Developmental Science

Developmental Science 16:5 (2013), pp 728–742 DOI: 10.1111/desc.12065

PAPER

The effect of early visual deprivation on the development of face detection

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Abstract

The expertise of adults in face perception is facilitated by their ability to rapidly detect that a stimulus is a face. In two experiments, we examined the role of early visual input in the development of face detection by testing patients who had been treated as infants for bilateral congenital cataract. Experiment 1 indicated that, at age 9 to 20, patients' accuracy and response times on a Mooney face detection task were normal. Experiment 2 revealed that the neural mechanisms underlying face detection in a similar group of adult patients are abnormal: the amplitude of both the P100 and N170 event-related potential were larger in patients than in visually normal controls, and the extent of augmentation was related to the duration of deprivation. Thus, early visual experience is necessary for the establishment of normal neural networks for face detection; abnormalities at these early processing stages may contribute to the deficits we previously reported in configural face processing for this patient cohort.

Introduction

Adults' expertise in face perception is facilitated by their ability to rapidly detect that a stimulus is a face, a task that is associated with neural markers that distinguish the processing of faces from the processing of non-face objects. Functional MRI (fMRI) studies indicate that some brain areas (e.g. middle fusiform gyrus, inferior occipital gyrus, and superior temporal sulcus) respond more to faces than to non-face objects, and electrophysiological studies indicate that the distinction between faces and non-face objects is observable within 200 ms of a stimulus being presented (e.g. Allison, McCarthy, Nobre, Puce & Belger, 1994; Bentin, Allison, Puce, Perez & McCarthy, 1996; Bötzel, Schulze & Stodieck, 1995; Desimone, Albright, Gross & Bruce, 1984; Kanwisher, McDermott & Chun, 1997; McCarthy, Puce, Gore & Allison, 1997; Perrett, Rolls & Caan, 1982; Puce, Allison, Gore & McCarthy, 1995; Rolls & Baylis, 1986; Tsao, Freiwald, Tootell & Livingstone, 2006).

Face detection is facilitated by the fact that all faces share the same ordinal relations of features: the two eyes are aligned with each other and positioned above the nose, which is above the mouth. As a result, and unlike other object categories, faces can be superimposed and the resulting composite retains a face-like structure. The ordinal relations have been described as the 'first-order relations' of faces, and they differ from the first-order relations among the features of other objects (Diamond & Carey, 1986). Adults have a remarkable ability to detect that a stimulus is a face even when some of the individual features are missing (e.g. a line drawing with eyes and nose but no mouth) and even when there are no normal facial features, as long as the components can be interpreted as having the correct first-order relations for a face. For example, they readily detect a face when presented with a painting by Arcimbaldo in which an

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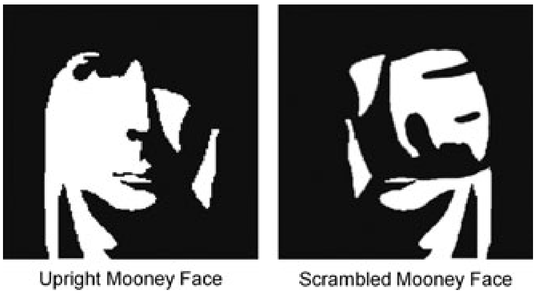
arrangement of fruit or vegetables forms the correct first-order relations for a face (Moscovitch, Winocur & Behrmann, 1997) and when looking at clouds in the sky (reviewed in Maurer, Le Grand & Mondloch, 2002). Similarly, at least when the stimuli are upright, they can detect a face in a two-tone Mooney stimulus (see Figure 1) in which the perception of individual features has been compromised by transforming all luminance values to black or white (Kanwisher, Tong & Nakayama, 1998). Faces may play a special role in capturing adults' attention: adult patients with visual neglect are more likely to detect a face presented in the neglected hemifield than they are to detect a scrambled face, a name, or a meaningless shape (Vuilleumier, 2000).

Even newborn infants orient preferentially toward some face-like stimuli: they orient preferentially toward a simple head outline with three 'blobs' arranged as facial features (a stimulus referred to as config) compared to the same head outline with the arrangement of features inverted (e.g. Goren, Sarty & Wu, 1975; Johnson, Dziurawiec, Ellis & Morton, 1991; Mondloch, Lewis, Budreau, Maurer, Dannemiller, Stephens & Kleiner-Gathercoal, 1999; Valenza, Simion, Macchi Cassia & Umiltà, 1996), a preference that might be mediated sub-cortically (Johnson & Morton, 1991). The newborn's preference is driven largely by the amplitude spectrum of the stimulus (amount of visible energy), although under some circumstances there are also influences of the phase spectrum (the organization of that energy; Kleiner & Banks, 1987; Mondloch *et al.*, 1999; Morton, Johnson & Maurer, 1990). The bias toward the upright config stimulus is also shaped by low-level perceptual biases such as top heaviness (number of elements in the top versus bottom half of the face) (Macchi Cassia, Turati & Simion, 2004), congruency (the fit between the shape of the external contour and the distribution of internal elements) (Macchi Cassia, Valenza, Simion & Leo, 2008), and contrast (features or blobs that are darker than the background and hence more face like) (Farroni, Johnson, Menon, Zulian, Faraguna & Csibra, 2005; but see Dannemiller & Stephens, 1988). Regardless of its basis, this early preference draws the attention of newborns to faces and may facilitate the development of more mature levels of face processing.


Upright Mooney Face

Scrambled Mooney Face

Figure 1 *A Mooney face (left), and a scrambled Mooney face (right) are shown. Mooney faces are comprised of black and white regions created by turning regions in a photographed face with above-average luminance to white and regions with below-average luminance to black. They lack veridical facial features and require closure for the face to be perceived.*

Infant preferences change over the first 2 to 3 months after birth. By 5 to 6 weeks of age, infants no longer prefer config over its inverted version (Johnson & Morton, 1991; Mondloch *et al.*, 1999), perhaps because config is such a degraded representation of a face, and they look preferentially at stimuli that have only the phase spectrum of a face when paired with stimuli that have only the amplitude spectrum (Kleiner & Banks, 1987; Mondloch *et al.*, 1999). By 12 weeks of age, babies look preferentially toward positive-contrast schematic faces when paired with negative-contrast schematic faces, a preference that is absent at 6 weeks of age (Dannemiller & Stephens, 1988; Mondloch *et al.*, 1999). There are continuing changes during later infancy. Although 10-month-old infants look preferentially toward an intact Mooney face over a scrambled version, 6-month-old infants do so only if they are first familiarized with the original photographic version of the face before it was transformed (Latour, Rousset, Deruelle & de Schonen, 1999). These results suggest a gradual process of cortical specialization for face detection, likely influenced by the frequent exposure babies have to faces, interacting with the baby's attentional biases.

These refinements in face detection require visual experience. Infants treated for bilateral congenital cataracts after 5 weeks of age ($n = 7$), that is, after the preference for config has disappeared in typically developing infants (Johnson *et al.*, 1991), had preferences like normal newborns rather than age-matched controls (Mondloch, Lewis, Levin & Maurer, 2013). Infants treated after 12 weeks of age ($n = 4$), that is, after the preference for a positive contrast face first emerges in infants with normal visual experience (Dannemiller & Stephens, 1988; Mondloch *et al.*, 1999), like normal newborns, failed to show that preference. The preference for the positive face ($n = 3$) emerged only after 12 weeks of visual experience.

