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Electrophysiological evidence of altered visual processing in adults who experienced visual deprivation during infancy

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Abstract

We examined the role of early visual input in visual system development by testing adults who had been born with dense bilateral cataracts that blocked all patterned visual input during infancy until the cataractous lenses were removed surgically and the eyes fitted with compensatory contact lenses. Patients viewed checkerboards and textures to explore early processing regions (V1, V2), Glass patterns to examine global form processing (V4), and moving stimuli to explore global motion processing (V5). Patients' ERPs differed from those of controls in that (1) the V1 component was much smaller for all but the simplest stimuli and (2) extrastriate components did not differentiate amongst texture stimuli, Glass patterns, or motion stimuli. The results indicate that early visual deprivation contributes to permanent abnormalities at early and mid levels of visual processing, consistent with enduring behavioral deficits in the ability to process complex textures, global form, and global motion.

KEYWORDS

congenital cataracts, ERP, form perception, motion perception, texture perception, vision development

1 | INTRODUCTION

It has long been known that early visual deprivation affects the organization of the visual cortex, an issue originally explored in the lid suture studies of Wiesel and Hubel (1963a, 1963b, 1965). Wiesel and Hubel (1965) explored the effects of depriving kittens of visual input to one or both eyes for varying periods of time after birth. A crucial part of their findings indicated that while monocular deprivation produces drastic changes in the organization of the visual system, binocular deprivation has a much smaller effect, resulting in a much better chance of recovering visual capabilities. Since then, others have studied visual deprivation by looking at congenitally blind humans and the adaptation of the brain to this drastic environmental change. For example, congenitally blind adults have apparent atrophy of the visual pathways as shown in MRI images (Ptito, Schneider, Paulson, & Kupers, 2008). Later, researchers demonstrated that there were changes to both white and gray matter throughout the occipital cortex (Voss, Pike, & Zatorre, 2014). Further developments occurred with the advancement of technologies allowing for the measurement of cortical thickness which revealed, for example, that early blind and congenitally blind individuals possess thicker occipital cortices than sighted individuals (Voss et al., 2014). In addition, congenital blindness can lead to functional changes in the cortex, that is, use of the visual cortex for other sensory modalities, a result suggesting that there might be crossmodal competition during early experience-dependent pruning (Leclerc, Segalowitz, Desjardins, Lassonde, & Lepore, 2005; reviewed in Maurer, Lewis, & Mondloch, 2005).

However, visual capabilities are not fully developed at birth and continue to mature well beyond the first year after birth. For example, although infants attend selectively to face-like stimuli within hours of birth (Mondloch et al., 1999; Simion, Macchi Cassia, Turati, & Valenza, 2001), their sensitivity is refined over the first few postnatal months (Mondloch et al., 1999), and sensitivity to subtle differences in facial identity and facial expression continue to improve into adolescence (Gao & Maurer, 2010; Mondloch, Le Grand, & Maurer, 2002; Thomas et al., 2007). These studies

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suggest that the visual system is extremely plastic and may be able to overcome functional alterations and renormalize once the deprivation ceases.

To test this hypothesis, we measured the ability to perceive faces in a cohort of patients (ages 18–29), who had been treated for dense bilateral congenital cataracts as infants (Mondloch et al., 2013). These infants had their cataracts removed surgically within the first year after birth and were then fitted with rehabilitative contact lenses. Until the cataracts were removed, all patterned input was blocked from reaching the retina. We hypothesized that, since the deprivation was bilateral and the cataracts were removed so early in life, little effect would be seen in face perception, an ability that continues to develop long after the child's first year. However, the event-related potential (ERP) data from these patients show that, despite normal behavioral performance on face detection tasks, their N170 is exaggerated in amplitude and latency compared to that of normals, an exaggeration that occurs specifically to face-stimuli but not to houses or objects. The same study also found that cataract-reversal patients have larger amplitudes and latencies to all stimuli including faces, houses, and objects in the P100, an early component of the visual evoked potential that originates in the extrastriate region of the occipital cortex (Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001).

The exaggerated ERPs suggest that patients achieved their normal performance on face detection at some cost. We hypothesized that this could be caused by an increased activation of face-specific networks or more widespread neural recruitment, and this enhanced activation could be a result of changes in how neural pruning progresses as a result of the early visual deprivation (Mondloch et al., 2013). In fact, we found a positive correlation between an index of the exaggeration, the amplitude of the difference between the N170 and the P100, and the number of days of visual deprivation.

Since face perception is a complicated higher-order process, one might expect that there would be similar deficits throughout the visual system for processes that require lower-level processing mechanisms. On the other hand, it may also be the case that a patient could have deficits in higher levels of processing without showing any deficits in the lower levels. That possibility is suggested by behavioral evidence collected from this cohort showing that the size of the acuity deficit, likely arising from damage at lower levels, does not correlate with higher level deficits (reviewed in Maurer & Lewis, 2013).

The current study investigated this same cohort of patients in order to determine whether there were neural deficits at other levels in the visual system. We examined this possibility utilizing four different stimulus sets to hone in on specific visual processing stages using ERP data.

The first stimulus set used a series of flashing alternating checkerboard patterns in order to target the lowest level of the visual processing system. Checkerboards are simple stimuli that elicit very early responses via low-level mechanisms in the primary visual cortex, reflected in the N75 component (Di Russo et al., 2001; Shigeto & Tobimatsu, 1998).

The second set was a series of textured stimuli that elicit both an initial N75 reflecting the sudden stimulus onset (Casco, Grieco, Campana, Corvino, & Caputo, 2005; Lachapelle, Ouimet, Bach, Ptito, & McKerral, 2004) and a later component related to the viewer's texture segregation abilities. Texture segregation represents an intermediate process that relies on low level visual characteristics including orientation and spatial frequency and that lead to higher processes such as shape discrimination (Arcand, Tremblay, & Vannasing, 2007). Texture segregation can be examined objectively since it is associated with a negative component at approximately 200 ms after stimulus onset which is thought to represent activation in the V2 association area and also the primary visual cortex (V1) via feedback from V2 (Bach & Meigen, 1997; Lamme, Van Dijk, & Spekreijse, 1992). We expected that the pattern found for textured stimuli might be different from that for the checkerboard stimuli because patients in this cohort have larger deficits in sensitivity to the direction of local motion defined by texture than by luminance cues (Ellemberg, Lewis, Defina, Maurer, Brent, Guillemot, & Lepore, 2005).

The third stimulus set used a series of Glass (1969) patterns. These stimuli are ideal for studying concentric structure in global form. They are made up of dots organized into concentric circles that generate the perception of a global form. By varying the percentage of signal dots (part of the concentric pattern) and noise dots (not part of the concentric pattern), it is possible to assess a person's sensitivity to global form. It is generally accepted that the processing of global form occurs in extrastriate regions. Area V4 is specifically central to the global integration of such patterns (Wilson, Wilkinson, & Asaad, 1997; Wilson & Wilkinson, 1998). Although one might also expect that very early components such as the N75 would also differentiate Glass stimuli, the onset of a Glass pattern produces only a very small change in the low-level characteristics that elicit early components. Thus, we expect that the differentiation of Glass patterns will be reflected in somewhat later ERP components at least 200 ms after stimulus onset and dependent primarily on the V4 region. Behavioral data indicate that patients in this cohort can see Glass patterns but have elevated thresholds; that is, they require more signal in order to perceive the form (Lewis, Ellemberg et al., 2002). This deficit persists despite the fact that patients were all treated during the first year after birth when sensitivity to global form is still very immature. In fact, the sensitivity to the form in Glass patterns has a long developmental trajectory, with improvements in sensitivity continuing until 9 years of age (Lewis, Ellemberg et al., 2004).

