial expressions or written words, respectively.

In adults, previous electrophysiological studies found that the magnitude of visual event-related potentials (ERPs) measured above the occipital region is sensitive to the SF content of stimuli. In particular, the P1 component (a positive peak arising between 80 and 140 ms) is evoked both by LSF and HSF stimuli, and can be either enhanced or reduced to HSF (relative to LSF) stimuli, depending on several factors, including contrast, structural complexity and possibly also task requirements (Baseler & Sutter, 1997; Boeschoten,

4

Kemner, Kenemans, & Engeland, 2005; Craddock, Martinovic, & Müller, 2013; Ellemberg, Hammarrenger, Lepore, Roy, & Guillemot, 2001; Hansen, Jacques, Johnson, & Ellemberg, 2011; Rokszin, Győri-Dani, Nyúl, & Csifcsák, 2016). Similarly, the subsequent N1 component (with a negative peak between 140-220 ms) reflects the cortical analysis of both LSF and HSF images, but its amplitude is modulated by the spectral content of stimuli in an inconsistent way, an effect that is probably paradigm-specific (Boeschoten et al., 2005; Craddock et al. 2013; Rokszin et al., 2016). Since the posterior P1 and N1 components reflect continuously unfolding, temporally overlapping processes of visual analysis such as feature detection, figure-ground segregation and structural encoding, and as outlined above, they are both influenced by SFs, these ERPs provide a unique measure for tracking the time course of SF processing in various groups of participants.

Visual ERPs evoked by LSF or HSF stimuli change with development across childhood: early cortical responses are differentially modulated by LSF vs. HSF square-wave gratings already in infancy (Zemon, Hartmann, Gordon, & Prünte-Glowazki, 1997), and the prominent P1 waveform observed exclusively for LSF stimuli during the first month of life suggests that the M-channel becomes functional more rapidly than the P-channel (Hammarrenger et al., 2003). In childhood and adolescence, age-related ERP effects were observed for both LSF and HSF stimuli between 3-15 (van den Boomen, Jonkman, Jaspers-Vlamings, Cousijn, & Kemner, 2015) or 10-18 years of age (Mahajan & McArthur, 2012), indicating ongoing maturation in this time period for the M- and P-channels. Importantly, while Mahajan & McArthur (2012) found that the dynamics of LSF vs. HSF processing (as indexed by both the P1 and N1 components) was comparable between 10-18 years of age, other work indicated delayed maturation for HSF (relative to LSF) analysis between 5-11 years (for steady-state visual evoked potentials; Gordon & McCulloch, 1999) or 7-10 years (in the N1 latency range; van den Boomen et al., 2015). With respect to how visual ERPs are

modulated by SFs, two studies found larger P1 amplitudes for LSF, but enhanced N1 components for HSF stimuli, as well as shorter latencies for LSF stimuli regardless of age (Mahajan & McArthur, 2012; van den Boomen et al., 2015), a pattern that has also been reported in adults (Rokszin et al., 2016), but is not entirely consistent with other studies (Boeschoten et al., 2005; Craddock et al., 2013). Altogether, previous research focusing on the development of visual ERPs evoked by different SFs provides evidence for the continued development of LSF and HSF processing in school-age, but to our knowledge, no ERP study found support for the prolonged maturation of LSF analysis, as highlighted by several behavioral studies (Adams & Courage, 2002; Benedek et al., 2003; Benedek et al., 2010; Gwiazda et al., 1997). Discrepancies between behavioral and electrophysiological work might stem from considerable variability in experimental protocols and from the fact that maturation patterns of behavioral performance and visual ERPs have not been compared to each other in the same group of participants, using the same experimental paradigm.

Despite our knowledge on how sensitivity to SFs matures during childhood and adolescence in paradigms using abstract stimuli, less is known about the impact of these developmental changes on the perception of more complex, meaningful images. Using colorful natural images, Batty and Taylor (2002) found that both behavioral and ERP correlates of animal vs. non-animal categorization keep developing during school-age (7-15 years), but the question of how these effects are influenced by the maturation of the LSF vs. HSF processing remains unknown. Given that LSF information was argued to be crucial for the rapid categorization of natural images (for review see: Fabre-Thorpe, 2011), it seems feasible to assume that in a more complex task involving decision-making based on semantic content, the putative prolonged maturation of LSF analysis during school-age (as suggested by behavioral studies) will also manifest in age-related changes in visual ERPs to LSF vs. HSF inputs. Given that the classification of everyday photographs containing objects was

argued to rely on fast feedforward information flow within the ventral visual pathway with bi-directional interaction between object and scene processing (Fabre-Thorpe, 2011), the finding that the influence of SFs on early ERPs changes throughout school-age would have developmental implications not only for object recognition, but also for scene processing.

The aim of the current study was to investigate how LSF and HSF information modulates behavioral performance and neural activity in children aged 7-15 years and adults when categorizing images as animals or vehicles. We presented grayscale photographs containing either animals or vehicles and their modified versions filtered at low or high spatial frequencies and analyzed modulations of classification accuracy, reaction time and visual ERPs (amplitude and latency of the posterior P1 and N1). Based on previous study results, we hypothesized that sensitivity to low and high spatial frequencies continues to develop in school-aged children, but at a different speed and pattern, with slower maturation of the LSF-associated M-channel. We anticipated that this effect would be detectable both on the behavioral and electrophysiological levels when participants are asked to categorize photographs based on their content.

Methods

Participants

Ninety-six participants aged between 7-30 years were clustered into five age groups: 7–8 (N=19, mean age=7.7, SD=0.45, 10 female), 9–10 (N=20, mean age=9.4, SD=0.51, 12 female), 11–12 (N=20, mean age=11.4, SD=0.5, 8 female), 13–15 year-old children (N=16, mean age=13.7, SD=0.77, 11 female), and adults (N=21, mean age=23.9, SD=3.44, 13 female). Children were recruited from two elementary schools; the majority of adults were university students. All participants had normal or corrected-to-normal vision. None of the subjects suffered from any developmental, psychiatric, neurological disorders (based on self-

report (adults) or parental report (children)), or learning problems (based on the report of the school's special education teacher (children)). The study conformed with the Declaration of Helsinki and was approved by the United Ethical Review Committee for Research in Psychology, Hungary (EPKEB). Before the procedure, written informed consent was obtained from adult participants and parents of all children/adolescents, whereas non-adults gave their oral (7-12 years) or written (13-15 years) assent to participation. No financial compensation for participation was received.

