Developmental Science

Developmental Science 2017; 20: e12384 DOI: 10.1111/desc.12384

PAPER

Reduced adaptability, but no fundamental disruption, of norm-based face coding following early visual deprivation from congenital cataracts

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Abstract

Faces are adaptively coded relative to visual norms that are updated by experience, and this adaptive coding is linked to face recognition ability. Here we investigated whether adaptive coding of faces is disrupted in individuals (adolescents and adults) who experience face recognition difficulties following visual deprivation from congenital cataracts in infancy. We measured adaptive coding using face identity aftereffects, where smaller aftereffects indicate less adaptive updating of face-coding mechanisms by experience. We also examined whether the aftereffects increase with adaptor identity strength, consistent with norm-based coding of identity, as in typical populations, or whether they show a different pattern indicating some more fundamental disruption of face-coding mechanisms. Cataract-reversal patients showed significantly smaller face identity aftereffects than did controls (Experiments 1 and 2). However, their aftereffects increased significantly with adaptor strength, consistent with norm-based coding (Experiment 2). Thus we found reduced adaptability but no fundamental disruption of norm-based face-coding mechanisms in cataract-reversal patients. Our results suggest that early visual experience is important for the normal development of adaptive face-coding mechanisms.

Research highlights

- Face identity aftereffects were reduced in cataract-reversal patients, indicating reduced updating of face norms by experience.
- Coding remained norm-based.
- Poor calibration of face norms by experience may contribute to face recognition difficulties in these patients.
- Our results demonstrate a role for early visual experience in the normal development of adaptive face-coding mechanisms.

Introduction

Adaptive coding mechanisms, which can calibrate a limited neural response range to the prevailing environment, are fundamental for efficient sensory coding (Clifford & Rhodes, 2005; Schwartz, Hsu & Dayan, 2007; Wark, Lundstrom & Fairhall, 2007). They also play an important role in face perception, with faces adaptively coded relative to visual norms that are updated by experience (Rhodes & Leopold, 2011; Webster & MacLeod, 2011). Norm-based coding of faces focuses processing resources on distinctive information and may contribute to face recognition ability (Armann, Jeffery, Calder, Bülthoff & Rhodes, 2011; Dennett, McKone, Edwards & Susilo, 2012; Rhodes, Jeffery, Taylor, Hayward & Ewing, 2014b).

The operation of these adaptive face-coding mechanisms can be seen in face identity aftereffects, where adaptation to a face biases perception towards an identity that lies opposite the adaptor in face-space (see Figure 1) (Jeffery, Rhodes, McKone, Pellicano, Crookes *et al*., 2011; Leopold, O'Toole, Vetter & Blanz,

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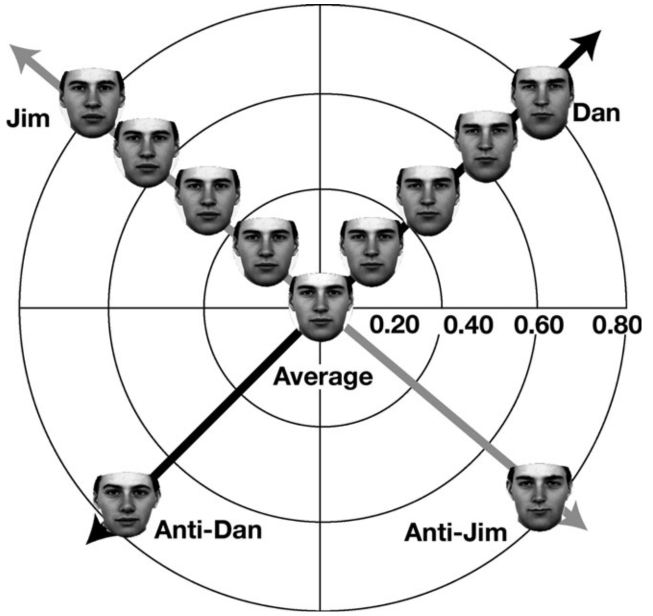

Figure 1 *A simplified (two-dimensional) face space with two faces, Dan and Jim, an Average face (created by morphing 20 male, Caucasian faces) and two antifaces, antiDan and antiJim. An antiface is made by morphing a face towards, and beyond, the Average, and has opposite properties from that face. Reduced-identity-strength versions of Dan and Jim, created by morphing those identities towards the Average, are also shown. Identity aftereffects occur when exposure to a face biases subsequent perception towards a face with opposite properties. For example, after viewing antiDan for a few seconds, we are biased (briefly) to perceive Dan.*

2001; Loffler, Yourganov, Wilkinson & Wilson, 2005; Rhodes & Jeffery, 2006). These identity aftereffects are larger for upright than inverted faces, consistent with adaptation of higher-level face-coding mechanisms that are tuned to upright faces (Rhodes, Evangelista & Jeffery, 2009). The selectivity of the bias for the opposite identity, with reduced aftereffects for equally perceptually dissimilar but non-opposite adapt-test face pairs (Jeffery *et al.*, 2011; Rhodes & Jeffery, 2006), suggests that the average face functions as a perceptual norm for coding identity.

The adaptive updating of face norms by experience may play an important functional role in our face recognition abilities. It can enhance face discrimination and recognition (Armann *et al.*, 2011; Wilson, Loffler & Wilkinson, 2002) (although this is not always found; Nishimura, Doyle, Humphreys & Behrmann, 2010; Rhodes, Maloney, Turner & Ewing, 2007). Moreover, individuals with more adaptable face-coding mechanisms, as indicated by larger identity-related face aftereffects, have better face recognition (Dennett *et al.*, 2012; Rhodes *et al.*, 2014b). Taken together, these findings suggest a functional role for adaptive norm-based coding in face recognition ability.