In the current study we investigated whether patients treated for congenital cataract recover from what appears to be an initial deficit in face detection. As was true for the infant patients described above, we tested patients who were deprived of early visual experience because they were born with dense and central cataracts in both eyes that blocked all patterned input from reaching the retina. Early visual input was delayed until later in infancy when the cataractous lenses were surgically removed and the eyes were fitted with rehabilitative contact lenses.

To determine whether early visual deprivation prevents the later development of normal face detection, in Experiment 1 we tested patients 9 to 20 years old with a history of early visual deprivation from bilateral cataracts on a face/non-face task using Mooney stimuli. We showed patients and visually normal control subjects brief presentations of a series of ambiguous stimuli – Mooney faces and scrambled Mooney faces – and asked them to classify each stimulus as a face or non-face. We selected Mooney faces because they are more difficult to classify than either gray-scale images or schematic faces and because they cannot be classified as faces based on individual features and hence require sensitivity to first-order relations. In Experiment 2, we investigated whether the face detection of patients treated for bilateral congenital cataracts is mediated by the same neural mechanisms associated with face detection in visually normal adults. We compared the P100 and N170 components of event-related visual evoked potentials while adult patients and visually normal controls passively viewed faces, houses, and objects and while they actively performed the Mooney Face Detection task. Separate patient groups were recruited for each experiment, although four patients participated in both.

Deficits in face detection would provide novel insights about previously identified deficits in face perception in this same population: when tested later in childhood, these patients do not process faces holistically (Le Grand, Mondloch, Maurer & Brent, 2004), they are less sensitive than age-matched controls to differences among faces in the spacing of features (a configural cue called sensitivity to second-order relations – Le Grand, Mondloch, Maurer & Brent, 2001; Robbins, Nishimura, Mondloch, Lewis & Maurer, 2010; de Heering & Maurer, 2012) and, perhaps as a result, they make more errors than age-matched controls when asked to recognize faces across different points of view (Geldart, Mondloch, Maurer, De Schonen & Brent, 2002; de Heering & Maurer, 2012). In contrast, these patients develop normal sensitivity to differences among faces in the shape of individual features (Le Grand *et al.*, 2001; Mondloch, Robbins & Maurer, 2010) and in the shape of the external contour (Mondloch, Le Grand & Maurer, 2003), and they develop normal accuracy in matching faces based on emotional expression, vowel being mouthed, and direction of eye gaze (Geldart *et al.*, 2002), at least when the differences are large.

Patients' higher-order deficits might be attributable, at least in part, to deficits in sensitivity to the first-order relations that define a stimulus as a face, which may be a prerequisite for the specialized processing underlying adult expertise in face recognition. This hypothesis is supported by a magnetoencephalography (MEG) study (Liu, Harris & Kanwisher, 2002) in which visually normal adults were presented with pairs of stimuli consisting of two faces, two houses, or one member of each category. Participants were asked to indicate whether the two stimuli were members of the same category or whether the two stimuli were identical exemplars (i.e. pictures of the same face). The earliest face-specific response (M100) was correlated only with correct categorization of the stimulus as a face whereas a later response (M170) was correlated with correct recognition of two faces as identical, a pattern suggesting that face detection precedes the recognition of facial identity.

The hypothesis that face detection precedes, and is necessary for, the processing of face identity is consistent with data from prosopagnosics suggesting that normal face detection may be necessary, but not sufficient, for normal processing of facial identity. For example, adult patients with acquired prosopagnosia have difficulty in detecting faces in Mooney stimuli and, by definition, have difficulty in identifying faces (Davidoff & Landis, 1990). Patient PHD, with acquired prosopagnosia, lacks an N170, a face-specific event-related potential (ERP) response, and has severe difficulty in both detecting and identifying faces (Eimer & McCarthy, 1999). Data from developmental prosopagnosics are mixed. In one study (Garrido, Duchaine & Nakayama, 2008) some, but not all, had deficits in a challenging face detection task in which faces (Task 1) or face parts (Task 2) had to be detected in an array of objects and scrambled face parts, respectively. In another study (Le Grand, Cooper, Mondloch, Lewis, Sagiv, de Gelder & Maurer, 2006) each of the eight adults with developmental prosopagnosia performed normally on the Mooney face detection task used in Experiment 1 of the current study (and similar to that used by Davidoff & Landis, 1990, in their study of acquired prosopagnosia). Only one of these individuals had a deficit in holistic processing as measured by a composite face task and only two had a deficit in sensitivity to the spacing of facial features. Overall, then, whether the prosopagnosia is acquired or developmental, it appears that the patients with deficits in face detection always have difficulty with facial identity while those with normal face detection have a more mixed pattern of deficits. Like the MEG data from normal adults, that pattern suggests that normal face detection may be a prerequisite for normal recognition of facial identity.

In this study we investigated whether patients treated for congenital cataract fail to develop normal holistic processing and sensitivity to feature spacing later in childhood because they never fully overcame the infant deficit in face detection.

Experiment 1

The purpose of Experiment 1 was to measure face detection in patients with an earlier history of visual deprivation from cataracts to determine whether the ability to detect a face had developed normally despite the absence of early visual input. Face detection was measured with Mooney faces and scrambled faces in the patients and age-matched controls.

Method

Participants

The participants included 11 patients (six females; 10 right-handed; nine Caucasian and two Asian) who were born with a dense, central cataract in each eye that prevented patterned stimulation from reaching the retina (for selection criteria, see Ellemberg, Lewis, Maurer & Brent, 2001). The eyes were treated by surgical removal of the natural lens and the fitting of a contact lens that provided focused visual input (mean duration of deprivation = 118 days from birth until optical correction, range = 62 to 161 days). The patients had a mean age of 14.5 years at the time of testing (range = 9 to 20 years), and had had at least 9 years of visual experience after treatment prior to testing. Testing was binocular, and visual acuity in the better eye at the time of the test ranged from 20/25 to 20/80 (geometric Mean = 20/45). When necessary, patients wore an additional optical correction to focus the eyes at the testing distance of 100 cm.

A group of 11 age-matched control subjects with normal visual experience were tested. None of the control subjects had a history of eye problems, and all met our criteria on a visual screening exam. Specifically, all participants had Snellen acuity of at least 20/20 in each eye without optical correction, worse acuity with a + 3 dioptre lens (to rule out hyperopia of greater than 3 dioptres), fusion at near on the Worth Four-dot test, and stereoacuity of at least 40 arc sec on the Stereo Fly Test. The control group matched the patient group on age (± 3 months), handedness, race, and gender.

Stimuli and apparatus

The stimuli were 13 black-and-white Mooney faces and a scrambled version of each of these faces (Figure 1). One example of each category was presented on practice trials, and the remaining 24 stimuli were presented on test trials. The Mooney faces were created by scanning colour photographs of adult female faces that were full frontal views taken under different lighting conditions (e.g. light coming from the top, from the right, etc.). The size of the images and the number of pixels per cm^2 were adjusted to the same value for all photographs. Using Adobe Photoshop, the contrast of each face was maximized and it was converted to a gray-scale image. Contrast was adjusted further such that all pixels were either black or white. Any isolated pixels (e.g. single black pixels in a white patch) were converted to match their surround. In pilot work, visually normal adults reported that the printed versions of these stimuli were all face-like.