The fourth stimulus set used random-dot kinematogram (RDKs) to investigate the neural correlates of patients' abilities to process global motion. A RDK consists of randomly positioned dots moving in random directions except for a certain percentage of the dots that move in the same direction. By varying the percentage of dots moving in the same direction, it is possible to examine a person's sensitivity to global motion. Binocular deprivation for even a few months beginning at birth results in the abnormal development of sensitivity to global motion (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; Hadad, Maurer, & Lewis, 2012), despite the fact that motion perception is very immature during early infancy (Banton, Bertenthal, & Seaks, 1999; Wattam-Bell, 1994, 1996) and is a skill that normally continues to develop into the teenage years (Hadad, Maurer, & Lewis, 2011). Previous research has identified the middle temporal visual area (MT) or V5 as central to

processing global motion (Maunsell & Newsome, 1987; Newsome & Pare, 1988). ERP components earlier than 120 ms post stimulus onset are not usually sensitive to motion stimuli, and generally components attributed to the V5 region are not seen (with some individual variation) until after 170 ms post stimulus onset (Schoenfeld, Heinze, & Woldorff, 2002). Therefore, we expected that later ERP components after at least 120 ms post stimulus onset, such as the N170 and P200 components, would be sensitive to the motion stimuli.

1.1 | The Current Study

Although the effects of early visual deprivation caused by congenital cataracts have been investigated using behavioral data, there has been no systematic study using EEG data. Such studies can identify where disruptions in processing occur, based on an analysis of the components of the event-related potentials. The current study involved four stimulus sets that investigated whether patients treated for congenital cataracts differ from controls in the way they process visual information and in the way they differentiate among stimuli. By manipulating the complexity of the stimuli across the experiments, we were able to inspect specific processing levels to determine what type of reorganization has occurred as a result of the early visual deprivation.

2 | METHODS

2.1 | Participants

The final sample consisted of thirteen patients (9 males) who were born with dense, central, bilateral cataracts. The cataracts prevented all patterned visual input until they were removed surgically, and the child was given compensatory optical correction with contact lenses (mean duration of deprivation from birth until optical correction after surgery = 125 days, range = 48–228 days). The patients had a mean age of 23.3 years at the time of testing (range = 18–28 years). Testing was binocular and visual acuity in the better eye ranged from 20/25 to 20/80 (geometric mean = 20/38.6). When necessary, patients wore additional optical correction to focus the eyes at the testing distance of 100 cm. All 13 of the patients participated in the Checkerboard task, 12 of the patients participated in the Texture and Motion tasks, and 11 participated in the Glass pattern task. Of the 13 patients, five showed fusion on the Worth4Dot test, and four showed some gross stereopsis on the Titmus test. Only two showed both fusion and stereopsis. All patients experienced amblyopia. Eight demonstrated better acuity in the right eye, three in the left eye, and two with equal acuity.

There were 42 control subjects in total, with a slight variation as to who supplied data for each comparison because of testing mishaps or noisy data sets.

2.2 | Procedure

The project received clearance from the Research Ethics Boards at Brock University, McMaster University, and The Hospital for Sick Children (Toronto). Testing began after the procedures were explained and the participant gave oral and written consent. Continuous EEG was recorded while participants sat with their chin in a chin rest and viewed all stimuli on a computer monitor (Dell Model # M782, 17" screen) from a distance of 100 cm.

2.3 | Checkerboard task

The stimuli were comprised of two black-and-white checkerboard patterns, one the inverse of the other, alternating back and forth. The diameter of the checkerboard was 12 cm (6.9° from the viewing distance of 100 cm); the individual checks had a diameter of 1 cm (.57°) (see Figure 1).

The stimuli were presented at the center of the screen and appeared for 250–550 ms before changing. As was the case for all tasks, a fixation stimulus was superimposed on each checkerboard and consisted of a single letter within a small white square box of 1.5 cm (0.86°) located about 1/3 of the distance from the bottom of the stimulus and centered horizontally. The fixation stimulus was positioned so that the checkerboard would be mostly in the upper visual field and would register on the ventral bank of the calcarine fissure, thus ensuring a negative initial (N75) response from the primary visual cortex (Di Russo et al., 2001). The participants' task was to press a button on a response pad with their index finger when the

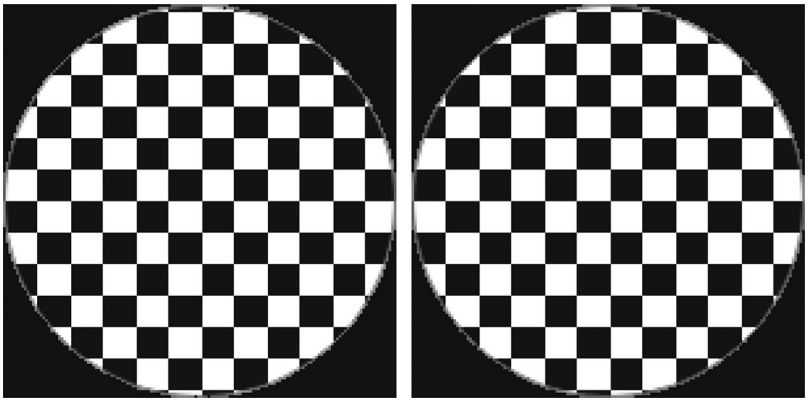

FIGURE 1 The stimuli used during the checkerboard task. A fixation letter (not shown) was superimposed one-third of the way up from the bottom of the stimulus

fixation letter changed. A total of 32 letter changes occurred during this task. As with the subsequent tasks, stimuli were presented in the same random order for each participant, and trials following fixation-letter changes were not included in the analysis. The first five stimuli appeared as practice trials and were not included in the analysis of the next 652 stimuli. As with the subsequent tasks, participants were instructed to respond as quickly and as accurately as possible to the letter changes. There were 620 trials in the final analysis (652 stimuli minus the 32 trials following letter changes). The task was divided into three blocks with a short rest break between blocks. The entire task took approximately 5 min to complete.

Twenty-nine adults (14 males) with a mean age of 21.2 years (range = 18–37 years) served as visually normal controls for the Checkerboard task.

2.4 | Texture task

The stimuli comprised four black-and-white texture patterns, taken from Lachapelle, Ouimet, Bach, Ptito, and McKerral (2004) with the kind permission of their creator Michael Bach (personal communication). The four stimuli were squares 13 cm wide (7.4°) containing oriented line segments, with a frequency of alternation of 0.31° for the simple stimuli and 0.37° for the complex stimuli. Two of the stimuli were simple, each with all lines oriented in the same direction; the other two stimuli were complex, each with lines oriented 90° away from those in the adjacent quadrant (see Figure 2). The stimuli were presented at the center of the screen and each appeared for 250 ms with a random inter-stimulus interval of between 750 and 900 ms. As with the checkerboards, a letter stimulus was superimposed on the changing patterns, with a total of 22 letter changes. Again, the first five texture stimuli appeared only as practice. The following 200 stimuli were presented in the same random order for each participant, with each stimulus appearing 50 times. The task was divided into three blocks with a 20-sec break between blocks. The entire task took approximately 8 min to complete.

Twenty-seven adults (7 males) with a mean age of 21.6 years (range = 18–37 years) served as visually normal controls for the Texture task.

2.5 | Glass pattern task

The stimuli were three different circular Glass patterns: 100% coherence, 60% coherence, and random coherence (see Figure 3), and were taken from Lewis, Ellemberg, Maurer, Dirks, and Wilkinson (2004).