Stimuli and procedure

Complex natural images (360 in total), containing either an animal or a vehicle (180-180) were selected from a commercial image database (Corel Photo Library). The pictures in both categories were chosen to be as varied as possible. The animal category included mammals, birds, insects, fishes and reptiles, while vehicles consisted of cars, trucks, trains, civil or military airplanes and boats. Since we rarely encounter isolated objects outside the laboratory, we used complex images with objects embedded in natural and man-made scenes, which is in contrast to previous studies presenting abstract stimuli or isolated objects on a homogeneous background (Craddock et al., 2013; Gordon & McCulloch, 1999; Mahajan & McArthur, 2012; van den Boomen et al., 2015). This way, image classification in our task would not only depend on object-specific processes, but also on the influence of contextual cues, which has been incorporated into models of object recognition (e.g. Bar, 2004; Oliva & Torralba, 2007). The size of the pictures was 256×256 pixels, corresponding to a visual angle of $9º \times 9º$ from a viewing distance of 110 cm.

Three stimulus types were used: intact stimuli and their modified versions with attenuated high or low spatial frequencies (see Figure 1. for examples). Color extraction and spatial frequency filtering were performed with Adobe Photoshop CS5 (Adobe Systems Inc.,

San Jose, USA). Low-pass filtering was done with a Gaussian blur filter (6.1 pixel kernel), whereas high-pass filtering was performed with a radius of 0.3 pixels (Bar et al., 2006). All images were luminance-adjusted with the SHINE toolbox (http://www.mapageweb.umontreal.ca/gosselif/shine/). The mean overall luminance was 6.95 ± 0.08 cd/m^2, 7.15 ± 0.11 cd/m^2 and 7.61 ± 0.39 cd/m^2 for intact, LSF and HSF stimuli, respectively, as measured with a Mavolux5032C luminance meter [$F(2,1077) = 1.698$, $p = 0.183$, $\eta p^2 = 0.003$].

Figure 1. Examples of animal and vehicle stimuli in the intact (left column), low spatial frequency (middle column) and high spatial frequency (right column) conditions.

The effect of image filtering was verified by analyzing of spectral content of our stimulus set in the following manner. Each image was windowed with a Tukey-window (tapered cosine function, spanning 10% of the image on each border) to remove boundary artifacts. The power spectrum of each windowed image was calculated by the discrete Fourier

transform, and then averaged over all images for a particular stimulus type (intact, LSF, HSF). The average power spectrum was mapped (resampled) from the Cartesian coordinate system to the polar (orientation angle, spatial frequency) coordinate system using 1 degree angular steps and the original (1 pixel) spatial frequency step using the inverse mapping strategy. This resulted in a polar representation of the Fourier spectrum with similar density as the original Cartesian Fast Fourier Transform matrix. The analysis revealed robust attenuation of spatial frequencies above 0.5 cycles/degree (cpd) for LSF and below 3.8 cpd for HSF pictures. These cut-off parameters are comparable with those reported earlier in the literature (LSF: 0.6 cpd and HSF: 3.3 cpd in Bar et al., 2006; LSF: 0.9 cpd and HSF: 4.7 cpd in Craddock et al., 2013).

The stimulus battery included 1080 pictures (3 x 360: intact, LSF and HSF) that were grouped into three stimulus sets of 360 images (120 per filtering condition, half of them containing animals and half of them vehicles). Stimulus sets differed in whether an image was present in its intact, LSF or HSF version. We made sure that within every stimulus set, approximately the same number of images belonging to one of the sub-categories (e.g., mammals, birds, cars, trains, etc.) was present for all three filtering conditions (intact, LSF, HSF). Each participant viewed one of the stimulus sets, counterbalanced across participants within each group. This way, every stimulus was presented only once to a given subject (either in its intact, LSF or HSF version), and all 3 versions of an image were presented to every participant group. Stimuli were presented in 4 experimental blocks, separated by short breaks. Each block consisted of 90 images (30 per filtering condition, 15-15 containing an animal or a vehicle), presented in a randomized order. The order of experimental blocks for each stimulus set varied between participants in a counterbalanced manner. Stimuli were presented on a 20 inch LCD screen (LG Flatron, resolution: 1024 x 768; refresh rate: 75 Hz, rectangular temporal window) using E-Prime software (Psychology Software Tools, Inc.,

Sharpsburg, USA). A forced-choice animal vs. vehicle categorization task was used, during which subjects were asked to press one of the two response buttons with their left or right index fingers. Response options for animals and vehicles were counterbalanced across participants. Images were presented for 2000 ms, but participants were asked to respond as quickly and accurately as possible. The rather long presentation time was necessary because our pilot results suggested that shorter presentation would substantially reduce classification accuracy in younger participants. Inter-stimulus interval was randomized between 1000 and 1500 ms. To ensure that each subject understood the task, each recording started with a training block with images (12 in total, 4 per stimulus filtering) that were not used later.

Electrophysiological recordings and data analysis

Electroencephalography (EEG) was performed with a 32-channel BioSemi ActiveTwo Amplifier (BioSemi B. V., Amsterdam, Netherlands), with the sampling rate of 512 Hz, without any frequency filters (a 30 Hz low-pass linear finite impulse response filter was applied to averaged data for data visualization purposes only). The Ag/AgCl electrodes were placed in accordance with the extended international 10/20 system (at positions Fp1, Fp2, AF3, AF4, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO3, PO4, O1, Oz, O2). The recording reference and the ground electrodes (Common Mode Sense and Driven Right Leg electrodes in the ActiveTwo System; Metting van Rijn, Peper, & Grimbergen, 1990) were placed in close proximity to the Cz position.

EEG was analyzed with the EEGLAB toolbox (Delorme & Makeig, 2004) for Matlab (MathWorks Inc., Natick, USA). The epoch count per filtering condition was 120. Epochs with 100 ms pre- and 1200 ms post-stimulus were extracted and visually inspected to remove those with ocular or other prominent artifacts (i.e. blinking monitored at electrodes Fp1/Fp2,

horizontal eye movements monitored at F7/F8, slow drifts, high-frequency noise due to muscle movement). ERPs were analyzed for trials with correct responses only. This protocol yielded an overall average rejection rate of 15.03%. Overall rejection rates (due to either incorrect responses or artifacts) differed between groups [$F(4, 91) = 2.996$, $p = 0.023$, $\eta p^2 = 0.116$], with significantly higher mean values in the youngest, 7-8 year-old group (17.94%) than for adults (12.76%; Bonferroni-corrected post hoc test: $p = 0.009$), but no differences for other comparisons (9-10 years: 15.01%; 11-12 years: 14.85%; 13-15 years: 14.77%; $p > 0.450$). Still, the lower number of averaged epochs in 7-8 year-olds corresponds to the mean of 98 epochs/stimulus filtering (range: 92-106 epochs), which is comparable to that reported by van den Boomen and colleagues (2015) and yielded a satisfactory signal-to-noise ratio (as it was evident from the ERP waveforms). Before data visualization, the epoch length was modified from -100 ms to 500 ms post-stimulus.