A scrambled version of each face was created by cutting each face into eight pieces and rearranging these pieces while maintaining, as much as possible, the total number of regions of each colour (i.e. we approximately equated the number of black/white transitions).

The stimuli were presented on a monochrome Radius 21-GS monitor controlled by a Macintosh LC-475 computer and Cedrus Superlab software. A fixation cross was presented prior to each face stimulus. Each bar of the fixation cross was 9 mm long (0.52 visual degrees from the testing distance of 100 cm) and 3 mm thick (0.17 visual degrees). All test stimuli were 10.2 cm wide and 15.2 cm high (5.8 × 8.7 visual degrees). Participants signalled their responses via a joystick, and the experimenter initiated each trial by pressing a key on the keyboard.

Procedure

Informed consent was obtained. The procedure was given ethics clearance by the Research Ethics Board at both McMaster University and The Hospital for Sick Children. The participant sat in a darkened room with his/her eyes 100 cm from the monitor. Prior to the test trials, the experimenter explained the task while displaying on the monitor one trial with a Mooney face and one trial with a scrambled Mooney face. The participant then saw each of these trials again at the normal presentation time of 100 ms and was asked to move the joystick forward if the stimulus was a face and backward if the stimulus was not a face. Participants were encouraged to respond as quickly as possible without making errors. Verbal feedback about accuracy was provided during the demonstration trials but not during the test trials.

Trials were initiated only when the experimenter, who could not see the stimuli on the screen, judged that the participant was fixating on the central fixation cross. Then the fixation cross was replaced by a face or scrambled face for 100 ms. Each participant was tested on 24 trials, which were presented in a different random order to each participant.

Results and discussion

For each subject, we calculated accuracy and median response time for correct trials (See Figure 2). For accuracy, a 2 (Group: Patients, Controls) × 2 (Stimulus: Face, Scrambled) mixed model ANOVA revealed a main effect of stimulus type, $F(1, 20) = 4.92$, $p = .038$, $\eta\rho^2 = .197$. Accuracy was higher on face trials (*M* proportion correct = .94) than on scrambled trials (*M* proportion correct = .86). The effect of group and the group × stimulus interaction were not significant, $p > .20$. For response time, the ANOVA revealed a main effect of stimulus type, $F(1, 20) = 30.22$, $p < .001$, $\eta\rho^2 = .602$; response times were faster on face trials (*M* RT = 734 ms) than on scrambled trials (*M* RT = 951 ms). The effect of group and the group × stimulus interaction were not significant, $p > .15$.

Patients' normal performance cannot be attributed to a ceiling effect: only one normal control obtained 100% accuracy. Moreover, there was no effect of visual deprivation on response time, a variable that is not limited by a ceiling effect. Unpublished data from our lab indicate that the task is difficult for children: both 6-year-old ($M = .73$, $SD = 0.14$) and 8-year-old ($M = .84$, $SD = .12$) children are less accurate than adults ($M = .95$, $SD = .06$) ($n = 24$ per group). Even when 6-year-olds see the stimuli for an unlimited time, their accuracy ($M = .68$, $SD = .18$) is well below that of adults and patients in the speeded condition used in Experiment 1. Thus, normal performance on this task cannot be attributed to the task being easy. Rather, our results suggest that the patients were able to develop normal sensitivity to first-order relations by 9–20 years of age, despite the absence of early visual input, even when no veridical facial features are present and when the task is difficult for 6- to 8-year-old children with normal visual histories.

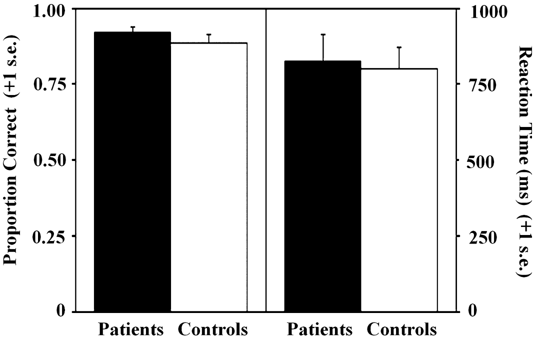


Figure 2 *Mean proportion correct and reaction times for patients and visually normal controls in Experiment 1.*

Experiment 2

In Experiment 1, patients performed normally on the Mooney face detection task, a task that cannot be solved based on featural processing and that school-aged children find difficult. We cannot conclude on the basis of these data that the underlying neural mechanisms are impervious to visual deprivation. One possibility is that patients treated for bilateral congenital cataract use the normal neural networks for face detection; alternatively, early plasticity may have extended the network to, or replaced it by, a different system that can, nevertheless, achieve normal accuracy and response time. We tested these alternative hypotheses in Experiment 2 by asking adult patients and visually normal controls to make face/non-face judgments while we recorded event-related potentials.

Studies using magnetoencephalogram (MEG), event-related potentials (ERPs), and functional magnetic resonance imaging (fMRI) have identified neural correlates of face detection. The earliest face-specific MEG response (M100) is correlated with correct categorization of a stimulus as a face (Liu *et al.*, 2002). In visually normal adults, the ERP negative potential called the N170 is larger for faces than for many other stimuli, including hands, houses, and cars (Bentin *et al.*, 1996; Itier & Taylor, 2004; Rossion, Gauthier, Tarr, Despland, Bruyer, Linotte & Crommelinck, 2000). In contrast, the earlier P100 ERP component is larger for faces only inconsistently, and in these cases is thought to be reflecting low-level stimulus characteristics differentiating the stimulus categories (Rossion & Jacques, 2008; Rousselet, Husk, Bennett & Sekuler, 2008). fMRI activation (which does not provide information about timing) in regions of the ventral occipitotemporal cortex, the inferior occipital gyrus, and the lateral fusiform gyrus (i.e. the fusiform face area – FFA) is greater for faces than for a variety of non-face objects, including cars, houses, hands, and furniture (Aguirre, Singh & D'Esposito, 1999; Haxby, Gobbini, Furey, Ishai, Schouten & Pietrini, 2001; McCarthy, Puce, Gore, and Allison, 1997).

The N170 shows a prolonged developmental timetable. The putative precursor of the N170 is a face-sensitive ERP component with similar morphology to the adult N170 characterized by a longer latency and smaller amplitude. It emerges during infancy (de Haan, Pascalis & Johnson, 2002) and becomes adult-like during childhood, although when during childhood this happens is uncertain (Kuefner, de Heering, Jacques, Palmero-Soler & Rossion, 2010; Taylor, Edmonds, McCarthy & Allison, 2001; Taylor, McCarthy, Saliba & Degiovanni, 1999). Evidence from adults suggests that the N170 may also be a marker for expertise. After extensive training with photographs of 'greebles' (a set of objects akin to chess pieces that share a small number of parts that differ slightly in shape and orientation), adults demonstrate a face-like N170 for upright greebles (Rossion, Gauthier, Goffaux, Tarr & Crommelinck, 2002), much as dog experts and bird experts do when shown stimuli from their category of expertise (Tanaka & Curran, 2001). The slow maturation of N170 for faces and the presence of an Nl70 following extensive training with non-face stimuli suggest slow maturation of the neural mediation for expertise with faces. The goal of Experiment 2 was to use ERPs to study whether the normal face detection observed in Experiment 1 that was evident despite early visual deprivation is based on the same neural processes as in visually normal adults. Because of the slow maturation of the N170 in visually normal children, we restricted the study to patients who were at least 18 years old.