Specifically, the circular stimuli consisted of single-pixel white dots on a gray ground (diameter = 12 cm or 6.9°) and were presented in the centre of a 1024 × 768 CRT screen. Each appeared for 250 ms with a random inter-stimulus interval between 750 and 900 ms. A total of 15 letter-fixation changes occurred during the task. Each stimulus was presented 100 times for a total of 300 trials. The task was divided into two sections with a 20-second break in between. The entire task took approximately 5 min to complete.

Twenty-five adults (7 males) with a mean age of 21.9 years (range = 18–37 years) served as visually normal controls for the Glass pattern task.

2.6 | Motion task

Motion stimuli consisted of five patterns of white dots on a gray background, similar to those in an earlier behavioral study (Ellemberg et al., 2002). The stimuli first appeared as a set of random dots at the center of screen created using VPixx v2.14. After 747 ms, the dots moved for 253 ms in one of the following directions: 100% toward center, 100% away from center, 70% toward center (and the other 30% moving in random directions), 70% away from center (and the rest moving in random directions), or randomly. Then the motion stopped and static dots remained on the screen for another 147 ms before disappearing, leaving only the gray background. There was an inter-stimulus interval of 0.8, 1, or 1.2 s. There were a total of 30 fixation-letter changes. The stimuli were presented in six blocks with a 20-s break between each block, providing a total of 61 trials for each stimulus type. The task took approximately 12 min to complete.

Twenty-four adults (4 males) with a mean age of 20.6 years (range = 18–27 years) served as visually normal controls for the motion task.

2.7 | Electrophysiological recordings

EEG was recorded continuously using the Electrical Geodesic System with a sampling rate of 500 points per second, referenced to the vertex electrode. Data were collected from some of the initial participants with a 256-channel montage and the remainder (most) with a 128-channel montage because of changes in lab procedure over time. We used an online bandpass filter from .01 to 100 Hz, kept impedances below 50 kΩ, and collected recordings with EGI NetStation software.

2.8 | EEG pre-processing

Offline, task-related EEG data were submitted to a pre-processing procedure to identify and remove eye and other artifacts with custom in-house code created in MATLab 2010, executed in Octave 3.6.3 on the Shared Hierarchical Academic Research Computing Network

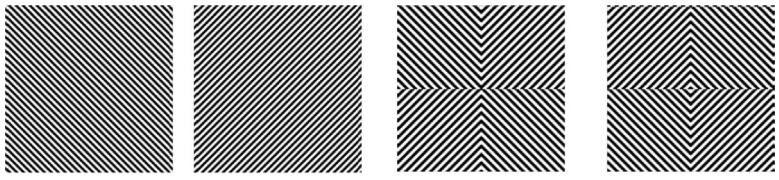

FIGURE 2 Four different black-and-white texture patterns from Lachapelle et al. (2004) used in the texture task

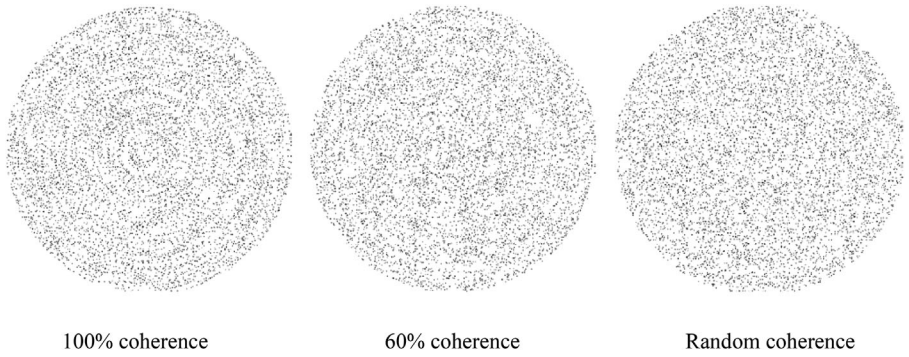

FIGURE 3 Three patterns from Lewis et al. (2004) used in the Glass task. The stimuli appeared as white dots on a gray background, but are black-white reversed here to be more visible when printed

(SHARCNet). These pre-processing steps follow closely those that have been described previously (Desjardins & Segalowitz, 2013; van Noordt et al., 2015, 2016).

2.9 | Segmentation

Stimulus-locked ERPs were calculated relative to the onset of the target stimuli. The responses for the Texture task were grouped into four categories, one for each of the four different texture stimuli. The Glass patterns were grouped into three categories: 100% coherence, 60% coherence, and 0% coherence (random). The Motion task stimuli were grouped into five categories: 100% inward motion, 100% outward motion, 70% inward motion, 70% outward motion, and random motion. The period of −200 to 0 ms relative to the stimulus onset was used as the baseline for all trials. Supplementary Appendix I shows the number of trials that contributed to the ERPs for each task and group, demonstrating the relatively few trials lost to artifacts and the comparability across groups.

2.10 | Peak size determination

Using the extended 10–20 system, the data were reduced to only the 20 posterior-occipital (PO) and occipital (O) channels. Maximum voltage values for the ERP peaks of interest were gathered for each of the channels. The ERPs of interest were determined by visually identifying peaks from the average waveforms of the segmented files. A summary of the ERP peaks of interest used in each task can be found in Table 1.

2.11 | Statistics

The peak values for each ERP for each participant were imported into SPSS for further analysis. For each individual and for each ERP component value for each stimulus, we averaged the data across a brain region (PO or O) on each side of the head (left or right). For all analyses, the Greenhouse-Geisser corrected p values are reported with original degrees of freedom.

3 | RESULTS

3.1 | Checkerboard task

A 2 (left, right) × 2 (patients, controls) ANOVA was done for each of the three components of interest: the N75, P100, and N170 ERPs (see Figure 4A).

3.1.1 | N75

The 2 × 2 ANOVA for the N75 revealed a main effect of side $F(1,40) = 8.79$, $p = .005$, with slightly larger amplitudes on the right side (L:−0.891 μV vs. R:−1.256 μV). A main effect of group, $F(1,40) = 9.94$, $p = .003$ was also found, with smaller amplitudes in the patient group than in controls (−0.442 μV vs −1.705 μV). A group by left/right side interaction was also found $F(1,40) = 4.64$, $p = .037$. Both patients and controls had a larger amplitude on the right side, but the difference was much larger in the controls (L: −1.390 μV vs. R: −2.021 μV) than the patients (L: −0.392 μV vs. R: −0.492 μV).

TABLE 1 Summary of scoring periods for each of the ERP components measured in each task

		Checkerboard	Texture	Glass	Motion
N75	Max negative 40–120 ms	✓	✓		
P100	Max positive 80–160 ms	✓	✓		
N170	Max negative 120–200 ms	✓	✓	✓	✓
P200	Max positive 200–380 ms			✓	✓

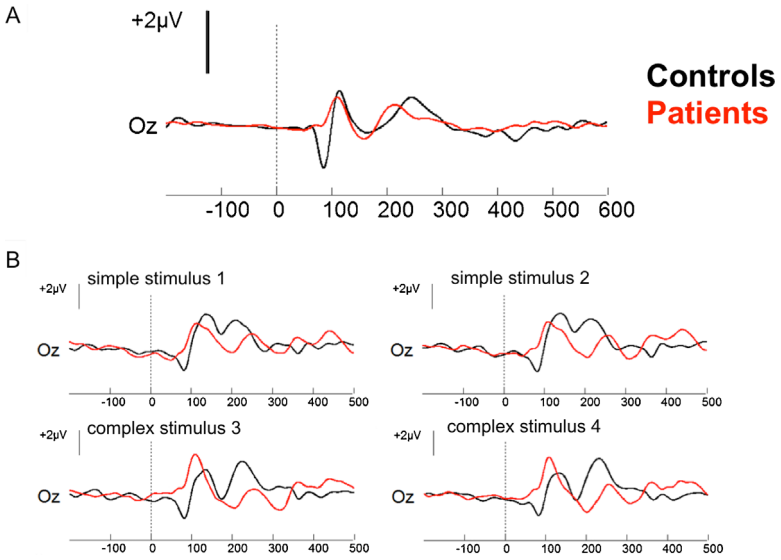

FIGURE 4 Patient and control overlays of the average ERP waveforms at Oz. (A) Checkerboard task. (B) Texture task.