Here we consider the developmental origins of these adaptive face-coding mechanisms. These mechanisms are qualitatively adult-like by early childhood (Jeffery, McKone, Haynes, Firth, Pellicano *et al.*, 2010; Jeffery, Read & Rhodes, 2013), but nothing is known about their earlier origins. One approach could be to measure identity aftereffects in infants, but in practice this would be difficult. Here we take a different approach, asking whether early visual experience is important for the normal development of adaptive face-coding mechanisms, as it is for other aspects of face perception. For example, by 2 days of age, infants have learnt to discriminate their mother's face from the faces of strangers (Bushnell, Sai & Mullin, 1989). Many aspects of early development may be directly related to adaptive norm-based coding. By 3 months, infants can form prototypes (averages/norms) of seen faces (de Haan, Johnson, Maurer & Perrett, 2001) and over the first year, ability to discriminate faces from familiar races and species improves and ability to discriminate within some unfamiliar face categories deteriorates (e.g. Kelly, Quinn, Slater, Lee, Ge *et al.*, 2007; Maurer & Werker, 2014; Pascalis, de Haan & Nelson, 2002). Infants are also initially better at discriminating female than male faces (Quinn, Yahr, Kuhn, Slater & Pascalis, 2002) and at forming prototypes of female than male faces (Ramsey, Langlois & Marti, 2005), patterns that match the predominance of female faces in their environment (Rennels & Davis, 2008; Sugden, Mohamed-Ali & Moulson, 2014). Thus, during the first year of life, face processing is already being calibrated by the infant's diet of faces.

Visual experience during infancy is crucial for normal visual development, including the development of face perception. Visual deprivation during the first year of life because of dense cataracts in both eyes that block patterned visual input results in enduring visual problems, despite early surgical removal of the cataracts and subsequent optical correction. As adults, these patients show reduced sensitivity at low temporal frequencies and high spatial frequencies, including abnormal acuity (Ellemberg, Lewis, Maurer, Lui & Brent, 1999), and deficits in global processing of shape and motion (Ellemberg, Lewis, Maurer, Brar & Brent, 2002; Lewis, Ellemberg, Maurer, Wilkinson, Wilson *et al.*, 2002). Face processing is also affected. Simple discrimination of facial feature shape seems intact (Le Grand, Mondloch, Maurer & Brent, 2001; Mondloch, Robbins & Maurer, 2010), but there are deficits in holistic processing as measured by the composite face effect (Le Grand, Mondloch, Maurer & Brent, 2004) (although it may develop later; de Heering & Maurer, 2014) and in matching faces across changes in point of view (de Heering & Maurer, 2014; Geldart, Mondloch, Maurer, De Schonen & Brent, 2002). There is also reduced sensitivity to the spacing of features in human faces (Le Grand *et al*., 2001; Robbins, Nishimura, Mondloch, Lewis & Maurer, 2010) but not monkey faces or houses (Robbins *et al*., 2010), a pattern which suggests that early visual exposure may be necessary for the later development of mechanisms used specifically for human face processing. As might be expected from these perceptual deficits, these patients also have trouble remembering faces, with lower accuracy in recognizing famous faces and poorer scores on the Cambridge Face Memory Test (de Heering & Maurer, 2014).

Neural mechanisms associated with face processing are also affected by this early visual deprivation. Patients show abnormal ERPs (larger P100 and N170 responses) during face-detection tasks even though behavioural performance is normal (Mondloch, Segalowitz, Lewis, Dywan, Le Grand *et al*., 2013). In addition, their face-selective regions show weaker specialization for faces over objects and altered connectivity with the extended face network (Grady, Mondloch, Lewis & Maurer, 2014). Moreover, this altered connectivity is linked to reduced sensitivity to feature spacing. Finally, responses of the face network are reduced during passive viewing of faces (Grady *et al*., 2014).

How might early visual deprivation from congenital cataracts affect the development of adaptive, norm-based face-coding mechanisms? Could the reduced responsiveness in face networks observed in cataract-reversal patients (Grady *et al*., 2014) be linked to reduced adaptability of face-coding mechanisms? One previous study has examined adaptive face-coding in cataract-reversal patients and found no face aftereffects at all (Robbins, Maurer, Hatry, Anzures & Mondloch, 2012). However, it used a complex orientation-contingent adapting paradigm, where participants viewed expanded upright faces together with contracted inverted faces (or vice versa), and did not measure direct (i.e. non-contingent) aftereffects for each distortion. The failure to find orientation-contingent aftereffects is, therefore, difficult to interpret. It could reflect a lack of aftereffects for either distortion. Alternatively, it could reflect similar aftereffects for each distortion that cancel out because face-coding mechanisms are poorly tuned to orientation in these patients. Moreover, (orientation-contingent) distortion aftereffects were calculated using attractiveness ratings, which is a very indirect way to measure perceived distortions. Therefore it is important to establish whether cataract-reversal patients do experience face aftereffects when tested with a simpler adaptation paradigm and whether those aftereffects may be reduced compared with those of controls.

Here we measured face identity aftereffects to index adaptive face-coding mechanisms (Leopold *et al*., 2001; Rhodes & Jeffery, 2006; Rhodes & Leopold, 2011) in cataract-reversal patients and typical controls. We used identity aftereffects, rather than the distortion aftereffects used by Robbins *et al*. (2012), because they are the face aftereffects that have been the most closely linked to adaptation of higher-level face coding mechanisms (Rhodes *et al*., 2009; Susilo, McKone & Edwards, 2010a). Therefore, failure to find identity aftereffects in patients, or a finding of reduced identity aftereffects, would indicate reduced adaptability of their face-coding mechanisms, and an important role for early visual experience in the normal development of those mechanisms.