The primary task in Experiment 2 was a Mooney Face Detection task similar to that used in Experiment 1. Using a larger set of Mooney faces and scrambled Mooney faces, we asked adult patients and visually normal controls to make face/non-face judgments while we recorded ERPs. We examined whether the N170 and the P100 components were differentially sensitive to face-like stimuli in the two groups. In another task, patients and visually normal controls performed a butterfly detection task while viewing non-target stimuli from three different categories: faces, houses, and objects. Analysis of the ERPs for each of the three non-target categories allowed us to determine whether any differences observed between patients and visually normal control participants were face-specific.

Method

Participants

We tested 13 patients (four females; eight right-handed; all Caucasian) comparable to those described in Experiment 1 who were born with a dense, central cataract in each eye that prevented patterned stimulation from reaching the retina (mean duration of deprivation = 125 days from birth, range = 48–228 days). The patients had a mean age of 23.7 years at the time of testing (range = 18–29 years), and thus had at least 18 years of visual experience after initial treatment. Four of these patients also participated in Experiment 1 but the testing was separated by more than 2 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 an additional optical correction to focus the eyes at the testing distance of 100 cm.

Sixteen right-handed adults (13 females, 15 Caucasian) with a mean age of 20.6 years (range = 18–26) served as visually normal controls for the Mooney Face Detection task. Fourteen of these controls and an additional 10 individuals in the same age range participated in the Face/House/Object task. All controls had normal or corrected-to-normal vision and had no signs of neurological or psychiatric disorders.

Stimuli

Stimuli in the Mooney Face Detection task comprised 50 black-and-white intact Mooney faces and a scrambled version of each of these faces, either from Experiment 1 (n = 13 pairs) or constructed in the same way (n = 37). Each image subtended a visual angle of 8.4 × 8.2 deg when viewed at a distance of 100 cm. An additional four images (two faces, two scrambled) were presented as practice trials. Stimuli in the Face/House/Object task comprised 64 unique photographs of stimuli from each of the three categories interspersed with pictures of 18 butterflies that were used as target stimuli (210 in all). All pictures were gray scale and subtended a visual angle of 8 × 8 deg when viewed at a distance of 100 cm.

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.

Mooney task. Continuous EEG was recorded while participants viewed the Mooney images presented sequentially in the centre of a computer monitor (Dell Model # M782, 17″ screen). They were instructed to make face/non-face judgments by pressing one button of a response pad with one index finger to indicate 'face', and a second button with the other index finger to indicate 'non-face' (with finger assignment counterbalanced across participants). Responses to the first four trials, made up of two intact and two scrambled Mooney faces, served as practice trials and were not included in analyses. The remaining 100 images were presented in the same random order for each participant. Each image appeared for 250 ms with a variable inter-stimulus interval ranging from 1200 ms to 1800 ms, using 50 ms increments. Participants were provided with a chin rest to reduce head movements and to help them keep their eyes fixated on the centre of the screen. They were instructed to respond as quickly and as accurately as possible. The task took approximately 5 minutes.

Face/House/Object task. Continuous EEG was recorded while participants performed the butterfly detection task. They were instructed to press a response pad button each time they detected a butterfly and not when they saw other images. Half of the participants were instructed to use their right index finger and half were instructed to use their left index finger. Participants viewed a randomly mixed presentation of the 64 houses, 64 faces, 64 objects, and 18 butterflies, all pseudo-randomly interspersed; trials were presented in the same order to all participants. As in the Mooney task, each image appeared for 250 ms with a variable inter-stimulus interval ranging from 1200 ms to 1800 ms, using 50 ms increments. Participants used the chin rest, and the task took approximately 7 minutes with two 20-second breaks. Both tasks were part of a larger battery of tests lasting approximately 2 hours.

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 due to changes in lab procedure over time. An online bandpass filter from 0.01 to 100 Hz was used. Impedances were kept below 50 kΩ. EGI NetStation software was used to average participants' raw EEG files into stimulus-locked ERPs. Data were bandpass filtered from 1 to 30 Hz to remove idiosyncratic slow wave components and better isolate the P100 and N170, and re-referenced to a common average reference. In order to standardize the site locations across all participants, the number of sites was reduced to the 81 channels of the extended standard 10–10 system (Nuwer, Comi, Emerson, Fuglsang-Frederiksen, Guérit, Hinrichs, Ikeda, Luccas & Rappelsburger, 1998) via spherical spline, a technique that maintains virtually all the original topological information in BESA (Scherg & Berg, 1996). The P100 was defined as the positive peak 75 to 200 ms after the stimulus onset centred around the O1 and O2 sites. The N170 was defined as the negative peak following the P100 125 to 250 ms after stimulus onset centred around P7 and P8 sites. However, as both components were clearly visible at both sets of sites, we conducted analyses for both at the four sites. Trials in which EEG exceeded ± 70 μV were rejected automatically. Baseline correction beginning at −200 ms and ending at 0.0 ms, locked to stimulus onset, was applied to all trials that did not exceed the rejection criterion. For the Mooney Detection task, only trials in which participants responded correctly were used for P100 and N170 analysis. The averaged waveforms were then exported to ERPScore (available from SJS) for peak scoring.

As mentioned above, peak amplitudes and latencies for both tasks were scored at the sites traditionally used for P100 and N170 scoring, namely O1, O2, P7 and P8. Exploratory analyses across a wider range of sites in this data set yielded identical or stronger results; to simplify analyses, we will report data only from these standard sites here. Greenhouse-Geisser corrections for violations of sphericity were applied, with the original degrees of freedom reported. The minimum number of trials per averaged ERP was 32 for the Mooney stimuli and 49 for the Face/House/Object stimuli, with the sole exception of one patient who demonstrated a nystagmus that reduced some averages to as low as 15 trials. Interestingly, his ERPs were otherwise scoreable and the results of the analyses were the same when his data were excluded, and therefore the statistics reported here include this participant.