3.1.2 | P100

The 2 × 2 ANOVA for the P100 did not show any main effects. A group by left/right side interaction was found, $F(1,40) = 7.33$, $p = .010$. The controls had a larger P100 amplitude on the right side (L:1.614 μV vs. R:2.134 μV) while the patients had a larger P100 amplitude on the left (L:1.608 μV vs. R:1.392 μV).

3.1.3 | N170

The 2 × 2 ANOVA for the N170 was not significant for side ($F(1,40) = 1.59$, $p = 0.21$), for group ($F(1,40) = 0.92$, $p = 0.34$) or for the side × group interaction ($F(1,40) = 2.20$, $p = 0.15$).

3.2 | Texture task

A repeated measures ANOVA was done on the average peak values for the N75, the P100, and the N170 ERP components (see Figure 4B). A 2(PO, O) × 2(left, right) × 4(four different stimuli, 2 simple and 2 complex) × 2(patients, controls) ANOVA was done for each of the three components of interest.

3.2.1 | N75

The 2 × 2 × 4 × 2 ANOVA for the N75 revealed a main effect of region, $F(1,37) = 4.80$, $p = .035$, with larger amplitudes occurring in the O region and a main effect of side, $F(1,37) = 3.91$, $p = .035$, with slightly larger amplitudes occurring on the right side. There was also a main effect of stimulus type, $F(3,111) = 7.21$, $p = .057 < .001$, and most importantly, a main effect of group, $F(1,37) = 11.88$, $p = .001$, with controls producing significantly larger N75 amplitudes than patients (−1.576 μV vs. −0.622 μV, respectively). This was superseded by a stimulus by group interaction, $F(3,111) = 5.51$, $p = .002$. A 2(stimuli) × 2 (left, right) × 2(PO,O) ANOVA was done for each pair of stimuli for each group separately in order to determine where these differences lie (see Figure 5). There were no differences in the amplitude of the N75 across stimuli for the controls (see Table 2).

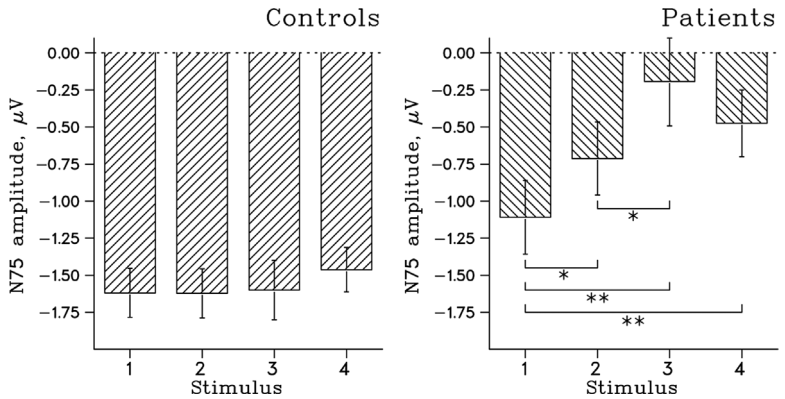

FIGURE 5 The average N75 component amplitudes in each group for each of the texture stimuli and the significant differences across stimuli within the patients. $^{**}p < .01$; $^{*}p < .05$

TABLE 2 Texture Task: Average N75 component amplitudes (and standard errors) in μV for the controls (C) and patients (P) and the *p*-value results from the ANOVA comparisons between each set of stimuli

N75 Amplitudes		Simple stimulus 1	Simple stimulus 2	Complex stimulus 3
C: −1.619 (.165) P: −1.109 (.248)	Simple stimulus 1			
C: −1.622 (.165) P: −0.712 (.247)	Simple stimulus 2	C: n.s. P: $p = 0.017$		
C: −1.600 (.200) P: −0.193 (.300)	Complex stimulus 3	C: n.s. P: $p = 0.001$	C: n.s. P: $p = 0.032$	
C: −1.463 (.150) P: −0.475 (.225)	Complex stimulus 4	C: n.s. P: $p = 0.008$	C: n.s. P: n.s.	C: n.s. P: n.s.

For the patients, the amplitude for stimulus 1, a simple texture, was significantly larger than the amplitude for stimulus 2, $F(1,11) = 7.87$, $p = .017$, another simple texture, and both complex textures, stimulus 3, $F(1,11) = 18.96$, $p = .001$, and stimulus 4, $F(1,11) = 10.53$, $p = .008$. The amplitude for simple stimulus two was significantly larger than for complex stimulus 3, $F(1,11) = 6.01$, $p = .032$.

There were also several interactions: a region by group interaction, $F(1,37) = 8.45$, $p = .006$, whereby the controls had larger amplitudes at the more posterior sites and the patients had a smaller increase at the more anterior region; a stimulus by region interaction, $F(3,111) = 4.72$, $p = .006$, whereby the increase at the occipital sites was greater for the simple stimuli over the complex stimuli; and a Left/Right by group interaction, $F(1,37) = 5.19$, $p = .029$, whereby the controls showed the larger amplitudes at the right side but the patients did not. No other effects were found.

3.2.2 | P100

The 2(PO,O) × 2(left, right) × 4(stimuli) × 2(groups) ANOVA for the P100 revealed no main effect of stimulus or group type, but did reveal a stimulus by group interaction, $F(3,111) = 8.17$, $p < .001$. A 2(stimuli) × 2(left, right) × 2(PO,O) ANOVA was done between each pair of stimuli for each group separately in order to determine where these differences lie (see Figure 6). The controls showed that the P100 peaks for the simple stimuli (stimulus 1 and stimulus 2) were significantly larger than for the complex stimuli (stimulus 3 and stimulus 4). Specifically, the P100 amplitude for stimulus 1, a simple texture, was significantly larger than both complex stimuli: stimulus 3, $F(1,26) = 11.22$, $p = .002$, and stimulus 4, $F(1,26) = 6.60$, $p = .016$. The P100 amplitude for stimulus 2, the other simple stimulus, was also significantly larger than both complex stimuli: stimulus 3, $F(1,26) = 9.71$, $p = .004$, and stimulus 4, $F(1,26) = 5.27$, $p = .030$. The patients showed the opposite effect with larger P100 amplitudes to complex stimuli than the amplitudes to the simple stimuli. The amplitude for stimulus three was significantly larger than for stimulus 1, $F(1,11) = 5.32$, $p = .042$, and stimulus 2, $F(1,11) = 5.07$, $p = .046$. The amplitude for stimulus four was larger than stimulus 1, $F(1,11) = 10.40$, $p = .008$ (see Table 3).