We also asked whether early visual experience is important for developing norm-based coding of face identity. To address this question, we examined how face identity aftereffects vary with adaptor identity strength (Experiment 2). If coding is norm based, then aftereffects should increase with increasing adaptor identity strength, because more extreme adaptors will adapt their preferred populations more strongly than less extreme adaptors. Several studies have shown this pattern for identity-related aftereffects (Jeffery *et al*., 2013; Jeffery *et al*., 2011; McKone, Jeffery, Boeing, Clifford & Rhodes, 2014; Robbins, McKone & Edwards, 2007; Susilo, McKone & Edwards, 2010b). Failure to observe this pattern in cataract patients could indicate a fundamental disruption of norm-based coding of faces. For example, a decrease in aftereffects with increasing adaptor strength would indicate non-norm-based, multichannel coding (for details, see Jeffery *et al*., 2011; McKone *et al*., 2014). More generally, failure to find the normal pattern of increasing aftereffects with increasing adaptor strength would suggest that early visual experience is important for the development of norm-based face-coding mechanisms.

Experiment 1

In Experiment 1, we measured face identity aftereffects in adults and adolescents whose early visual experience was compromised by dense bilateral congenital cataracts that blocked all patterned input for the first few months of life. Because identity aftereffects with this paradigm are adult-like by age 4 (Jeffery *et al*., 2013), all patients were compared to adult controls. Reduced aftereffects in cataract patients would suggest that reduced early visual experience can affect the development of adaptive face-coding mechanisms.

Method

Participants

The patient group consisted of 12 individuals (8 male, Mean age = 20.8 years, range = 11–28 years) born with bilateral cataracts that prevented any patterned visual input until they were surgically removed and the eyes fitted with contact lenses during their first year of life. The duration of deprivation from birth until first contact lenses ranged from 34 to 294 days ($M = 129$). Acuity in the better eye on the day of testing ranged from 20/25 to 20/125 ($M = 20/50$). Table 1 lists clinical details for each patient. One additional patient was tested, but excluded, because no aftereffects could be calculated (due to poor curve fits). The control group consisted of 24 undergraduate students (12 male; Mean age = 19.3 years, range = 18–24 years) who participated for course credit. All had normal vision as indicated by 20/20 acuity on the Lighthouse chart and normal performance on the Titmus test of stereoacuity.

Stimuli

The stimuli were taken from a previous study of identity aftereffects and are shown in Figure 1 (Rhodes & Jeffery, 2006). Grey-scale images of two male faces (Dan and Jim) served as target identities to be learned. Test images consisted of these target identities at reduced identity strengths (0, 20, 40, 60, 80%). Adapting images were 80% antifaces (anti-Dan and anti-Jim), which have opposite characteristics from their matched target faces relative to an average male face created by morphing 20 adult Caucasian male faces (for details see Rhodes & Jeffery, 2006). For example, if Dan has a bigger-than-average forehead, then anti-Dan has a smaller-than-average forehead. Test and adapting faces were 7.6 cm × 7.8 cm on the screen (4.35° × 4.45° of visual angle when viewed from 100 cm).

Procedure

Participants viewed the stimuli on a 19.5″ Dell Trinitron monitor with OS 9.2.1 operating system from a distance of 100 cm. A chin rest was used to keep testing distance constant. Room lights were turned off to minimize distractions. Acuity was measured before the aftereffects task.

Following previous studies, the aftereffects task was presented as a game. The entire experiment was self-paced as participants initiated each trial by pressing the space bar when ready. During the first training phase, participants were shown the two faces with 100% identity strength, 'Dan' and 'Jim'. After 100% Dan and Jim were introduced to the participants on the screen side by side with their names shown underneath each face, each face was shown individually, without its label, five times for a total of 10 trials, and the participant was asked to report which face they had seen by pressing the 'x' key if the face was of Dan and the comma key if the face was of Jim. The keys were labelled with stickers reading 'Dan'

Table 1 *Cataract patient information for Experiment 1. Table shows the patients' visual acuity in the better eye on the day tested and days of deprivation prior to cataract surgery and optical correction during infancy. Any secondary complications are also shown. Patients with glaucoma were included only if the increased pressure was controlled and there was no sign of retinal damage, as indicated by the cup:disc ratio*

					Duration of deprivation (days)		
Initials	Gender	Age	Acuity in better eye (logMAR)	Better eye	Right eye	Left eye	Complications
AB	M	17	0	Right	106	106	Glaucoma
AC	M	27	0.4	Left	196	161	
AD	M	23	0.6	Left	97	97	Glaucoma
CB	F	23	0.1	Left	91	91	
CP	M	28	0.2	Left	187	187	
DO	M	11	0.3	Right	61	61	
IW	M	27	0.1	Right	181	294	
JF	M	18	0.3	Left	100	100	
MM	M	18	0.2	Equal	48	48	Glaucoma
NA	F	19	0.8	Right	134	134	Nystagmus
RT	F	21	0.2	Left	62	478	
VO	F	13	0.4	Equal	34	34	Glaucoma

and 'Jim', respectively. Faces were shown on the screen for an unlimited duration until a response was made. Following this first block, participants completed another block of 10 trials in which faces were shown for only 200 msec. This block of 10 trials was repeated until participants answered all 10 trials correctly. Auditory feedback was given on each trial. Patients completed the first training phase in an average of 1.3 blocks (range 1–3 blocks) and all controls did so in one block.