Results

Behavioural responses

For each subject, we calculated accuracy and mean response time for correct trials (see Figure 3). For accuracy, a 2 (Group: Patients, Controls) × 2 (Stimulus: Face, Scrambled) mixed model ANOVA revealed a main effect of stimulus type, $F(1, 28) = 6.53$, $p = .016$, $\eta\rho^2 = .189$; accuracy was higher on face trials (M proportion correct = .91) than on scrambled trials ($M = .86$). The effect of group was not significant, $p > .15$, but the group × stimulus interaction approached significance, $F(1, 28) = 3.94$, $p = .057$, $\eta\rho^2 = .123$. Patients' performance did not differ from that of controls on Mooney Face trials ($M_{Pt} = .914$ vs. $M_C = .912$), but they tended to make more errors than controls on Scrambled trials ($M_{Pt} = .811$ vs. $M_C = .899$), $t(28) = 1.76$, $p = .09$. Patients, $t(12) = 2.51$, $p = .028$, but not normal controls, $t < 1$, were more accurate on face trials than scrambled trials. These data indicate that patients may have more difficulty than controls in rejecting non-face stimuli. For response time, the ANOVA revealed a main effect of stimulus type, $F(1, 28) = 18.56$, $p < .001$, $\eta\rho^2 = .399$; response times were faster on face trials (M RT = 547 ms) than on scrambled trials

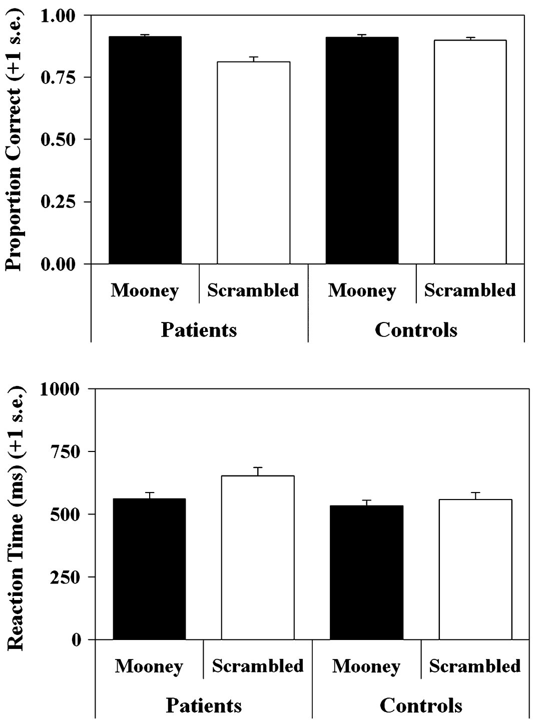


Figure 3 *Mean proportion correct and reaction times for patients and visually normal controls in Experiment 2. Results are shown separately for Mooney face vs. Scrambled trials.*

(M RT = 607 ms). The effect of group was not significant, $p > .10$, but there was a significant group × stimulus interaction, $F(1, 28) = 5.85$, $p < .0001$, $\eta\rho^2 = .173$. Patients were slightly slower than controls on Mooney Face trials ($M_{Pt} = 560$ vs. $M_C = 533$ ms), but were significantly slower on Scrambled trials ($M_{Pt} = 654$ ms vs. $M_C = 560$ ms, $t(28) = 2.29$, $p = .03$. Patients, $t(12) = 5.70$, $p < .001$, but not normal controls, $p = .22$, were faster on face trials than scrambled trials.

Errors on the Face/House/Object task consisted of missing a butterfly or false alarms to the non-butterfly stimuli, neither of which were scored for ERPs. In all, there were eight missed targets out of 594 trials across all participants (1.3%), with seven of these attributable to one patient and one to another patient. When we redid the ERP analyses without the patient who missed seven targets, the results were identical. Of the 6435 Face/House/Object nontarget stimuli across all subjects, there were only 10 false alarm responses (0.16%).

ERP responses

Mooney Face Detection task. Averaged ERP waveforms for the Mooney and scrambled faces are shown for each group in Figure 4. Topographical maps of the P100 and N170 components associated with Mooney faces for patients and controls are illustrated in Figure 5 and the amplitude and latency results are illustrated in Figure 6. To analyse each of the ERP components we conducted a mixed model ANOVA with Group (Patients, Controls) as a between-subjects factor and Stimulus Type (Mooney, Scrambled), Site (Occipital, Parietal), and Side (Left, Right) as repeated measures.

P100: The patients had larger P100 amplitudes than controls, $F(1, 26) = 8.50$, $p = .007$, $\eta\rho^2 = .246$, with on average double the amplitude (3.94 vs. 1.85 μV). There was no main effect of stimulus type (Mooney vs. scrambled) or interaction between stimulus type and group, ps > .21, perhaps reflecting the sensitivity of this component to low-level visual factors rather than object categories. P100 latencies were sensitive to site, $F(1, 26) = 7.06$, $p = .013$, $\eta\rho^2 = .214$, being shorter at occipital (105.5 ms) than parietal (109.5 ms) sites, and side, being shorter on the left, $F(1, 26) = 5.56$, $p = .026$, $\eta\rho^2 = .176$, left = 105.6 ms, right = 109.7 ms. There was a trend toward a longer P100 latency for the patients (113.3 ms) compared to controls (102.0 ms), $F(1,26) = 3.06$, $p = .09$, $\eta\rho^2 = .105$. There was no effect of stimulus or interaction of stimulus and group for latency, ps > .61.

N170: There was a reliable stimulus effect on the N170 amplitude, $F(1, 26) = 16.9$, $p < .001$, $\eta\rho^2 = .394$, with the Mooney faces eliciting a larger N170 (−2.20 μV) compared to the scrambled faces (−1.70 μV). The N170 amplitude differed across groups, $F(1, 26) = 5.49$, $p = .027$, $\eta\rho^2 = .174$, with the patients (−2.74 μV) showing a much larger amplitude than the controls (−1.16 μV). There were no significant interactions for amplitude. N170 latency was not different between Mooney and scrambled faces ($p = .97$). Patient N170 latency (168.9 ms) was longer than that of the controls (153.4 ms), $F(1, 26) = 4.98$, $p = .034$. N170 latency was shorter at the occipital sites (158.3 ms) than parietal sites (164.5 ms), $F(1, 26) = 20.1$, $p < .001$, $\eta\rho^2 = .437$. There were no significant interactions for latency.

The Face/House/Object task. To analyse each of the ERP components we conducted a mixed model ANOVA with Group (Patients, Controls) as a between-subjects factor and Stimulus Type (Face, House, Object), Site (Occipital, Parietal), and Side (Left, Right) as repeated measures. The amplitude and latency results are illustrated in Figure 7.

P100: As with the Mooney task, the P100 amplitudes for all stimuli were on average double for the patients (2.64 versus 1.26 μV), $F(1, 34) = 5.90$, $p = .021$, $\eta\rho^2 = .148$. There was a main effect of stimulus, with the P100 amplitude differing across faces, houses, and

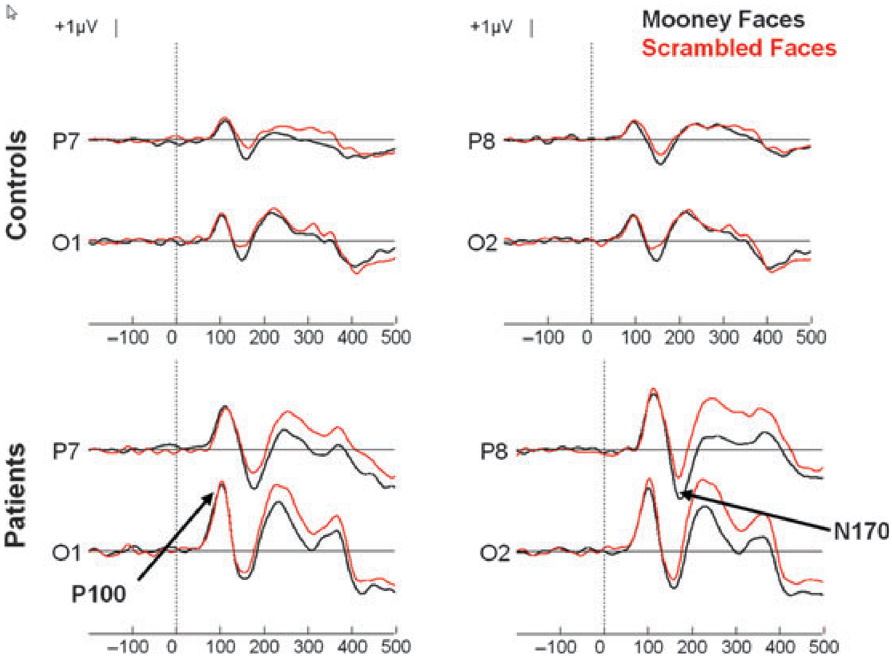


Figure 4 *Averaged ERP waveforms illustrating the response to Mooney versus Scrambled faces for controls (top panel) and patients (bottom panel) during the Mooney Task. Patients produced larger P100 and N170 amplitudes.*