Another examination of the stimulus x group interaction described in Figure 6 suggests that the groups are similar on the simple stimuli but considerably different on the complex stimuli. We investigated this further in two 2(PO,O) × 2(left, right) × 2(stimuli) × 2(groups) ANOVAs, one for the simple stimuli and one for the complex stimuli. As expected from Figure 6, the analysis of the simple stimuli did not yield an effect of group or region by group interaction ($Fs < 1$) but did show an interaction of side × stimulus × group, $F(1,37) = 4.37$, $p = .044$, indicating slight left–right differences in stimulus effects for the two groups, but with no difference in group amplitudes. There was also a main

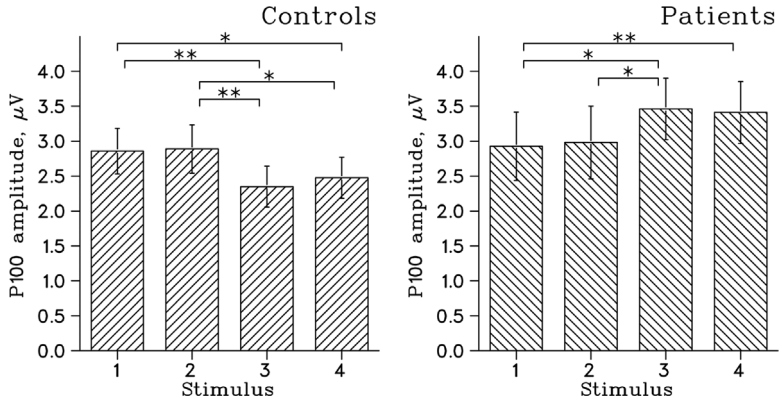

FIGURE 6 The average P100 component amplitudes in each group for each of the texture stimuli and the significant differences across stimuli. $^{**}p < .01$; $^{*}p < .05$

TABLE 3 Texture Task: Average P100 component amplitudes (and standard errors) in μV for the controls (C) and patients (P) and the associated *p*-value from the ANOVA comparisons between each set of stimuli

P100 amplitudes		Simple stimulus 1	Simple stimulus 2	Complex stimulus 3
C: 2.858 (.327) P: 2.927 (.490)	Simple stimulus 1			
C: 2.888 (.348) P: 2.981 (.522)	Simple stimulus 2	C: n.s. P: n.s.		
C: 2.349 (.293) P: 3.461 (.439)	Complex stimulus 3	C: $p = 0.002$ P: $p = 0.042$	C: $p = 0.004$ P: $p = 0.046$	
C: 2.474 (.295) P: 3.411 (.442)	Complex stimulus 4	C: $p = 0.016$ P: $p = 0.008$	C: $p = 0.030$ P: n.s.	C: n.s. P: n.s.

effect of region, with larger amplitudes at occipital sites, $F(1,37) = 24.09$, $p < .001$. The analysis of complex stimuli yielded several effects of interest: In terms of group-related effects, there was a marginal between-group main effect, $F(1,37) = 3.95$, $p = .054$. It was evident that regions contributed differently to this effect as this was superseded by a significant region by group interaction, $F(1,37) = 7.63$, $p = .009$; a significant effect of region was also found with larger amplitudes at the occipital sites, $F(1,37) = 14.85$, $p < .001$. To further investigate this, analyses were run separately for the occipital and parietal-occipital regions. There was no group effect in the parieto-occipital region ($p = 0.11$), but there was a group effect in the occipital region, $F(1,37) = 5.06$, $p = .031$.

A main effect of region was also found, $F(1,37) = 22.36$, $p < .001$, with P100 amplitudes being much larger in the occipital region than in the parietal-occipital region. This main effect was superseded by a region by stimulus type interaction, $F(3,111) = 6.50$, $p = .003$, whereby the complex stimuli elicited a slightly greater amplitude in the PO region and the simple stimuli a slightly greater amplitude in the O region, and a three-way interaction of region by stimulus type by left/right side, $F(3,111) = 4.66$, $p = .007$, whereby the two-way interaction appeared stronger on the right side than the left. No other effects were found.

3.2.3 | N170

The 2 × 2 × 4 × 2 ANOVA for the N170 revealed a main effect of stimulus type, $F(3,111) = 9.36$, $p < .001$, and a main effect of group, $F(1.37) = 6.06$, $p = .019$, with the patients producing significantly larger N170 amplitudes than the controls (−1.879 μV vs. −0.860 μV). This was superseded by a stimulus by group interaction, $F(3,111) = 4.17$, $p = .016$. A 2(stimuli) × (left, right) × 2(PO,O) ANOVA was done between each pair of stimuli for each group separately in order to determine where these differences lie (see Figure 7).

In the control group, the amplitudes for the N170 for complex stimuli (stimulus 3 and stimulus 4) were larger than for the simple stimuli (stimulus 1 and stimulus 2). The amplitude of stimulus 3 was significantly larger for both stimulus 1, $F(1,26) = 25.71$, $p < .001$, and stimulus 2, $F(1,26) = 35.03$, $p < .001$. The amplitude for stimulus 4 was also significantly larger than both stimulus 1, $F(1,26) = 18.57$, $p < .001$, and stimulus 2, $F(1,26) = 23.26$, $p < .001$. There were no significant differences among the four stimuli in the patient group. See Table 4.

A region by stimulus type interaction, $F(3,111) = 11.85$, $p < .001$, whereby the complex stimuli elicited larger amplitudes especially in the O region compared to the PO region, and a region by left/right interaction, $F(1,37) = 5.16$, $p = .029$, whereby the PO region showed an overall right side amplitude advantage but the O region no bias, were also found. There was also a left/right by stimulus type interaction showing a right side increase for complex stimuli whereas the simple stimuli were bilaterally more equal, $F(3,111) = 6.90$, $p = .001$. No other effects were found.

3.3 | Glass pattern task

A repeated measures ANOVA was done on the average peak values for the N170 and the P200 ERP components (see Figure 8A). A 2

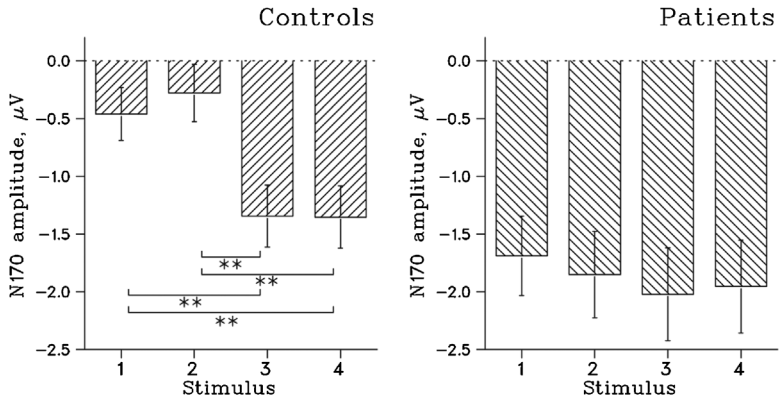

FIGURE 7 The average N170 component amplitudes in each group for each of the texture stimuli and the significant differences across stimuli. $^{**}p < .01$; $^{*}p < .05$

TABLE 4 Texture Task: Average N170 component amplitudes (and standard errors) in μV for the controls (C) and patients (P) and the *p*-value results from the ANOVA comparisons between each set of stimuli

N170 amplitudes		Simple stimulus 1	Simple stimulus 2	Complex stimulus 3
C: −0.462 (.229) P: −1.689 (.344)	Simple stimulus 1			
C: −0.279 (.249) P: −1.851 (.374)	Simple stimulus 2	C: n.s. P: n.s.		
C: −1.345 (.267) P: −2.022 (.401)	Complex stimulus 3	C: $p < 0.001$ P: n.s.	C: $p < 0.001$ P: n.s.	
C: −1.353 (.269) P: −1.955 (.403)	Complex stimulus 4	C: $p < 0.001$ P: n.s.	C: $p < 0.001$ P: n.s.	C: n.s. P: n.s.