We assessed the visual P1 and N1 components at pooled occipital (Oz, O1, O2) electrodes. Baseline-to-peak amplitudes and peak latencies (measured from stimulus onset) were measured using the ERPLAB (http://erpinfo.org) plug-in for EEGLAB. Peak amplitudes and latencies were detected in a semi-automatic manner: first, ERPLAB searched over the corresponding time intervals (P1: 120-170 ms; N1: 170-250 ms) for the most positive (P1) or negative (N1) peaks that were not surpassed by ±9.8 ms (5 time points) and then, these peaks were verified by one of the investigators (R.A.A) and manually corrected when deemed necessary. Although mean amplitudes or area under the curve data might be more suitable for capturing the dynamic change in neural activity, we chose to quantify individual peaks to enable better comparison with previous results (Batty & Taylor, 2002; Mahajan & McArthur, 2012; van den Boomen et al., 2015). Because amplitude effects detected at later ERP components might be simply due to carry-over effects from earlier peaks (as it has been shown for age-related N1 amplitude modulations by Mahajan & McArthur (2012), we also

performed peak-to-peak amplitude analysis for the N1 component. Peak-to-peak values were calculated by subtracting P1 data from N1 data.

Statistical analysis

Mean classification accuracy (percentage of correct responses relative to the total number of stimuli) and median reaction times (RTs in milliseconds for correct responses) were calculated for each participant and filtering condition separately. Age- and spatial frequency-related changes in behavioral and electrophysiological data were assessed using repeated-measures analysis of variance (ANOVA) with stimulus FILTER (intact, LSF, HSF) as within-subject and with age GROUP (7-8, 9-10, 11-12, 13-15-year-olds and adults) as between-subject factors. Where significant interaction between FILTER and GROUP was detected, two additional ANOVAs were performed. The effect of spatial frequency in each age group was analyzed with separate repeated-measures ANOVAs with FILTER as within-subject factor. In addition, to study whether such changes might be due to the different developmental patterns of intact, LSF and HSF processing, three univariate ANOVAs were performed for each stimulus filtering with GROUP as fixed factor. Bonferroni post hoc tests were used for pairwise comparisons. For violations of sphericity, Greenhouse-Geisser corrected p values and the relevant epsilon (ε) corrections are reported. In order to demonstrate the magnitude of the observed effects, partial eta-squared (ηp^2) values are also shown. Effects with $p < 0.05$ were considered as statistically significant.

Results

Behavioral data

Behavioral results regarding changes in classification accuracy and reaction times for the three filtering conditions and age groups are presented in Figure 2.
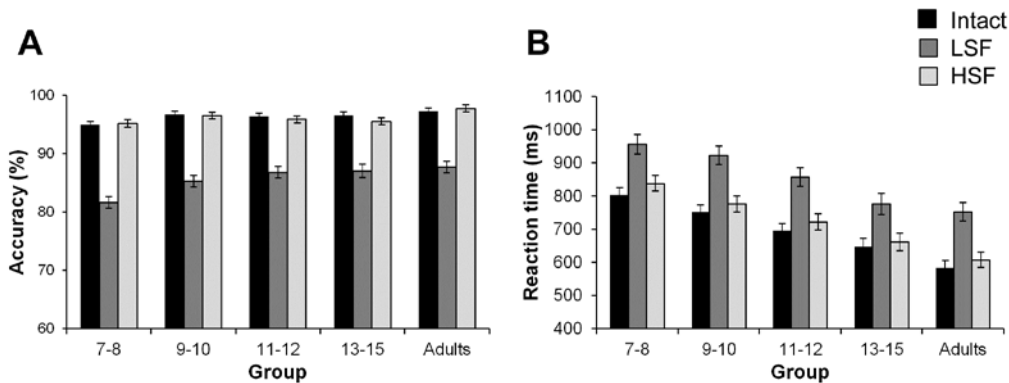
Figure 2. Age-related effects on classification accuracy (A) and reaction times (B) for intact, low spatial frequency (LSF), and high spatial frequency (HSF) filtering conditions.

Response accuracy

With respect to classification accuracy, a significant main effect of FILTER was found $[F(1.41, 128.354) = 620.391, \varepsilon = 0.705, p < 0.001, \eta p^2 = 0.872]$, with substantially worse accuracy for LSF pictures than for the other two filtering conditions (Bonferroni-corrected post hoc tests: $p < 0.001$ for both comparisons). The main effect of GROUP was also significant $[F(4, 91) = 5.559, p < 0.001, \eta p^2 = 0.192]$. This was qualified by an interaction between FILTER and GROUP $[F(5.642, 128.354) = 3.94, \varepsilon = 0.705, p = 0.002)$. Results for the main effect of FILTER and GROUP in the follow-up repeated-measures ANOVA tests are presented in Supplementary Tables 1 and 2. Bonferroni-corrected post hoc tests revealed that 7-8 year-olds were the only group that was significantly worse at classifying images than adults (Supplementary Table 3). This was true for all filter conditions, although they were disproportionately worse for LSF images. Furthermore, 7-8 year-olds performed worse than 11-15 year-old children for LSF images only, while performance was comparable to this age group for other filter settings.

Reaction time

14

When analyzing reaction times, repeated-measures ANOVA revealed a significant main effect of FILTER [$F_{(1.258, 114.453)} = 520.793$, $\varepsilon = 0.629$, $p < 0.001$, $\eta p^2 = 0.851$]. Bonferroni post hoc analysis showed that all three filtering conditions differ from each other ($p < 0.001$ for all comparisons), with shortest reaction time for intact images and longest for LSF stimuli. Response latencies decreased with age [GROUP main effect: $F_{(4, 91)} = 13.773$, $p < 0.001$, $\eta p^2 = 0.377$], with a significant post hoc effect between non-neighboring age groups ($p < 0.019$), but no significant differences between neighboring age groups ($p > 0.784$). The FILTER $\times$ GROUP interaction was not significant (Figure 2).