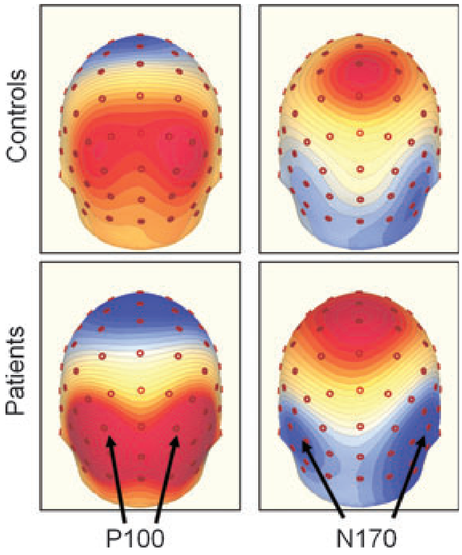


Figure 5 *The topographical distribution of electrocortical activity elicited by Mooney faces at P100 (left panels) and N170 (right panels) peaks. Data are for controls (top panels) and patients (bottom panels).*

objects (2.23, 2.10, 1.53 µV, respectively), $F(2, 68) = 14.2$, $p < .001$. These two effects were superseded by their interaction, $F(2, 68) = 3.91$, $p = .028$, $\eta\rho^2 = .103$, with the larger P100 in patients being more reliable for faces ($p = .013$) and houses ($p = .017$) than for objects ($p = .077$).

The P100 amplitude also differed by site, $F(1, 34) = 12.6$, $p = .001$, $\eta\rho^2 = .271$, larger at occipital (2.32 µV) than parietal (1.59 µV) sites, with this effect interacting with stimulus, $F(2, 68) = 12.8$, $p < .001$, $\eta\rho^2 = .273$, such that the occipital advantage was greater for faces and houses than for objects. In addition there was one three-way interaction, $F(1, 34) = 6.27$, $p = .017$, $\eta\rho^2 = .156$, whereby the occipital advantage over the parietal sites was 1.2 µV for the left sided sites in the patient group and only .4 to 1.7 µV for the other three cells. The only latency effect was a faster P100 peak, $F(1, 34) = 4.23$, $p = .047$, $\eta\rho^2 = .111$, at the occipital compared to parietal sites (102.6 versus 105.0 ms).

N170: Overall, the N170 amplitudes were considerably larger for faces (−1.84 µV) than for houses (−.53 µV) or objects (−.75 µV), $F(2, 62) = 13.7$, $p < .001$, $\eta\rho^2 = .306$, but this effect was modified by an interaction with site, $F(2, 62) = 7.08$, $p = .002$, $\eta\rho^2 = .186$, such that the advantage for faces was larger at the parietal sites as is traditionally found, rising to −2.2 vs. −.50 and −.75 µV. Furthermore, this interaction itself interacted with group, $F(2, 62) = 5.44$, $p = .007$, $\eta\rho^2 = .149$, with a group by stimulus effect at parietal sites, $F(2, 62) = 5.29$, $p = .022$, $\eta\rho^2 = .146$, and not at the occipital sites, $p = .827$. At the parietal site, patients' N170 amplitudes for faces considerably

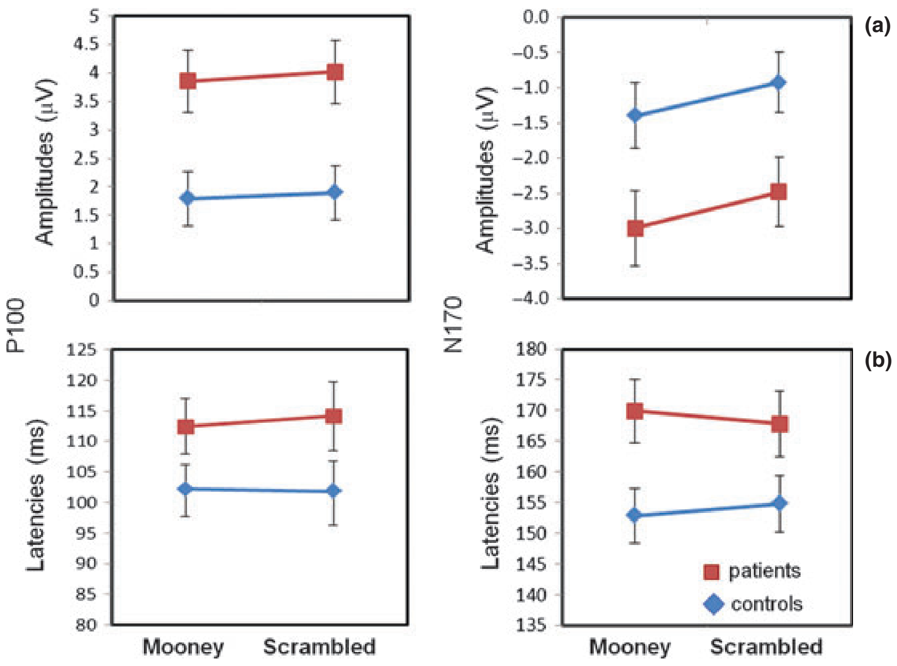


Figure 6 *Amplitudes and latencies for P100 (left) and N170 (right) for patients (squares) and controls (diamonds) for Mooney faces and Scrambled images. Vertical bars indicate standard errors. Results for the two categories are connected for ease of comparison across groups.*