(PO, O) × 2(left, right) × 3(100% coherence, 60% coherence, 0% coherence) × 2(patients, controls) ANOVA was done for each of the components of interest.

3.3.1 | N170

The 2 × 2 × 3 × 2 ANOVA for the N170 revealed a main effect of left/right side, $F(1,34) = 7.94$, $p = .008$, with larger amplitudes on the right side. Although the patients produced N170s with lower amplitudes, the effect of group was not significant. There was also a main effect of stimulus type, $F(2,68) = 4.16$, $p = .026$, but this was superseded by a stimulus by group interaction, $F(2,68) = 4.41$, $p = .022$. A 2(2 stimuli) × 2(left, right) × 2(PO,O) ANOVA was done between each pair of stimuli for each group separately in order to determine where these differences lie. There were no significant differences in the N170 amplitudes among the three stimuli in the patient group (see Figure 9).

In the control group, the Glass patterns with 100% coherence created the largest N170 amplitude. This was significantly larger than both the 60% coherence stimuli ($F(1,24) = 4.82$, $p = .038$) and the 0% coherence (random) stimuli ($F(1,24) = 13.70$, $p = .001$). The N170 produced by the 60% coherence stimuli was also significantly larger than the one produced by the 0% coherence (random) stimuli, $F(1,24) = 7.95$, $p = .009$. See Table 5.

3.3.2 | P200

The ANOVA for the P200 revealed a main effect of region, $F(1,34) = 9.14$, $p = .005$, with larger amplitudes occurring in the occipital region than more anteriorly. A main effect of left/right side, $F(1,34) = 11.56$, $p = .002$, was also found with larger amplitudes occurring on the right side. These effects were superseded by a region by stimulus interaction, where the amplitude ordering at the PO and O regions were slightly different, $F(2,68) = 4.10$, $p = .023$. No other effects were found.

3.4 | Motion task

A repeated measures ANOVA was done on the average maximum and minimum peak values for the N170 ERP component. A 2(PO, O) × 2(left, right) × 5(100% inwards, 100% outwards, 70% inwards, 70% outwards, random) × 2(patients, controls) ANOVA was done for each of the three components of interest (see Figure 8B).

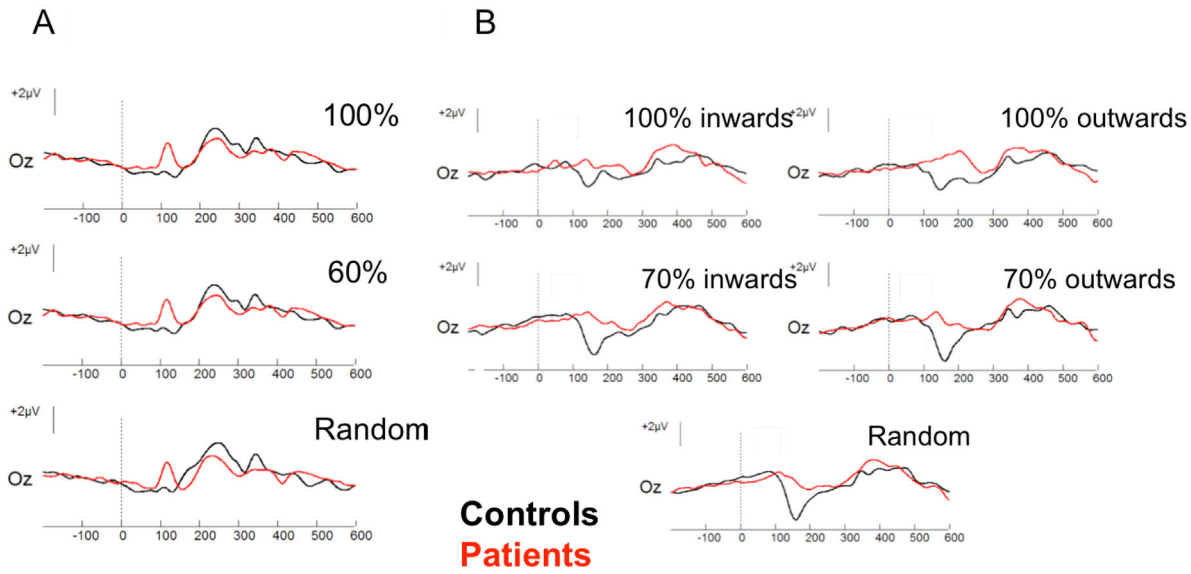

FIGURE 8 Patient and control overlays of the average ERP waveforms at Oz for each of the stimuli: (A) Glass task; (B) Motion task

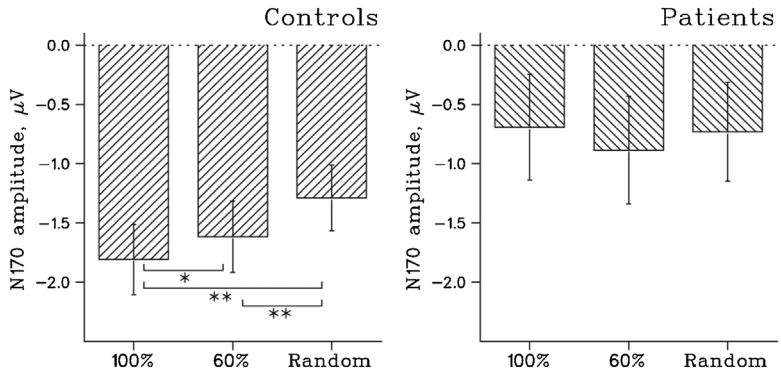

FIGURE 9 The average N170 component amplitudes in each group for each of the Glass patterns and the significant differences across stimuli. $^{**}p < .01$; $^{*}p < .05$

3.4.1 | N170

The ANOVA for the N170 revealed a main effect of stimulus type, $F(4,136) = 8.46$, $p < .001$, and a main effect of group, $F(1,34) = 19.52$, $p < .001$, with controls producing significantly larger N170 amplitudes than patients (−1.941 μV vs. −0.162 μV), for each of the stimuli. This was superseded by a stimulus by group interaction, $F(4,136) = 3.79$, $p = .015$. A 2(stimuli) × 2(left, right) × 2(PO,O) ANOVA was performed for each pair of stimuli for each group separately in order to determine where these differences lie (see Figure 10).

There were no significant differences in the patient group in the N170 amplitudes across the five stimulus types, which were consistently small. In the control group, 100% inward motion produced the smallest N170 amplitude, with its N170 amplitudes significantly smaller than those for 100% outward motion, $F(1,23) = 6.57$, $p = .017$, 70% inward motion, $F(1,23) = 11.11$, $p = .003$, 70% outward motion, $F(1,23) = 45.57$, $p < .001$, and random motion, $F(1,23) = 27.10$, $p < .001$. The 70% outward motion also produced significantly larger ERPs than both 70% inwards motion, $F(1,23) = 6.66$, $p = .017$, and 100% outwards motion, $F(1,23) = 18.81$, $p < .001$. Random motion produced an N170 ERP that was also larger than the 100% outwards motion, $F(1,23) = 11.78$, $p = .002$. See Table 6.

There was also a region by group interaction whereby the controls showed larger amplitudes in the PO region and the patients a slight increase in the O region, $F(1,34) = 11.39$, $p = .002$, and a region by stimulus type interaction, $F(4,136) = 6.42$, $p = .002$, which does not relate to group by stimulus effects of central concern here. No other effects were significant.

The P200 was not consistently present in either group and so was not scored. A summary of the results are presented in Table 7.