Electrophysiological data

Grand average ERPs obtained for all three filtering conditions, separately for children and adults are shown in Figure 3.
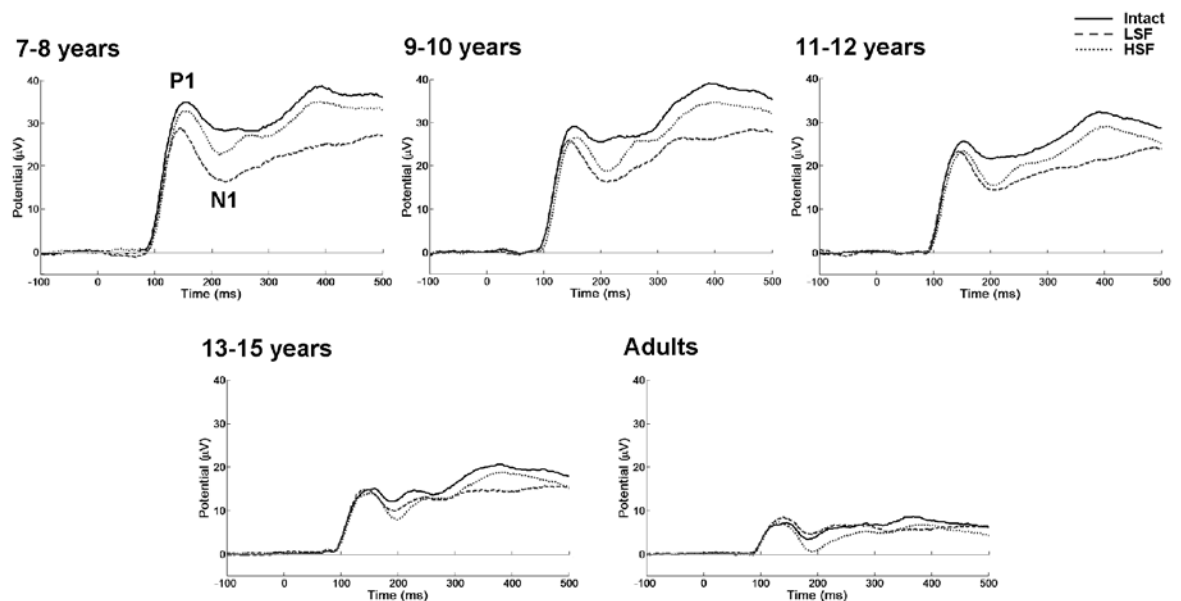

Figure 3. Modulatory effects of spatial frequencies on event-related potentials for children and adults at the occipital region (pooled data of electrodes O1, Oz and O2). LSF: low spatial frequency; HSF: high spatial frequency

P1 amplitude

For the P1 amplitude, the main effect of FILTER was significant [$F(1.84, 167.468) =$ 23.463, $\varepsilon = 0.92$, $p < 0.001$, $\eta p^2 = 0.205$], with a larger positivity to intact images than to LSF and HSF pictures ($p < 0.001$ for both). Developmental changes were also observed [GROUP main effect: $F(4, 91) = 41.645$, $p < 0.001$, $\eta p^2 = 0.647$], since the P1 amplitude decreased with age ($p < 0.035$ for all comparisons except for the effect between groups 7-8 vs. 9-10 years and 9-10 vs. 11-12 years). Moreover, the interaction between FILTER and GROUP was significant [$F(7.361, 167.468) = 8.133$, $\varepsilon = 0.92$, $p < 0.001$, $\eta p^2 = 0.263$]. The P1 amplitude was significantly larger for HSF than LSF images in the 7-8 year-old group, there were no significant differences between the P1 for HSF and LSF stimuli for other children/adolescent groups, but the P1 was significantly enhanced for LSF compared to HSF stimuli in adults (Figure 4; Table 1; Supplementary Table 1). In addition, the P1 showed less pronounced reductions for LSF stimuli between 7-12 years of age (Supplementary Tables 2, 4).
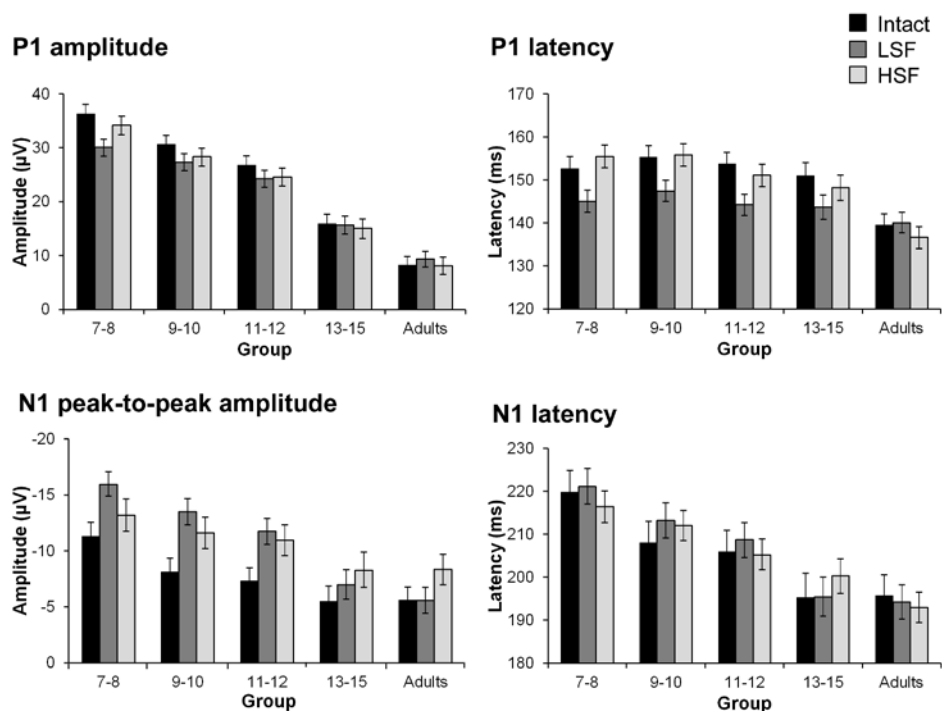

Figure 4. The effects of spatial frequencies on the amplitudes and latencies of the P1 and N1 components in all groups. LSF: low spatial frequency; HSF: high spatial frequency

Table 1. Results of Bonferroni-corrected pairwise comparisons between filtering conditions in each age group for behavioral and electrophysiological data.