In the second training phase, the weaker identity strengths (40% and 60%) of Dan and Jim were introduced as 'the brothers' of Dan and Jim. Dan and his brother were referred to as 'Team Dan' and Jim and his brothers were referred to as 'Team Jim'. Participants were asked to press the button for 'Dan' whenever they saw a face from Team Dan, and to press the button for 'Jim' whenever they saw a face from Team Jim. In the first block, faces were shown individually (twice per face) for an unlimited duration until a response was made. For subsequent blocks, faces were shown for 200 msec. Participants were required to repeat the block until they answered 4/5 of the final trials correctly that showed the 40% or 60% identity faces. Auditory feedback was given on each trial. Patients completed the second training phase in an average of 1.2 blocks (range 1–2 blocks) and controls did so in an average of 1.8 blocks (range 1–2 blocks).

The third phase tested recognition in the absence of adaptation. During this phase, 0, 20, 40, 60, 80% Dan and Jim faces were shown individually for 200 msec. Participants were asked to indicate whether each face belonged to 'Team Dan' or 'Team Jim' by a key press. Each face was shown six times so that we could measure how well participants had learned the Dan and Jim identities and how well they could recognize them at lower identity strengths. No feedback was given.

In the fourth phase, adaptation, the task was explained as a game in which Teams Dan and Jim were trying to 'catch the robbers'. An adapting face (anti-Dan or anti-Jim) was shown for 5 seconds before the test face was shown for 200 msec. Participants were instructed to look at the adapting face for the whole duration. The experimenter was seated beside the participant and all participants appeared to follow this instruction well. The adapting face was described as the robber's face, and the test face as the face of the person 'who caught the robber'. Participants were asked to indicate whether the person who caught the robber belonged to Team Dan or Team Jim. Each test face (0, 20, 40, 60, 80% Dan and Jim faces) followed each adapting face six times, for a total of 60 trials. Auditory feedback was not given. Breaks were offered after every 10 trials and taken as needed. Each session lasted 45–60 minutes.

Results and discussion

After training, participants could identify the two target faces (80% identity strength versions) (phase 3) with perfect scores for all but one participant in each group. To further characterize identification performance in the absence of adaptation, we fitted cumulative Gaussians to the proportion of 'Team Dan' responses for each participant, plotted as a function of test stimuli ranging from 80% Jim to 80% Dan. Function fits were excellent, with high R^2 values for both groups (controls: $M = .97$, $SD = .03$; patients: $M = .96$, $SD = .04$). The *SD*s of the fitted functions serve as a measure of precision, with smaller *SD*s indicating better discrimination of the two identities. There was no significant difference between the groups in identification precision, $t(34) = .06$, $p = .95$ (controls: $M = .21$, $SD = .10$; patients: $M = .20$, $SD = .19$). Nor was there any significant difference in PSEs (i.e. the point at which Dan and Jim responses are equally likely), which measure response bias, $t(34) = 0.39$, $p = .70$ (controls: $M = .05$, $SD = .13$; patients: $M = .02$ $SD = .22$). Therefore, after training, the groups did not differ in how well they discriminated the two target identities in the absence of adaptation. This result likely reflects the simple nature of the discrimination required (between two identities) and the extensive training given.

To quantify adaptation, we fitted a cumulative Gaussian function to the proportion of 'Team Dan' responses plotted as a function of test stimuli ranging from 80% Jim to 80% Dan, for each adaptation condition, for each participant. Adaptation to antiDan should bias perception to Dan and increase the proportion of 'Team Dan' responses. Adaptation to antiJim should bias perception to Jim and decrease the proportion of 'Team Dan' responses. Therefore the adapt antiDan function should be shifted left of the adapt antiJim function. To index the curve positions we determined the point of subjective equality (PSE) (the mean of the cumulative Gaussian, where responses are 50% 'Team Dan' responses), for each function (Figure 2). Following previous studies, we defined the size of the aftereffect as the difference in PSEs for these two adapting conditions (PSE after adapting to antiJim minus PSE after adapting to antiDan) (e.g. Pellicano, Jeffery, Burr & Rhodes, 2007). Again curve fits were excellent for both groups (controls: $M = .97$, $SD = .04$; patients: $M = .95$, $SD = .08$).

Patients' aftereffects were significantly greater than zero, $t(11) = 4.74$, $p < .001$. Thus, we demonstrate for the first time that cataract-reversal patients show face aftereffects and, therefore, that their face-coding mechanisms are adaptable by experience. Importantly, however, their aftereffects were significantly reduced compared with those of control participants, $t(34) = 2.20$, $p = .035$,

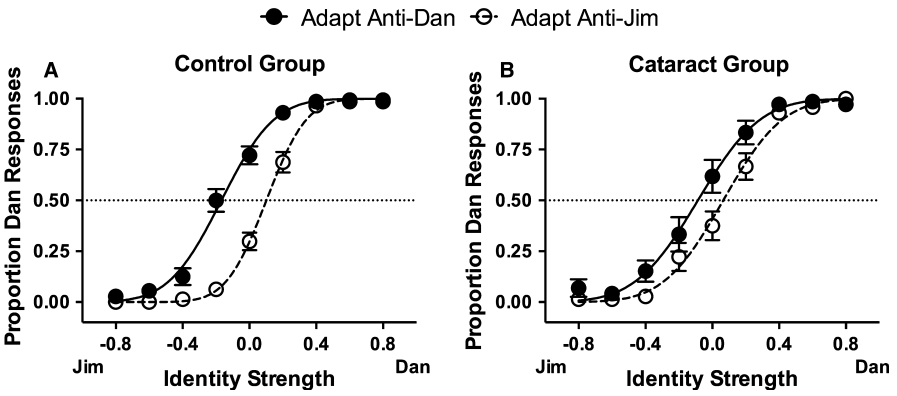

Figure 2 *Proportion of 'Dan' responses as a function of test face identity strength for each adapting condition for (A) control participants and (B) cataract-reversal patients in Experiment 1. Error bars show one standard error either side of the mean.*