3.5 | Effects of days of deprivation and final acuity

Although all patients were optically corrected for the testing distance, all had bilateral deprivation amblyopia, that is, reduced acuity in each eye. Acuity was better in the left eye for nine patients, in the right for three, and equal in the two eyes for one. However, since all the tests were conducted binocularly, we tested whether any of the results of interest correlated significantly with acuity in the better eye (using the log of the denominator of the acuity score), and found that none did. However, the number of days from birth until removal of the cataracts and fitting of the contact lens did predict a few of the ERP effects, always in the direction of a longer period of deprivation relating to an attenuated ERP peak. The most notable was that the N75 from the texture stimuli were increasingly attenuated in those with longer periods of deprivation, with statistical significance only for simple stimulus 1, $r = 0.639$, $p = .025$. Similarly, in the checkerboards task, the N170 (averaged over both sides of the head) was attenuated for those with a longer period of deprivation, $r = 0.595$, $p = .032$. These correlations were also significant on each side of the head (right: $r = 0.643$, $p = .018$; left: $r = 0.522$, $p = .067$). Similarly, the P200 to Glass stimuli was more attenuated with longer duration of deprivation, $r = -0.686$, -0.675, and -0.642, $p = .020$, $.023$, and $.033$, for the three stimuli, respectively, although the relation was caused by a split at about 120 days. Of the five patients with fewer than 120 days of visual deprivation, four were the only ones with P200 amplitudes greater

TABLE 5 Glass Task: Average N170 component amplitudes (and standard errors) in μV for the controls (C) and patients (P) and the *p*-value results from the ANOVA comparisons between each set of stimuli

N170 amplitudes		100% coherence	60% coherence
C: −1.808 (.296) P: −0.693 (.446)	100% coherence		
C: −1.616 (.301) P: −0.887 (.454)	60% coherence	C: $p = 0.038$ P: n.s.	
C: −1.289 (.277) P: −0.732 (.418)	Random coherence	C: $p = 0.001$ P: n.s.	C: $p = 0.009$ P: n.s.

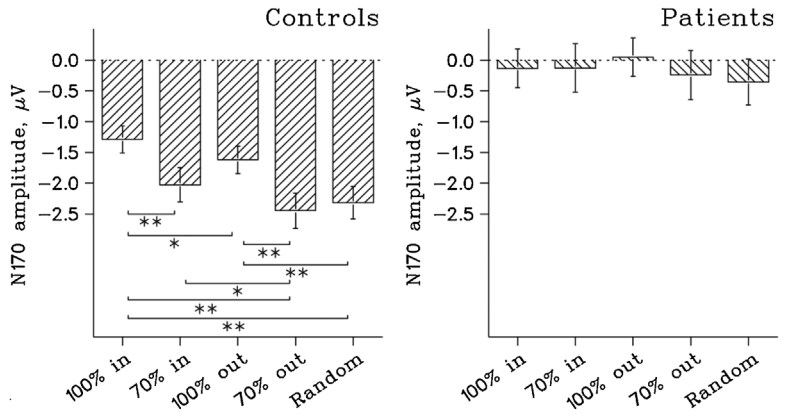

FIGURE 10 The average N170 component amplitudes in each group for each of the Motion stimuli and the significant differences across stimuli. $^{**}p < .01$; $^{*}p < .05$

than 4.5 μV; the rest (including one with 91 days deprivation, and the rest ranging up to 228 days) had P200 amplitudes below 3μV with no relation to duration of deprivation.

3.6 | Effects of measures of fusion and of stereopsis

Five of the patients could fuse images and four showed stereopsis. In order to see whether the effects of days of deprivation on ERP amplitudes might be related to either of these factors, we examined whether the amplitudes for the N75, N170, and P200 described above related to either fusion or stereopsis; we found that neither did.

4 | DISCUSSION

Earlier behavioral studies of patients treated for congenital cataract who had pattern vision restored during infancy indicate that some visual processing deficits remain even after decades of normal or nearly normal visual input (Ellemberg, Lewis, & Maurer, 1999; Lewis & Maurer, 2009; Maurer, Mondloch, & Lewis, 2007). More recent work at the electrophysiological level has indicated that processing complex stimuli elicits some abnormal ERP responses (Mondloch et al., 2013). The goal of this study was to expand our understanding of early visual processing stages in these patients by examining ERPs elicited by a variety of stimuli ranging from very simple to integrative geometric forms, without having overt responses depend on stimulus meaning. Thus, these results complement those of the earlier ERP study that focused on faces and objects.

The current study demonstrated early ERP component differences between the patient and control groups. The observed differences are likely to be caused by the early visual deprivation and not merely by correlated deficits like reduced acuity and stereopsis, although we cannot totally rule out some contribution from those deficits. None of the deficits correlated with the patients' acuity on the day of testing, which ranged from a mild deficit of 20/25 to a moderate deficit of 20/80, when viewing with the better eye. Moreover, the ERP data indicated that patients saw the stimuli well enough to differentiate the stimuli in each set. Nor did the deficits relate to whether or not there was any preserved binocular vision. When there were correlations, they were with the duration of early binocular deprivation, a pattern pointing to deprivation as the main source of differences between patients and controls.

The earliest component investigated was the N75, and both the checkerboard and texture stimuli indicated reduced N75 amplitudes in

TABLE 6 Motion Task: Average N170 component amplitudes (and standard errors) in μV for the controls (C) and patients (P) and the *p*-value results from the ANOVA comparisons between each set of stimuli

N170 amplitude		100% motion inwards	70% motion inwards	100% motion outwards	70% motion outwards
C: −1.286 (.221) P: −0.133 (.313)	100% motion inwards				
C: −2.028 (.279) P: −0.128 (.394)	70% motion inwards	C: $p = 0.003$ P: n.s.			
C: −1.622 (.222) P: 0.048 (.314)	100% motion outwards	C: $p = 0.017$ P: n.s.	C: n.s. P: n.s.		
C: −2.449 (.284) P: −0.242 (.401)	70% motion outwards	C: $p < 0.001$ P: n.s.	C: $p = 0.017$ P: n.s.	C: $p < 0.001$ P: n.s.	
C: −2.319 (.264) P: −0.355 (.373)	Random motion	C: $p < 0.001$ P: n.s.	C: n.s. P: n.s.	C: $p = 0.002$ P: n.s.	C: n.s. P: n.s.

TABLE 7 Summary of group effects across the conditions

		Checkerboard	Texture	Glass	Motion
N75	Max negative 40–120 ms	C>P	C>P esp on complex		
P100	Max positive 80–160 ms	C>P on right	C = P but interactions		
N170	Max negative 120–200 ms	-	P>C; Cs only stim effects	Cs only show stim effects	C>P; Cs show stim effects
P200	Max positive 200–380 ms			C = P	N/A

the patient group. There were two types of texture stimuli, simple and complex, and the patients showed larger N75 amplitudes to the simple than to the complex stimuli while the N75 of controls did not differentiate among the stimuli. Nevertheless, for the simple texture stimulus, the attenuation was greater for patients with longer periods of deprivation.

The P100 elicited by the texture stimuli showed differentiation of the complex stimulus from the two simple textures in both groups, but much more reliably in the controls. Interestingly, the P100 for the complex stimuli was larger in the patients, while the controls showed a larger P100 for the simple stimuli, that is, the groups differed by only 0.1 μV to the simple textures, but by over 1.1 μV for the complex stimuli. This parallels the findings from Mondloch et al. (2013), where the P100s to faces and houses (complicated stimuli) were larger in the patients than in controls. The current results from the N75 and the P100 components indicate that, at the neural level, the patients are able to differentiate between the simple and complex stimuli at an early stage of processing, but the patients process the information via a mechanism different from that of controls. Since these ERP components occur so early, this is an indication of a difference that occurs at the earliest level of visual processing—in V1 and V2 (Di Russo et al., 2001).