		Accuracy	P1 ampitude	P1 latency	N1 peak-to-peak amplitude
7-8	**Intact vs. LSF**	<0.001	<0.001	0.043	0.015
	Intact vs. HSF	n.s.	0.006	n.s.	n.s.
	LSF vs. HSF	<0.001	<0.001	0.001	n.s.
9-10	**Intact vs. LSF**	<0.001	0.01	0.001	<0.001
	Intact vs. HSF	n.s.	0.035	n.s.	0.008
	LSF vs. HSF	<0.001	n.s.	0.01	n.s.
11-12	**Intact vs. LSF**	<0.001	0.021	0.011	<0.001
	Intact vs. HSF	n.s.	0.014	n.s.	<0.001
	LSF vs. HSF	<0.001	n.s.	n.s.	n.s.
13-15	**Intact vs. LSF**	<0.001	n.s.	0.035	n.s.
	Intact vs. HSF	n.s.	n.s.	n.s.	0.003
	LSF vs. HSF	<0.001	n.s.	n.s.	n.s.
Adults	**Intact vs. LSF**	<0.001	n.s.	n.s.	n.s.
	Intact vs. HSF	n.s.	n.s.	n.s.	<0.001
	LSF vs. HSF	<0.001	0.043	n.s.	<0.001

Note: These tests were only performed for measures with significant FILTER × GROUP interactions.

P1 latency

P1 peak latencies were influenced by spatial frequencies [FILTER main effect: $F_{(2, 182)} = 15.286$, $p < 0.001$, $\eta p^2 = 0.144$], which was due to shorter latency to pictures containing LSF information only (LSF vs. intact: $p < 0.001$; LSF vs. HSF: $p < 0.001$). The main effect of GROUP was also significant [$F_{(4, 91)} = 7.099$, $p < 0.001$, $\eta p^2 = 0.238$]: adults' P1 peak latencies were shorter than children's (7-8 years vs. adults: $p = 0.001$, 8-9 years vs. adults: $p < 0.001$, 11-12 years vs. adults: $p = 0.003$, 13-15 years vs. adults: $p = 0.054$), but there were no differences among younger groups. Finally, the effect of spatial frequencies varied with age groups as revealed by a significant FILTER × GROUP interaction [$F_{(8, 182)} = 2.383$, $p = 0.018$, $\eta p^2 = 0.095$]. Age-related changes were observed in the case of intact and

HSF stimuli only (Supplementary Table 2), with significantly shorter latencies for adults than for children (Figure 4; Supplementary Table 5).

N1 peak-to-peak amplitude

Results of the baseline-to-peak N1 amplitude analysis are presented in Supplementary Results. Here, we report peak-to-peak amplitude statistics, because this measure is independent of P1 effects. The main effect of stimulus FILTER was significant [$F(1.873, 170.455) = 40.960$, $\varepsilon = 0.937$, $p < 0.001$, $\eta p^2 = 0.310$] due to differences between intact vs. LSF and intact vs. HSF stimuli ($p < 0.001$ for both comparisons). The main effect of GROUP was also significant [$F(4, 91) = 6.076$, $p < 0.001$, $\eta p^2 = 0.211$]. However, whereas baseline-to-peak data indicated an age-related increase in the N1 amplitude, peak-to-peak differences showed a reduction (Figure 4), with significant differences between 7-8 vs. 13-15 years of age ($p = 0.003$) and 7-8 year-olds vs. adults ($p < 0.001$). Due to the significant FILTER $\times$ GROUP interaction [$F(7.493, 170.455) = 5.098$, $\varepsilon = 0.937$, $p < 0.001$, $\eta p^2 = 0.183$], additional tests were carried out. The effect of stimulus filtering was significant in all age groups (Supplementary Table 1), since no group of children showed adult-like patterns of HSF images producing significantly larger N1 than LSF stimuli (Table 1). Details of the post hoc analysis are reported in Supplementary Results.

N1 latency

The N1 latency varied with age [main effect of GROUP: $F(4, 91) = 7.951$, $p < 0.001$, $\eta p^2 = 0.259$]. N1 latencies decreased with age, but significant differences were found between groups 7-8 vs. 13-15 years ($p = 0.001$), 7-8 years vs. adults ($p < 0.001$) and 9-10 years vs. adults ($p = 0.01$) only. The effect of spatial frequency filtering and its interaction with age were not significant (Figure 4).

Discussion

In this study, we aimed to determine how low and high spatial frequencies influence visual processing in school-age (between 7-15 years) and adults, using a task requiring participants to discriminate photographs based on their semantic content. Given that previous research focusing on the behavioral correlates of SF sensitivity indicated that the processing of LSF information might lag behind that of HSF (Adams & Courage, 2002; Benedek et al., 2003; Benedek et al., 2010; Gwiazda et al., 1997), we hypothesized to find evidence for this phenomenon not only by evaluating behavioral responses, but also by analyzing early electrophysiological markers of visual processing. Overall, the results confirmed our expectations, since only 7-8-year-old children showed poorer classification accuracy than adults, but while this was true for all three filter settings, performance was disproportionately worse with LSF images. In addition, 7-8 year-olds were less accurate than all other groups of children for LSF, but not for HSF or intact images. With respect to ERPs, HSF images elicited larger P1 amplitudes than LSF images in 7-8-year-old children, but not in any other group of children. From 9-10 years, the P1 amplitude became comparable for LSF and HSF images, but the adult group was the only one showing enhanced P1 amplitudes for LSF images relative to HSF stimuli. Similarly, only adults (but not children) showed significantly enhanced N1 peaks to HSF compared to LSF images. Regarding latency data, P1 latency for HSF stimuli was shorter in adults compared to all other groups, but there were no age-related latency changes in the P1 for LSF stimuli. N1 latencies were also shorter in adults than children younger than 11 years of age, but both for LSF and HSF stimuli. Taken together, it seems that LSF and HSF processing are still maturing during the school-age years, but in a non-linear fashion, as LSF analysis clearly lags behind that of HSF at the age of 7-8 years. Below, we shall discuss our behavioral and ERP results in detail, with special focus on the development of scene processing and on the relationship between maturation of SF processing and activity of the M- and P-channels.

Effects of development and spatial frequencies on behavioral performance

We found robust modulations of classification accuracy and reaction times with increasing age, with both parameters indicating better performance in older participants. Similar patterns have been reported earlier in other tasks (Batty & Taylor, 2002; Itier & Taylor 2004a, 2004b), which might reflect a general, task-unspecific effect in school-aged children. While this might hold for reaction time (Kail, 1993), for which no interaction between image filtering and aging was found, the different developmental patterns for response accuracies in the LSF vs. HSF conditions point toward a stimulus-specific effect, affecting early visual processing as revealed by our ERP analysis.