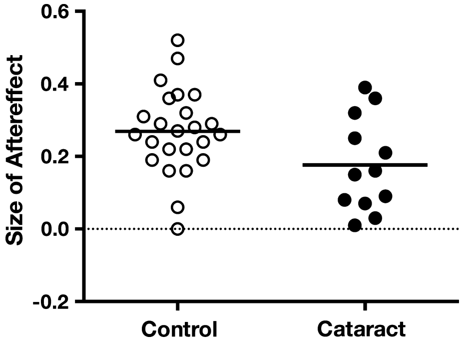

Figure 3 *Size of identity aftereffects for control participants and cataract-reversal patients in Experiment 1. Individual participant scores are shown. Horizontal bars indicate group means. SEM bars are shown. Aftereffects are measured as the difference (in identity strength) between PSEs for 'Dan' response curves after anti-Dan and anti-Jim adaptation (see Figure 2).*

Cohen's $d = 0.764$ (Figure 3). This result suggests that early visual experience is important for the normal development of adaptive face-coding mechanisms.

The size of the aftereffects correlated strongly with acuity in the better eye (in logMAR, high values reflect poor vision), $r = -0.683$, $p = .007$ (one-tailed), $N = 12$ (Figure 4). This finding raises the possibility that poor acuity explains the reduced aftereffects in the patient group, which we will consider further in the General Discussion. There was no significant difference in size of aftereffects for patients with and without additional visual complications (glaucoma, nystagmus), $t(10) = 0.95$, $p = .363$.

There was no correlation between the size of the aftereffect and duration of deprivation in the eye with better acuity, whether acuity was controlled, $r = -0.110$, $p = .374$ (one-tailed), $N = 12$, or not, $r = -0.009$, $p = .489$ (one-tailed), $N = 12$.

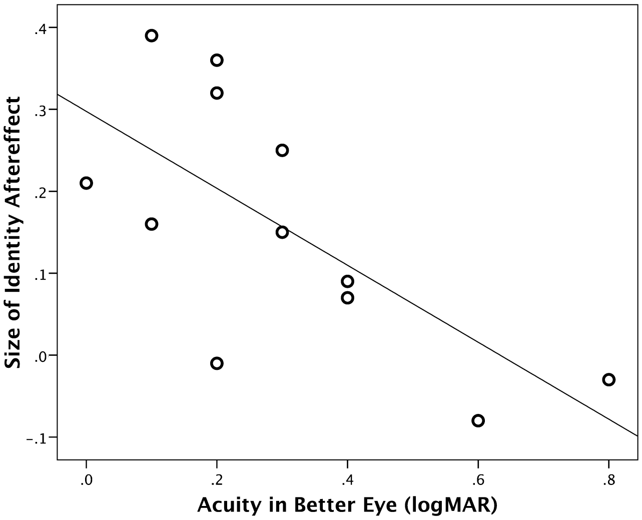

Figure 4 *Scatterplot with best-fitting regression line illustrating the relationship between size of identity aftereffects and acuity (logMAR) in the better eye. Larger logMAR values indicate poorer acuity. The best fitting regression line is shown.*

The groups were matched on mean age (patient $M = 20.8$ years; control $M = 19.3$ years, $t(34) = 1.23$, $p = .24$, unequal variances t-test), although the range was greater in the patient group (13–28 years) than the control group (18–24 years). However, this difference cannot explain reduced aftereffects in the patient group, because identity aftereffects are adult-like well before the youngest age tested here (Jeffery *et al.*, 2013; Nishimura, Maurer, Jeffery, Pellicano & Rhodes, 2008) and remain stable during early adulthood (17–29) (Rhodes, Pond, Burton, Kloth, Jeffery *et al.*, 2015). Furthermore, age did not correlate with the size of aftereffects in either the patient group, $r = 0.004$, $p = .990$, $N = 12$, or the control group, $r = -.27$, $p = .20$, $N = 24$.

Experiment 2

Experiment 1 showed that cataract-reversal patients had smaller face identity aftereffects than typical adults. This finding suggests that early visual deprivation may have lasting effects on the adaptability of face-coding mechanisms. In Experiment 2, we investigated whether there was any more fundamental disruption of those mechanisms. In typical adults and children identity-related aftereffects increase with increasing adaptor strength (distance from the average), consistent with norm-based coding of identity (Jeffery *et al.*, 2013; Jeffery *et al.*, 2011; McKone *et al.*, 2014; Rhodes, Ewing, Jeffery, Avard & Taylor, 2014a; Robbins *et al.*, 2007; Susilo *et al.*, 2010b). Here we asked whether patients would also show this pattern. We measured the change in perceived identity of the average face rather than full psychometric functions (so that the testing session did not become too long). This shorter procedure has been used successfully to measure identity aftereffects in special populations (Rhodes *et al.*, 2014a; Walsh, Maurer, Vida, Rhodes, Jeffery *et al.*, 2015). We also included test faces with 80% identity strength (easy trials) to help maintain motivation and to check that participants remembered the target identities. Importantly, we introduced a size change between adapting and test faces to minimize the contribution of lower-level retinotopic adaptation.

Method

Participants

The patient group consisted of 14 patients (8 male; mean age 19.9, *SD* = 5.2, range 13–31 years) born with bilateral congenital cataracts. The duration of deprivation (in the better eye) from birth until the infant first received compensatory contact lenses after the surgery to remove the cataracts ranged from 28 to 294 days (*M* = 119.4, *SD* = 73.6). Acuity in the better eye on the day of testing ranged from 0.1 to 0.8 logMAR (*M* = 0.4, *SD* = 0.2, range = 0.1 to 0.8). Five patients had participated in Experiment 1, always at least 1 year earlier (range 1–5 years). Table 2 lists clinical details for each patient. The control group consisted of 20 adults (10 M; age 18–27, *M* = 19 years) who participated for course credit. All met the same visual screening criteria as in Experiment 1. There was no significant age difference between the patients and controls, $t(16.31) = 0.37$, $p = .713$ (equal variances not assumed, Levene's test for equality of variances $F = 5.88$, $p = .021$). One additional patient was tested, but excluded due to poor identification of target identities (80% identity strength) in the adaptation task (*M* = 40% correct, chance = 50%).