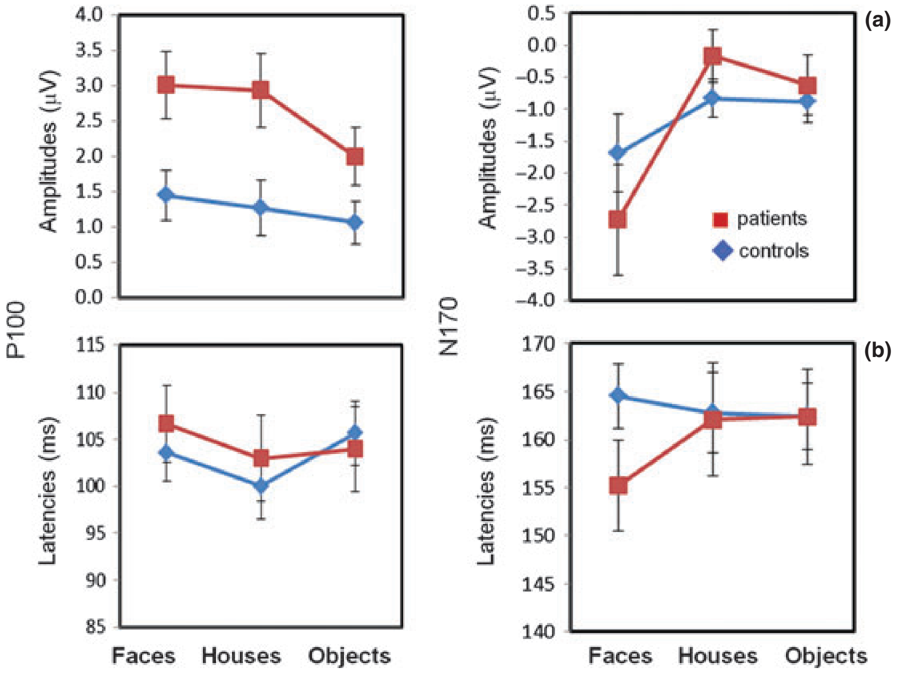


Figure 7 *Amplitudes and latencies for P100 (left) and N170 (right) for patients (squares) and controls (diamonds) for Faces/Houses/Objects. Vertical bars indicate standard errors. Results for the two categories are connected for ease of comparison across groups.*

exceeded those for the other stimuli (by 2.57 and 2.11 µV over those to houses and objects), compared to smaller differences between faces and objects/houses for controls (.86 and .81 µV) (see Figure 7). At the occipital sites, the advantages for faces were all small, between .69 and .95 µV for both groups.

The main effect for N170 latency was not significant, but a stimulus × group interaction, $F(2, 62) = 3.09$, $p = .054$, $\eta\rho^2 = .091$, indicated a trend for the patients to have a slower N170 for faces (155.3 versus 163.0 ms, for controls and patients, respectively), but not for houses and objects, for which the mean latencies ranged between 159 and 161 ms. Other effects include a 3-ms faster response at occipital sites, $F(1, 31) = 11.2$, $p = .002$, $\eta\rho^2 = .265$, an effect that interacted with stimulus, $F(2, 62) = 8.02$, $p = .001$, $\eta\rho^2 = .205$, whereby the parietal and occipital sites had similar latencies for faces (159.9 and 159.1 ms), but for houses and objects there was a slowing down at the parietal sites and a speeding up at the occipital sites.

Follow-up analyses of ERP responses to faces/objects/houses. Given that the patient group demonstrated larger P100 and N170 amplitudes than controls in response to face stimuli, we sought to determine the source of this general augmented neural response. We focused on the parietal sites as the face effects were clearly strongest there. We first determined whether individuals in the patient group with a larger P100 also had a larger N170. These correlational analyses (Table 1, left columns) revealed that for both the left and right electrode sites P7 and P8, the P100 and N170 amplitudes were related to each other such that individuals with larger positive P100 amplitudes also had larger negative N170 amplitudes as evidenced by reliable negative correlations. This result was not simply present for the faces stimuli, but for the houses and objects as well.

In the control group, there was no general relationship between the amplitudes of the P100 and the N170 (Table 1, right columns). The one correlation that reached statistical reliability (i.e. for houses) was positive – larger P100, smaller N170 – suggesting a general positivity drift, contrary to the pattern in the patients. Thus, the relation between the two ERP components is specific to the patient group and the augmentation may relate to the early abnormal experience.

Table 1 *Pearson correlations between amplitude of P100 and N170 at left (P7) and right (P8) parietal sites as elicited by face, house, and object stimuli for patients and controls*

	Patients		Controls	
Stimulus Type	P7	P8	P7	P8
Faces	−.78**	−.69*	−.04	−.29
Houses	−.67*	−.69*	.44*	−.09
Objects	−.73*	−.58†	.03	.17

Note: ** $p < .01$; * $p < .05$; † $p = .06$.

In order to examine the relation between the augmented response and the duration of deprivation, we calculated the P100-to-N170 peak-to-peak amplitude (total degree of augmentation) and correlated it with the number of days of visual deprivation the patients experienced after birth. All six correlations (P7/P8 × faces/houses/objects) indicated that the degree of augmentation indeed did relate to the duration of visual deprivation, *rs* = .593 to .662, *ps* = .054 to .027. The number of days of visual deprivation after birth accounted for 43% of the variance in the average of the six peak-to-peak measures, $r = .656$, $p = .029$ (see Figure 8).

We further tested to see whether this effect could be attributed to differences in visual acuity, possibly related to the duration of deprivation. Within the patient group, (log) acuity in the better eye did not relate to the number of days of deprivation nor to the P100-N170 peak-to-peak amplitude, *ps* > 0.15. When we recalculated the correlation between the duration of visual deprivation and the average degree of ERP augmentation with acuity in the better eye partialled out, the correlation increased slightly to 0.683. Therefore, it is clear that the relation between days-of-deprivation and ERPs is not confounded by the degree of visual acuity impairment.

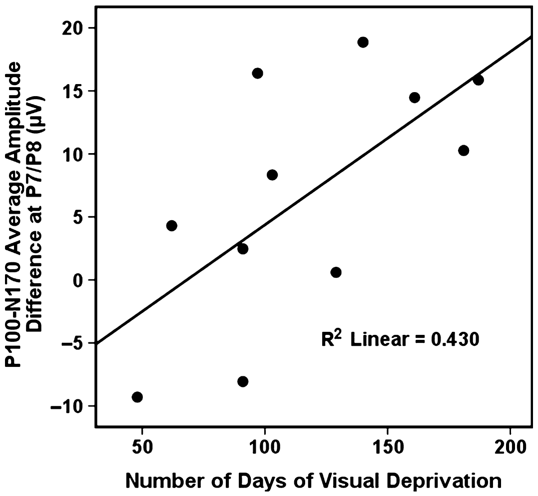


Figure 8 *A scatterplot of the amplitude difference between the P100 and N170 peaks averaged over P7 and P8 sites and averaged over face, house, and object stimuli as a function of the number of days of visual deprivation beginning from birth to the receipt of first optical correction after cataract surgery. Two patients are omitted because at least one of their 12 peaks going into the amplitude difference calculation was not scorable.*

Discussion

The P100 of patients was consistently larger than that of controls, both when performing the Mooney Face Detection task and when performing the Face/House/Object task. Because this effect held across stimulus types, it likely reflects an early neural response to low-level stimulus characteristics and suggests that patients' visual cortex consistently activates to a greater extent in the initial processing of visual stimuli. The augmentation of the P100 in patients relative to controls was smaller for objects than the other categories, with no difference between faces and houses or between intact and scrambled Mooney faces, a pattern that may have arisen from the objects being less visually complex than the other categories.