In all participants, LSF images were classified with more errors and longer RTs than HSF or intact ones. This suggest that LSF images were more difficult to recognize than HSF or intact stimuli, despite literature data supporting the dominance of magnocellular processes in rapid categorization of natural images (Fabre-Thorpe, 2011). It is possible that LSF information is crucial for shaping behavioral responses only when stimuli are presented very briefly, but not when there is enough time for more elaborate processing of stimulus details, conveyed by the P-channel. This notion is consistent with our results, but also with previous work using relatively long stimulus presentation times (Bar et al., 2006; Craddock et al., 2013, Rokszin et al., 2016).

The effect of development on ERPs

We observed a reduction in the P1 amplitude with increasing age, a result that is in accordance with literature data (Batty & Taylor, 2002, Itier & Taylor, 2004a, 2004b; Mahajan & McArthur, 2012; van den Boomen et al., 2015). Although the N1 baseline-to-peak amplitude was increasing with age, this effect could have been carried over from the P1 peak,

as it was also suggested by other authors (Mahajan & McArthur, 2012). Indeed, our peak-to-peak N1 amplitude analysis revealed a different developmental pattern, with age-related reduction of this component, which is in line with the results reported by van den Boomen and colleagues (2015) for black-and-white grating stimuli. In general, developmental effects on ERP amplitudes can be linked to structural changes in the gray matter, more specifically, to reductions in cortical volume due to the process of 'synaptic pruning', but also to other phenomena such as alterations in neurotransmitter levels, hormonal effects or increasing head volume and skull thickness (Segalowitz, Santesso, & Jetha, 2010; Whitford et al., 2007). However, the main focus of this research was not on age-associated ERP modulations, but on the impact of development on the cortical analysis of SF information.

The effect of spatial frequencies on ERPs

To our knowledge, this work is the first to report opposite patterns of SF-sensitivity of the P1 and N1 components in early school-age relative to adulthood, with the involvement of several age groups. The finding that the P1 is larger for HSF images at 7-8 years but is gradually tuned towards LSF stimuli with age, while the N1 is characterized by the opposite pattern even after controlling for carry-over effects from the P1 (peak-to-peak analysis) implies that SF analysis in the visual cortex undergoes substantial maturation between 7-15 years of age. Thus far, developmental studies evaluating age-related modulations of the P1 amplitude evoked by either black and white checkerboard stimuli or luminance gratings found increased P1 amplitudes for LSF (relative to HSF) and enhanced N1 amplitudes for HSF (relative to LSF) stimuli (Mahajan & McArthur, 2012; van den Boomen et al., 2015), a pattern that we observed in adults only. This discrepancy might be due to numerous factors, since (1) we used natural images, (2) required participants to classify stimuli based on their semantic content, and (3) produced modified images with different filter settings (with lower

cut-off values for our LSF and HSF stimuli; LSF: 0.5 vs. 0.83 vs. 0.75 cpd; HSF: 3.8 vs. 4 vs. 6 cpd in the current, Mahajan & McArthur (2012) and van den Boomen et al. (2015) studies, respectively). Nevertheless, we are also aware of three studies that reported results resembling the ERP patterns we detected in children. Using black and white gratings, Boeschoten, Kenemans, Engeland and Kemner (2007) recorded greater P1 amplitudes for HSF (6 cpd) relative to LSF (0.75 cpd) stimuli in 9-10-year-olds, a pattern that we found in 7-8-year-olds. Furthermore, two ERP studies focusing on the development of configural face processing found that sensitivities of the P1 component to face inversion is still developing in adolescence in an SF-specific manner (Grose-Fifer et al., 2015; Peters, Vlamings, & Kemner, 2013). Notably, the latter two studies used well-recognizable complex images rather than abstract stimuli, with SF filter settings also differing from ours (LSF: ≤ 2 cpd; HSF: ≥ 6 cpd in Peters et al., 2013). Thus, it is likely that the discrepancy between our findings and those of van den Boomen and colleagues (2015) and Mahajan & McArthur (2012) might primarily stem from differences in experimental paradigms.

Relevance to scene processing in school-age

It is well-known that the context in which objects are presented can either facilitate or hinder object recognition, depending on object-scene congruence (Joubert, Fize, Rousselet, & Fabre-Thorpe, 2008). Behavioral and computational studies have argued that global image statistics (i.e. the power spectrum) of natural images can directly facilitate the process of object identification, and that the effect of scenes on object recognition depends both on LSF and HSF information (Joubert et al., 2008; Oliva & Schyns, 1997; Oliva & Torralba, 2006; Rousselet, Joubert, & Fabre-Thorpe, 2005; Torralba & Oliva, 2003). Taking this into account, our finding of ongoing maturation of SF processing in 7-15 year-old participants might also limit scene categorization and scene-object priming in this age group. This might particularly

apply to 7-8 year-old children, since they were the only group not showing adult-like classification accuracy for LSF images. In the future, it would be interesting to investigate if similar age- and SF-associated behavioral and ERP effects would emerge by changing the task from object to scene categorization.

Relevance to the development of the magno- and parvocellular channels

In most developmental studies focusing on the effect of SFs on visual processing, age-related changes in LSF vs. HSF sensitivities were linked to the maturation of the M- and P-subcortical channels that convey information from the retina to the primary visual cortex (V1) via the lateral geniculate nucleus (LGN; Livingstone & Hubel, 1988). In this context, our results also point towards M- and P-channel development during school-age, although one has to keep in mind that our paradigm did not allow direct measurement of M- and P-inputs to the primary visual cortex (V1). In fact, the P1 and the N1 are generated in extrastriate areas and do not reflect V1 activity (di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2001; Schendan & Lucia, 2010). Even projections from V1 to these extrastriate regions are not exclusively dominated by thalamocortical (M- and P-channel specific) inputs (Douglas & Martin, 2007; Logothetis, 2008). Rather, activity in the visual cortex is heavily influenced by feedback projections from other cortical regions (Douglas & Martin, 2007; Logothetis, 2008), and also by activity in subcortical structures other than the LGN, such as the superior colliculus, amygdala or the pulvinar (Johnson, 2005; Vuilleumier, Armony, Driver, & Dolan, 2003). This is particularly important when interpreting LSF-related results, because all the aforementioned subcortical nuclei as well as non-visual areas such as the orbitofrontal cortex were shown to be particularly sensitive to LSF information and hence contribute to coarse, gist-like analysis of the visual environment (Bar et al., 2006; Vuilleumier et al., 2003). Therefore, the slower development of LSF relative to HSF processing at 7-8 years might just as well reflect delayed

M-channel maturation as structural changes in other subcortical or prefrontal regions. In fact, our finding that LSF-associated P1 latency was constant across all age groups indicates that the myelination of the M-channel is largely finished by the age of 7 years and thus, supports the contribution of other brain structures to the observed developmental lag in LSF processing.