The texture task also produced group differences in the amplitude of the N170, likely the same component as the N200 component described in earlier studies (Casco et al., 2005). Specifically, the texture task, like the faces task reported earlier (Mondloch et al., 2013), revealed a significantly larger N170 component in patients than in controls, again pointing to differences between patients and controls in the organization of early visual processing. However, the N170 components elicited by the patients did not differentiate between complex and simple stimuli whereas controls' N170s did. Contrary results were found in the N170 component from the motion task where the patients had much smaller N170 component amplitudes than did the controls, but as with the Texture task, the N170 did not differentiate between the motion stimuli. The differences in the characteristics of the N170 amplitude between tasks (larger for faces in Mondloch et al., 2013, and for textures in this study; smaller for motion stimuli) may indicate that this component is dependent on different regions of visual cortex during the two tasks. The N170 component in the Glass task, although not significantly different in amplitude between the two groups, also showed that controls but not patients differentiated between stimuli with this component. As we suggested in Mondloch et al. (2013), this group difference may reflect an altered history of pruning in the visual cortex, which would be consistent with the thicker visual cortex found in congenitally blind individuals (Guerreiro, Erfort, Henssler, Putzar, & Röder, 2015; Voss et al., 2014). Another possibility, however, is that early visual deprivation reduces the development of inhibitory synapses in the visual cortex needed for sophisticated integration of information. This would be consistent with the findings that early visual input is needed for the normal 3-fold increase in GABA-ergic circuits in the early critical period for experience-dependent plasticity in the visual cortex (Morales, Choi, & Kirkwood, 2002). Such a reduction in inhibitory circuits may account for the increased amplitude of some of the ERP components. Whether it would account for differences in holistic processing, discussed further below, is open to speculation.

The overall pattern of results suggests that the generator of the N170 components receives different information concerning the stimuli in controls than in patients who experienced deprivation of visual input during infancy. By the time the N170 is generated, most likely in fusiform cortex (Sadeh, Podlipsky, Zhdanov, & Tovel, 2010) but possibly also in lateral occipito-temporal cortex (Schweinberger, Pickering, Hentzsch, Burton, & Kaufman, 2002), the visual cortex has processed enough detail in controls to have aspects of stimulus complexity decoded. The patients, in contrast, appear to be reacting strongly with clear P100 and N170 responses, but in a way that does not support the same fine discriminations. The poverty of response in patients to motion stimuli suggests a considerable deterioration of this function, which accords with earlier behavioral results (Ellemberg et al., 2002; Hadad et al., 2012).

These results can be divided easily into two categories. The early ERP components (the N75 and the P100) indicate that the patients are able to differentiate among stimuli. The differences in the component amplitude size between the groups, however, may point to a different mechanism or pathway used by the patients to process the visual information. The later visual ERP components (the N170 and the P200) show that the patients do not differentiate among stimuli in later processing stages reflected in the ERP. Again, the differences in the component amplitude size between the two groups may point to a different pathway that the visual information is taking or a different schedule of information processing with the result that the ERP components of the patients do not discriminate between stimuli.

Overall, it appears that patients are able to differentiate between stimuli at early processing stages by reorganizing neural processes,

while at later stages such compensation may be more problematic and differentiation among stimuli does not occur. Furthermore, our data also indicate that the changes that occur in the patients are not a simple reduction in the degree of responsiveness of the system. In some cases the ERP components are larger in the patients than in the controls.

4.1 | Holistic processing deficit?

An underlying reason for the differences in ERP differentiation of stimuli in the two groups may be because of the patients' long delay in developing the ability to process information holistically (de Heering, Wallis, & Maurer, 2012; Le Grand, Mondloch, Maurer, & Brent, 2004). It has been shown that patterned visual input immediately after birth is necessary to set up and preserve the neural mechanisms required for the development of the visual system (Lewis & Maurer, 2009). In humans, the low spatial frequencies that infants can see may prepare the system for further development of contrast sensitivity and acuity. Other visual capabilities that do not develop prenatally require input from birth to ensure their proper later development. Holistic processing is one such capability. When asked to perform a composite-face task, patients performed much better than controls, a pattern indicating that they did not process the faces holistically, but rather attended selectively to different parts of the face (Le Grand et al., 2004). Although adult patients indicated evidence of developing holistic processing after childhood (de Heering et al., 2012), a history of perceiving the world in a piecemeal fashion may have prevented the development of other forms of integrative processing. This may account for why the patients' ERP components elicited by the Motion and Glass tasks did not differentiate among stimuli. These tasks are measures of global motion and global form, tasks on which this patient cohort shows behavioral deficits (Ellemberg et al., 2002; Hadad et al., 2012; Lewis et al., 2002). Patients who do not develop the proper neural mechanisms for integrative processing would not be able to differentiate or properly process stimuli that differ on a holistic processing continuum.

Deficits in holistic processing may also explain a number of our other findings. Checkerboards are simple stimuli not inducing holistic or integrative processing and elicit normal P100 amplitudes in the patients. The texture task provides us with the first contrast. Whereas the complex textures elicit a smaller P100 amplitude in controls, suggesting a faster automatic processing, patients produced larger P100 amplitudes for complex stimuli, as if they cannot take advantage of the holistic option. More complex stimuli in the Motion or Glass tasks appear to require much more integration that is simply missing in the patients, at the time of the N170 at least.

Dramatic differences between the controls and the patients were also seen in the N75 component: the amplitude was larger in controls, especially for the complex texture stimuli. The N75 should be highly sensitive to the retinal response to such low-level characteristics that might differentiate the groups, but not the interaction with stimulus complexity in the texture task. Thus, it may be that the compromised visual system is affected by subtle differences in stimulus complexity even at the earliest stages. However, we need also to keep in mind that reductions in N75 amplitude may be caused by decreased consistency of response trial-to-trial, a factor that is not easily discerned in traditional ERP studies such as the present one (Desjardins & Segalowitz, 2013). However, whether the reduced N75 amplitude reflects inconsistency of response or some other factor, it is reasonable to consider that such alterations in early stages of visual processing may be responsible for alterations in later processing seen in both ERPs and behavioral testing. Behavioral measures on their own have not been able to address this issue of the timing of initial alterations in the processing of visual input.

One of the interesting, and unexpected, findings involves group differences in the regions producing the ERP response as well as the laterality of the ERP response. In some cases, controls produced larger ERP amplitudes over occipital sites while patients' responses were biased toward more anterior sites. This group difference lends support to the suggestion that patients process visual information using a different mechanism from that of controls. In other cases, the group differences manifested in the patients producing larger ERP amplitudes over the left side while the controls' responses were biased toward the right side. It is tempting to link this distinction to the traditional differentiation of hemispheric function involving the analytic-holistic distinction in processing. Although it is easy to overplay this contrast in hemispheric functioning (Hellige, 1993), it does appear a number of times in the visual processing literature when stimuli are carefully controlled (Romei, Thut, Mok, Schyns, & Driver, 2012; Segalowitz, Bebout, & Lederman, 1979; Yovel, Yovel, & Levy, 2001) and fits with the suggestion given above that the patients are less adept at automatic holistic processing, which would lead to less responsivity in the right hemisphere.

Whatever the underlying reason, the present study demonstrates clearly that early visual deprivation contributes to permanent abnormalities in mechanisms that underlie the processing of visual stimuli and are consistent with behavioral evidence of enduring deficits in the ability to process complex textures, global form, and global motion.

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