Stimuli

The face stimuli were taken from previous studies of the identity aftereffect and have been described in detail previously (Walsh *et al.*, 2015). Briefly, there were two male target identities ('Ted' and 'Rob') (different from the identities used in Experiment 1). The adapting faces were 40% and 80% antifaces of these target identities. The test faces were an average male face, used to measure the aftereffect, and 80% identity strength versions of the target identities, used to provide easy trials to maintain motivation. The images were all grey-scale and a grey mask matching the background surrounded the external contour of the face to hide the hair. Adapting anti-faces

Table 2 *Cataract patient information for Experiment 2. Table shows the patients' visual acuity in the better eye on the day tested and days of deprivation prior to cataract surgery and optical correction during infancy. Secondary complications are also shown. Glaucoma was well controlled with no evidence of retinal damage*

					Duration of deprivation (days)		
Initials	Sex	Age	Acuity in better eye (logMAR)	Better eye	Right eye	Left eye	Complications
CB	F	28	0.2	Right	91	91	
IW	M	31	0.3	Left	181	294	
JF	M	21	0.2	Left	100	100	
MM	M	19	0.1	Left	48	48	Glaucoma
NA	F	20	0.6	Left	134	134	Nystagmus
DI	M	20	0.8	Left	139	139	Strabismus; glaucoma
Jsu	F	20	0.2	Right	152	152	Strabismus; glaucoma
JS	F	17	0.2	Left	92	92	Strabismus; glaucoma
WS	M	16	0.4	Left	65	65	Glaucoma
TA	F	13	0.3	Left	50	50	
ZC	M	25	0.7	Right	142	142	Nystagmus; glaucoma
BB	M	14	0.6	Left	28	28	
JB	F	14	0.4	Right	98	98	Strabismus
CR	M	20	0.1	Right	91	91	Glaucoma

were 6.4 cm by 6.4 cm and subtended a visual angle of 7° when viewed from 52 cm. The test faces were 5.2 cm high by 4.8 cm wide or 5.7° by 5.3° from the same viewing distance.

Procedure

Participants viewed the stimuli on a 15″ MacBook Pro laptop with OSX operating system from a distance of 52 cm. The room lights were turned off during testing. Participants keyed in their responses by pressing the 'x' key for Ted and the '.' key for Rob. These keys were labelled with stickers saying T or R.

The experiment consisted of three phases, presented in the context of a game. In the first training phase, the faces of 'Ted' and 'Rob' at 100% identity strength were shown side by side and introduced as police captains who specialize in catching Robbers. Once participants indicated they had sufficient time to learn the faces, they were given six trials with the faces one at a time and asked to identify them by pushing the appropriate key and then use the space bar to advance to the next trial. They were required to be correct on all six trials, three with each identity, presented in random order. If not, the 6 trials were repeated. All participants met this criterion on the first run. Next, participants were given 12 trials with the 100% identity strength faces presented for 400 msec and were required to be correct on 10/12 trials. One patient (DI) required two runs of this phase to meet this requirement; all others achieved it on the first run. Auditory feedback was given throughout this first training phase.

In the second training phase, the weaker identity strengths (40% and 60%) of Ted and Rob were introduced as 'brothers' serving under the captains as 'Team Rob' or 'Team Ted'. Participants were presented with one team (40%, 60%, 100%) until they felt they could identify it and then the other team. In the first block, faces with these three levels of identity strength were shown individually for an unlimited duration until the participant pushed a key to identify the team it belonged to. Participants were required to be correct on 8 out of 12 trials. If they were not, the block was repeated. For subsequent blocks, faces were shown for 400 msec. Participants were required to repeat the block if they made 4 or more errors in 12 trials. Both groups met the criterion for this part of the training on the first try. Auditory feedback was given on each trial of the second training phase. Trial duration was increased from the 200 msec used in Experiment 1 because decisions were expected to be harder in the trials of Experiment 2 following adaptation with a weaker (40%) anti-face.

In the third phase, adaptation, participants were shown the anti-faces, which were described as 'robbers' and instructed to identify the test face that followed as belonging to 'Team Rob' or 'Team 'Ted', as this was the team that caught the robber. An adapting face (anti-Ted or anti-Rob) was shown for 5 seconds, then following an interstimulus interval of 150 msec, the test face appeared for 400 msec. No feedback was given. The next adapting face appeared as soon as the participant keyed in a response and pressed the space bar. Participants were instructed to pay close attention to both the adapting and test faces. On the 120 adaptation trials, the adapting face was either the 40% (near) or 80% (far) face of anti-Ted or anti-Rob. The test face was either the average face (80 trials) or an 80% identity strength face of Ted or Rob (40 trials).[1] All participants received the same pseudo-random order, which was constrained by the requirement that no more than two adapting faces could be of the same identity, to avoid cumulative adaptation. The trials were divided into blocks of 24 trials each, with two 'refresher' trials with 80% Ted and Rob at the beginning of each block presented for 400 msec. Participants were required to identify these two faces correctly before proceeding to the next test block and were given auditory feedback only on these two reminder trials. Breaks were offered between blocks as needed. Together, the three phases of the experiment took about 30 minutes.