Limitations and future perspectives

One novel aspect of our task was that we investigated the influence of SFs on visual processing in a semantic categorization task. There is ample evidence that neural responses are category-specific, especially when contrasting activity for living vs. non-living items (Caramazza & Mahon, 2003), and such effects can also be detected with ERPs (Sitnikova, West, Kuperberg, & Holcomb, 2006). Therefore, it would have seemed reasonable to evaluate if (1) such category-specific effects are changing between 7-15 years of age, and (2) if they are modulated by SFs. However, this was not our primary aim when designing the experiment, and thus, our protocol with 60 stimulus/image category/filtering did not allow comparison of ERPs for animals vs. vehicles (due to the resulting low signal-to-noise ratio). Perhaps, by the exclusion of intact images, one could investigate the interaction between aging, SFs and image categories by adding more images to both stimulus categories.

In addition, currently it is not clear if the sensitivity of our paradigm to the maturation of SF processing was primarily due to our stimulus set, task requirements, or both. This question could be investigated in the future by simple experimental manipulations (e.g. 'passive viewing of natural images' or 'active discrimination of abstract stimuli') to assess if the P1 and N1 effects were primarily stimulus- or task-driven.

Finally, alternative measures for quantifying ERPs such as area under the curve or fractional area latency could have been used for assessing differences between developmental groups.

Conclusions

In this study, we provide behavioral and electrophysiological evidence for the slower development of LSF relative to HSF analysis at early school-age. Moreover, we show that sensitivity of the P1 and N1 components to LSF and HSF information changes from 7-8 years to adulthood, indicating ongoing maturation of cortical processing of both low and high spatial frequencies. The fact that other developmental studies did not observe such ERP effects points towards the potential utility of our experimental paradigm in monitoring spatial frequency-dependent maturation of visual responses with EEG in childhood and adolescence. The successful identification of electrophysiological markers sensitive to the maturation of LSF and HSF processing can have implications for neurodevelopmental disorders that typically emerge in this sensitive period (Gori et al., 2016; Vlamings et al., 2010).

Acknowledgements

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Supplementary Results

N1 baseline-to-peak amplitude

In the case of the baseline-to-peak N1 amplitude, the statistical analysis revealed a significant main effect of stimulus filter, $F(1.657, 150.789 = 103.679, \varepsilon = .829, \text{p} < .001, \eta\text{p}^2 = .533$, as intact stimuli evoked smaller N1 amplitudes than LSF or HSF images ($p < .001$ for both comparisons). Developmental effects were also observed [group main effect: $F(4, 91) = 17.307, p < .001, \eta\text{p}^2 = .432$]: adults' N1 amplitudes were larger (more negative) than those of children aged 11 and 12 years and younger ($p < .001$ for all comparisons), while the N1 amplitude of 13- to 15-year-old participants differed from the amplitudes of 9- and 10-year-olds ($p = .009$) and 7- and 8-year-olds ($p < .001$). In addition, a significant Filter × Group interaction was found, $F(6.628, 150.789) = 19.012, \varepsilon = .829, p < .001, \eta\text{p}^2 = .455$. Significant effects of filter were detected in all age groups (Supplementary Table 1). The pattern observed for LSF versus HSF stimuli differed in childhood relative to adulthood, since LSF images evoked significantly larger N1 waveforms in children aged 7-8 and 9-10 years ($p < .039$), no LSF versus HSF difference was found in 11- and 12-year-olds, but increased N1 amplitudes for HSF stimuli were detected in 13- to 15-year-old adolescents and adults ($p < .02$). Effects of age were significant for all three filtering conditions (Supplementary Table 2). Here, the main finding was that the gradual increment of the N1 between 7-15 years of age was less prominent for LSF images than for HSF and intact ones (Supplementary Table 6; Supplementary Figure 1).
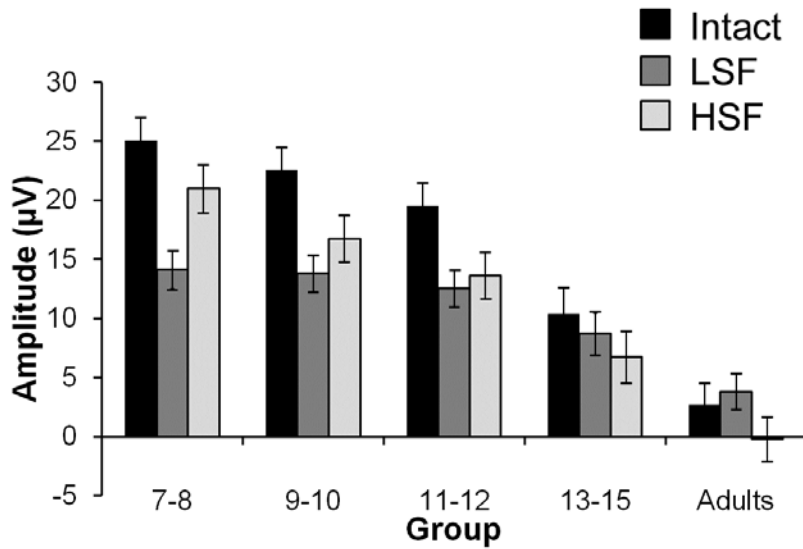
Supplementary Figure 1. The effects of spatial frequencies on baseline-to-peak N1 amplitudes in all groups. LSF: low spatial frequency; HSF: high spatial frequency

N1 peak-to-peak amplitude

With respect to age-related changes for each stimulus filtering, the effect of group was significant for intact and LSF images only (Supplementary Table 2). Post hoc tests revealed that for LSF stimuli children between 7-10 years differed from adults, and children between 7-12 years differed from 13- to 15-year-olds, while group differences were less pronounced for intact images (Supplementary Table 7). These results are in stark contrast to baseline-to-peak data, since developmental changes for HSF stimuli (relative to LSF pictures) were more robust for baseline-to-peak amplitudes, but absent for peak-to-peak data.

Supplementary Table 1. ANOVA results conducted for the main effect of filtering in each developmental group separately.