Patients, like controls and as expected from the literature on normal adults (e.g. McCarthy *et al.*, 1997), had a larger N170 to faces than to other stimulus categories. Patients' N170 to faces was also generally larger and later than that of controls both when performing the Mooney Face Detection Task and when viewing faces in the Face/House/Object task. Because the amplitude of both the P100 and N170 of patients was larger, it is evident that the N170 effect was not caused by the confounding factor of a slow negative drift in the ERP waveform after the onset of the stimuli, but rather to the fact that the patients had larger ERP responses at both the P100 level (reflecting the early response to stimulus characteristics) and at the N170 level (reflecting the activation associated with structural integration of the stimuli). This group difference in the amplitude and latency of the N170 was specific to the conditions in which faces were being processed.

In contrast to (nearly) normal behavioural performance on the Mooney face task, patients had a larger electrocortical response to visual stimuli than controls, a finding that is particularly notable given their reduced visual acuity. Their larger electrocortical response was evident in the first stages of visual processing that reflect low-level stimulus characteristics (the P100) and then more specifically for faces at the next integrative stage (the N170). This augmentation was not related to the size of the deficit in acuity, but was positively related to duration of deprivation. Combined, the results suggest that many years of nearly normal visual input following early deprivation was sufficient to achieve the (nearly) normal face detection revealed in the behavioural measures of Experiments 1 and 2 but left a sustained abnormality at the level of the visual cortex that was correlated with the duration of the initial deprivation.

General discussion

The normal performance of adult patients on the Mooney face detection task suggests that early visual deprivation does not prevent the eventual development of normal face detection and indicates that patients' poor acuity does not prevent them from detecting facial structure in Mooney stimuli. The absence of a permanent behavioural deficit in sensitivity to the first-order relations in faces contrasts with the permanent deficits in sensitivity to second-order relations (i.e. the spacing among features in individual faces). Patients are less accurate than visually normal control subjects when making same/different judgments about pairs of faces that differ only in the spacing among features (de Heering & Maurer, 2012; Le Grand *et al.*, 2001; Robbins *et al.*, 2010), an ability that continues to improve in visually normal children past 10 years of age (Mondloch, Le Grand & Maurer, 2002; Mondloch *et al.*, 2003). Our current behavioural findings also contrast with deficits in holistic processing that are evident in the same cohort, at least until early adulthood. Typically developing adults show a robust composite face effect (Hole, 1994; Young, Hellawell & Hay, 1987): their ability to make same/different judgements about the top halves of faces is impaired when those top halves are fused with the bottom halves of different faces, an effect that is robust in typically developing children by 4–6 years of age (de Heering, Houthuys & Rossion, 2007; Macchi Cassia, Picozzi, Kuefner, Bricolo & Turati, 2009; Mondloch, Pathman, Maurer, Le Grand & De Schonen, 2007) and that can be observed indirectly in babies by 3 months of age (Turati, Di Giorgio, Bardi & Simion, 2010). This effect was absent in patients tested between 9 and 23 years of age (Mean = 15 years) (Le Grand *et al.*, 2004), although at least some patients recover when retested 8–9 years later (de Heering & Maurer, 2012).

The findings based on event-related potentials challenge the conclusion that patients' face detection is normal and highlight the value of research that integrates behavioural and neurophysiological methodologies. Like visually normal control participants, our adult patients produced an N170 that was larger for Mooney faces than scrambled images in the Mooney Face Detection task and for faces than either houses or objects in the Face/House/Object task. These data indicate that patients do process faces differently from non-face objects, as do adults with normal visual histories. However, adult patients differ from adults with normal visual histories in several key ways. The N170 face effect was exaggerated in patients. Compared to controls, their N170 was larger in amplitude and longer in latency for faces in both the Mooney Face Detection task and in the Face/House/Object task. Although the larger N170 may reflect abnormalities in several aspects of face perception, the results indicate that it emerges even when the viewer is not required to recognize facial identity because the task is restricted to face detection (Experiment 1) or the task is only passive viewing (Experiment 2), thus ensuring that the effect was not restricted to conditions in which patients may adopt a different strategy from visually normal controls.

In contrast, the amplitude of their N170 did not differ from that of controls for houses and objects (see Figure 7), indicating that by 170 ms post-stimulus presentation, differences between patients and controls may be stimulus-specific. These patterns, like those for the P100, are unlikely to be related to the patients' generally poorer acuity because the augmentation was related to the duration of the initial deprivation and not to the patient's current acuity.

In visually normal adults, inverting faces consistently increases the latency of the N170 and in many, but not all, cases increases its amplitude (Itier & Taylor, 2004; Rossion *et al*., 2000; reviewed in Macchi Cassia, Keufner, Westerlund & Nelson, 2006), despite their ability to detect that the inverted stimulus is a face. These effects have been attributed to increased task difficulty that leads to increased activation of face-specific networks or to more widespread neural recruitment (e.g. the involvement of object areas; Sadeh & Yovel, 2010). The larger N170 observed in patients relative to controls when presented with upright Mooney stimuli is consistent with either of these explanations. Indeed when visually normal adults' sensitivity to first-order relations is impaired by disrupting either vertical symmetry or the canonical top-heavy pattern, the N170 is delayed and, for vertically asymmetrical stimuli only, larger (Macchi Cassia *et al*., 2006). Differences in the N170 of patients versus controls suggest that, despite (nearly) normal behavioural performance on our Mooney task, they achieved normal face detection at a cost and that they found the task more difficult. This is consistent with patients failing to develop holistic processing during childhood and performing less well than controls when asked to recognize faces based on feature spacing and across changes in point of view (Geldart *et al*., 2002; Le Grand *et al*., 2001, 2004; Robbins *et al*., 2010; de Heering & Maurer, 2012) or to remember famous or recently learned faces (de Heering & Maurer, 2012), perhaps because the non-face object systems recruited are incapable of mediating normal holistic face processing or sensitivity to second-order relations in faces. It is also possible that patients would perform worse than controls on more demanding face detection tasks in which faces must be detected among a larger array of stimuli (e.g. Garrido *et al*., 2008).

The mechanism accounting for larger N170s for faces will not, however, account for the group differences in the P100 amplitudes, which were larger in patients than in visually normal controls for all visual stimuli. Such enhanced activation may be the result of a change in neural or dendritic pruning after early visual deprivation, by a compensatory increase in synapses that serves to enhance the perception of visual stimuli and/or by increased top-down innervation due to increased difficulty in processing.

It appears that it is only by recruiting more neural processing than normal that patients are able to demonstrate (nearly) normal face detection with Mooney stimuli. If face detection precedes holistic processing and the processing of feature spacing, as suggested by MEG data (Liu *et al*., 2002) and the pattern of deficits observed in prosopagnosics (Davidoff & Landis, 1990; Eimer & McCarthy, 1999; Le Grand *et al*., 2006), it may be that the processes underlying face detection in patients are not adequate to produce normal holistic processing during childhood, normal sensitivity to small differences among faces in feature spacing, or normal memory for faces. In any event, normal visual input during infancy is necessary for the brain to later develop normal neural efficiency in distinguishing between faces and other categories.

Acknowledgements

We thank Scania de Schonen and Thomas McKeef who created the Mooney stimuli for us and Allison Flynn for her help in coordinating the collection and management of the ERP data. This research was funded by grants from the Natural Sciences and Engineering Research Council of Canada (DM, CJM, SJS, JD), the Canadian Institutes for Health Research (DM & TLL, SJS, JD) and the Social Sciences Research Council of Canada (DM).

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Received: 1 November 2011
Accepted: 4 February 2013