Results and discussion

The 80% identity strength test faces were identified very well, indicating that participants remembered the identities during the adaptation task. Accuracy was very high for both the control group (M = .97, SD = .02, range = .90–.98) and the patient group (M = .94, SD = .04, range = .85–.98), with controls performing significantly better than patients, $t(16.61) = 3.10$, $p = .007$ (equal variances not assumed, Levene's test for equality of variances, $F = 13.55$, $p = .001$).

We calculated the size of the aftereffect as the proportion of 'Ted' responses after adapting to anti-Ted (which should increase 'Ted' responses) minus the proportion of 'Ted' responses after adapting to anti-Rob (which should increase 'Rob' responses and thus reduce 'Ted' responses). The mean aftereffect in each condition for each group is shown in Figure 5.

We conducted a two-way repeated measures ANOVA on the size of the aftereffects, with group (patient, control) as a between-participants factor and adaptor

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[1] Because of a coding error, one trial in block 5 with 80% Ted as the test face was omitted.

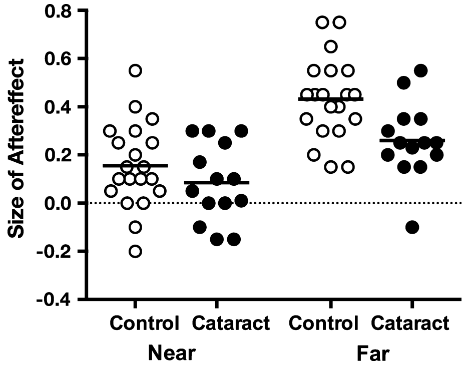

Figure 5 *Size of identity aftereffects for control participants and cataract-reversal patients for near (40%) and far (80%) adaptors in Experiment 2. Individual participant scores are shown. Horizontal bars indicate group means. SEM bars are shown. Aftereffects are measured as the proportion of 'Ted' responses after adapting to anti-Ted (which should increase 'Ted' responses) minus the proportion of 'Ted' responses after adapted to anti-Rob (which should increase 'Rob' responses and thus reduce 'Ted' responses).*

strength (near [40%], far [80%]) as a repeated measures factor. There was a significant main effect of group, $F(1,32) = 6.12$, $p = .019$, $\eta_p^2 = .161$, with smaller aftereffects for the patient ($M = .17$, $SD = .04$) than for the control ($M = .29$, $SD = .03$) group. This finding replicates the results of Experiment 1, under conditions that minimize the contribution of lower-level adaptation (by using adapting and test faces of different sizes). It therefore strengthens the evidence for reduced adaptability of higher-level face coding mechanisms in cataract-reversal patients.

There was also a significant effect of adaptor strength, $F(1, 32) = 51.32$, $p < .0001$, $\eta_p^2 = .616$, with larger aftereffects for far ($M = .35$, $SD = .03$) than near ($M = .12$, $SD = .03$) adaptors. Importantly, there was no significant interaction between identity strength and group, $F(1, 32) = 2.63$, $p = .114$, $\eta_p^2 = .076$. Additional planned t-tests confirmed that aftereffects were significantly larger for far than near adaptors for the patient group, $t(13) = 3.29$, $p = .006$, as well as the control group, $t(19) = 7.38$, $p < .0001$. Thus, both groups showed a pattern consistent with norm-based coding of identity, so there was no evidence of any more fundamental disruption of adaptive face-coding mechanisms in the patient group.

We also conducted separate one-sample t-tests for each group and adaptor strength, to test whether the aftereffects were significantly greater than zero. For the control group, the aftereffects were significantly greater than zero for both far adaptors, $t(19) = 11.30$, $p < .0001$, and near adaptors, $t(19) = 3.94$, $p = .001$. For the patients, the aftereffects were significantly greater than zero for far adaptors, $t(13) = 6.17$, $p < .0001$, and marginally greater than zero for near adaptors, $t(13) = 1.95$, $p = .073$.

Importantly, the size of aftereffects did not correlate significantly with acuity (logMAR) (in the better eye) for either near adaptors, $r = -.08$, $p = .39$ (one-tailed), $N = 14$, or far adaptors, $r = -.224$, $p = .22$ (one-tailed), $N = 14$ (Figure 6). Indeed, for far adaptors, where floor effects were not a problem, the two patients with best acuity had aftereffects (.25) that fell below the lower bound of the 95% confidence interval for control participants (.357). Therefore, unlike in Experiment 1, the reduced aftereffects cannot be attributed to poor acuity.

The size of patients' aftereffects was not related to other visual problems (present in 9 of the 14 patients – see Table 2), with no significant difference between patients with and without visual problems for either near aftereffects, $t(12) = 1.23$, $p = .244$, or far aftereffects, $t(12) = 1.50$, $p = .160$. These effects were even smaller when we removed one patient with visual problems who failed to show any aftereffects at all (perhaps due to visual problems), $ts < 1.26$, $ps > .235$. We note that excluding this participant did not change the results of the main ANOVA described above, which still yielded significant effects of group, $F(1, 31) = 4.45$, $p = .043$, $\eta_p^2 = .125$, and adaptor strength, $F(1, 31) = 52.06$, $p < .0001$, $\eta_p^2 = .627$, but no interaction, $F(1, 31) = 1.90$, $p = .178$, $\eta_p^2 = .058$. Overall, therefore, we have no evidence that reduced aftereffects in the patients are due solely to their visual problems.