Measure	Group	df	F	p	ε	ηp²
	7-8 years	1.334, 24.01	183.853	< .001*	.667	.911
	9-10 years	1.264, 24.02	121,113	< .001*	.632	.864
Accuracy	11-12 years	1.472, 27.963	115.148	< .001*	.736	.858
	13-15 years	2, 30	64.953	< .001*	-	.812
	adults	1.366, 27.329	172.807	< .001*	.683	.896
	7-8 years	2, 36	37.201	< .001*	-	.674
	9-10 years	2, 38	6.367	.004*	-	.251
P1 amplitude	11-12 years	2, 38	4.989	.012*	-	.208
	13-15 years	2, 30	1.326	.281	-	.081
	adults	2, 40	4.924	.012*	-	.198
	7-8 years	2, 36	7.977	.001*	-	.307
	9-10 years	2, 38	10.56	< .001*	-	.357
P1 latency	11-12 years	2, 38	6.048	.005*	-	.241
	13-15 years	2, 30	3.363	.048*	-	.183
	adults	2, 40	0.695	.505	-	.034
	7-8 years	1.377, 24.791	29.6	.001*	.689	.622
N1 baseline-to-	9-10 years	2, 38	47.105,	< .001*	-	.713
peak	11-12 years	2, 38	50.661	< .001*	-	.727
amplitude	13-15 years	2, 30	20.484	< .001*	-	.577
	adults	2, 40	41.074	< .001*	-	.673
	7-8 years	2, 36	6.205	.005*	-	.256
N1 peak-to-	9-10 years	1.332, 25.303	15.983	< .001*	.666	.457
peak	11-12 years	2, 38	24.685	< .001*	-	.565
amplitude	13-15 years	2, 30	9.731	.001*	-	.393
	adults	2, 40	24.195	< .001*	-	.547

Note: These tests were only performed for measures with significant Filter × Group interactions. Stars denote significant ($p < .05$) main effects of filter.

Supplementary Table 2. ANOVA results conducted for the main effect of group for each stimulus filtering separately.

Measure	Stimulus filtering	df	F	p	ηp^2
Accuracy	Intact	4, 91	2.812	.03*	.11
	LSF	4, 91	6.062	< .001*	.21
	HSF	4, 91	3.371	.013*	.129
P1 amplitude	Intact	4, 91	46.268	< .001*	.67
	LSF	4, 91	31.401	< .001*	.58
	HSF	4, 91	39.151	< .001*	.632
P1 latency	Intact	4, 91	5.464	.001*	.194
	LSF	4, 91	1.213	.311	.051
	HSF	4, 91	9.115	< .001*	.286
N1 baseline-to-peak amplitude	Intact	4, 91	22.977	< .001*	.502
	LSF	4, 91	7.877	< .001*	.257
	HSF	4, 91	18.144	.001*	.444
N1 peak-to-peak amplitude	Intact	4, 91	3.668	.008*	.139
	LSF	4, 91	13.737	< .001*	.376
	HSF	4, 91	2.195	.076	.088

Note: These tests were only performed for measures with significant Filter $\times$ Group interactions. Stars denote significant ($p < .05$) main effects of group.

Supplementary Table 3. Results of Bonferroni-corrected post hoc tests of between-group differences in classification accuracy for each stimulus type.

		Accuracy		
		Intact	LSF	HSF
7-8 versus	**9-10**	n.s.	n.s.	n.s.
	11-12	n.s.	.003	n.s.
	13-15	n.s.	.004	n.s.
	Adults	.018	< .001	.015
9-10 versus	**11-12**	n.s.	n.s.	n.s.
	13-15	n.s.	n.s.	n.s.
	Adults	n.s.	n.s.	n.s.
11-12 versus	**13-15**	n.s.	n.s.	n.s.
	Adults	n.s.	n.s.	n.s.
13-15 versus	**Adults**	n.s.	n.s.	n.s.

Supplementary Table 4. Results of Bonferroni-corrected post hoc tests of between-group differences in the P1 amplitude for each stimulus type.

		P1 amplitude		
		Intact	LSF	HSF
7-8 versus	**9-10**	n.s.	n.s.	n.s.
	11-12	.001	n.s.	.001
	13-15	< .001	< .001	< .001
	Adults	< .001	< .001	< .001
9-10 versus	**11-12**	n.s.	n.s.	n.s.
	13-15	< .001	< .001	< .001
	Adults	< .001	< .001	< .001
11-12 versus	**13-15**	< .001	.003	.002
	Adults	< .001	< .001	< .001
13-15 versus	**Adults**	.026	n.s.	n.s.

Supplementary Table 5. Results of Bonferroni-corrected post hoc tests of between-group differences in the P1 latency for each stimulus type.

		P1 latency		
		Intact	LSF	HSF
7-8 versus	**9-10**	n.s.	n.s.	n.s.
	11-12	n.s.	n.s.	n.s.
	13-15	n.s.	n.s.	n.s.
	Adults	.011	n.s.	< .001
9-10 versus	**11-12**	n.s.	n.s.	n.s.
	13-15	n.s.	n.s.	n.s.
	Adults	.001	n.s.	< .001
11-12 versus	**13-15**	n.s.	n.s.	n.s.
	Adults	.004	n.s.	.002
13-15 versus	**Adults**	n.s.	n.s.	.038

Supplementary Table 6. Results of Bonferroni-corrected post hoc tests of between-group differences in the N1 baseline-to-peak amplitude for each stimulus type.

		N1 baseline-to-peak amplitude		
		Intact	LSF	HSF
7-8 versus	**9-10**	n.s.	n.s	n.s.
	11-12	n.s.	n.s.	n.s.
	13-15	< .001	n.s.	< .001
	Adults	< .001	< .001	< .001
9-10 versus	**11-12**	n.s.	n.s.	n.s.
	13-15	.001	n.s.	.01
	Adults	< .001	< .001	< .001
11-12 versus	**13-15**	.023	n.s.	n.s.
	Adults	< .001	.001	< .001
13-15 versus	**Adults**	n.s.	n.s.	n.s.

Supplementary Table 7. Results of Bonferroni-corrected post hoc tests of between-group differences in the N1 peak-to-peak amplitude for each stimulus type.

		N1 peak-to-peak amplitude		
		Intact	**LSF**	**HSF**
7-8 versus	**9-10**	n.s.	n.s.	n.s.
	11-12	n.s.	n.s.	n.s.
	13-15	.02	< .001	n.s.
	Adults	.012	< .001	n.s.
9-10 versus	**11-12**	n.s.	n.s.	n.s.
	13-15	n.s.	.003	n.s.
	Adults	n.s.	< .001	n.s.
11-12 versus	**13-15**	n.s.	n.s.	n.s.
	Adults	n.s.	.002	n.s.
13-15 versus	**Adults**	n.s.	n.s.	n.s.