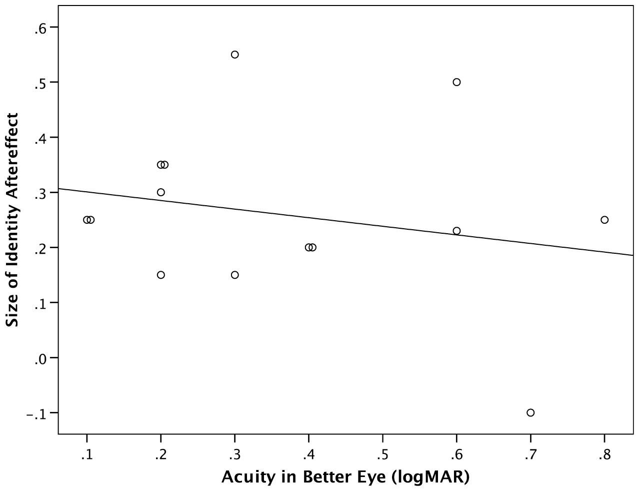

Figure 6 *Scatterplot with best-fitting regression line, illustrating the relationship between the size of identity aftereffects for far adaptors and acuity in the better eye (logMAR) in Experiment 2.*

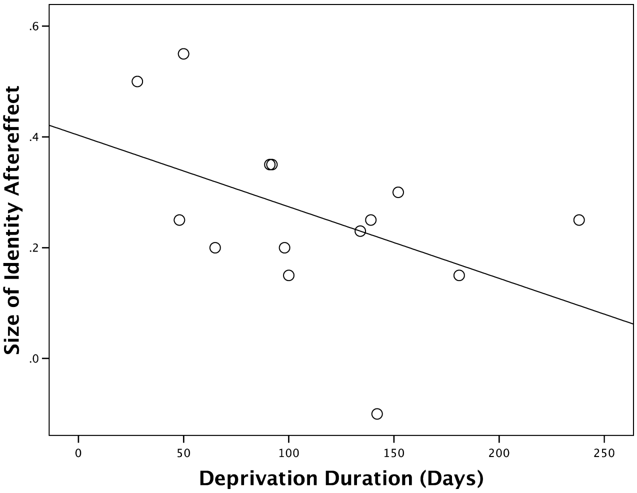

Figure 7 *Scatterplot with best-fitting regression line, illustrating the relationship between the size of identity aftereffects for far adaptors and the duration of visual deprivation during infancy in the eye with better acuity in Experiment 2.*

There was a moderate negative correlation between the size of aftereffects for far adaptors and duration of deprivation in the eye with better acuity, $r = -.495$, $p = .036$ (one-tailed), $N = 14$. This correlation remained significant when acuity in the better eye was controlled, $r = -.485$ $p = .046$ (one-tailed), $N = 14$. Thus, longer periods of deprivation were associated with smaller aftereffects (Figure 7). Aftereffects for near adaptors, which were small and contaminated by floor effects, did not correlate with duration of deprivation in the better eye, whether acuity was controlled, $r = .066$, $p = .415$ (one-tailed), $N = 14$, or not, $r = .056$, $p = .424$ (one-tailed), $N = 14$.

General discussion

Face identity aftereffects were reduced in cataract-reversal patients, indicating reduced adaptation to identity-related information in faces. The aftereffects were reduced when measured using full psychometric functions (Experiment 1) and when measured as changes in perceived identity of the average face (Experiment 2), both well-established methods. Moreover, longer periods of deprivation in the first year of life were associated with smaller aftereffects. These results suggest that early visual experience is important for the normal development of adaptive face-coding mechanisms.

We found no evidence of more fundamental disruption of adaptive face-coding mechanisms in the cataract-reversal patients. Their face identity aftereffects increased with increasing adaptor strength, like those of controls, suggesting intact norm-based coding of identity. Thus experience with faces in the first months of life may not be necessary to develop norm-based face-coding mechanisms, although it may be critical for efficient ongoing calibration of those mechanisms by our diet of faces.

We have attributed reduced adaptability of face-coding mechanisms in cataract-reversal patients to their lack of early visual experience. But could it instead be due to ongoing visual atypicalities, such as poor acuity? In Experiment 1 patients with worse acuity had smaller aftereffects, consistent with this possibility. However, there was no link with acuity in Experiment 2 (despite greater power). Moreover, the two patients with the best acuity in that experiment still had aftereffects well below the lower bound of the 95% confidence interval for control participants. More generally, it is not clear that poor acuity would be expected to affect performance on our identification task. This is because poor acuity reduces sensitivity to high spatial frequencies, not to the middle spatial frequencies that are typically used to discriminate facial identity (Gao & Maurer, 2011) and to which sensitivity is intact in this patient cohort (Ellemberg *et al*., 1999). Therefore, it seems unlikely that poor acuity per se can explain reduced face adaptation in these patients. Nor was there any significant difference in the size of aftereffects for patients with and without visual problems (glaucoma, nystagmus, strabismus) in either experiment. Of course power was low for those comparisons, so caution is needed in interpreting these null effects. Overall, however, we suggest that reduced aftereffects in the patient group are unlikely to be entirely the result of ongoing visual problems.

We suggest instead that reduced identity aftereffects in cataract patients reflect reduced adaptability of higher-level face-coding mechanisms. This interpretation is based on evidence that identity aftereffects tap adaptation of higher-level, face-coding mechanisms in typical adults (Rhodes *et al*., 2009). It is also consistent with the reduced responsivity to faces observed in the face networks of cataract-reversal patients (Grady *et al*., 2014), because less activation means less opportunity for adaptation.

Although we interpret our results as evidence for reduced adaptability of face-coding mechanisms in cataract-reversal patients, it remains an open question whether this reduced adaptability is face-selective. Indeed, it may not be, because face-coding neural networks in such patients are themselves not very face-selective (Grady *et al*., 2014). Therefore, even if the aftereffects measured here tap the same face-coding networks in patients as they do in typical individuals, adaptation may not be face-selective simply because those networks respond strongly to non-face objects. Importantly, however, our conclusion that early visual experience is important for normal development of adaptive face-coding mechanisms does not hinge on whether or not the reduced adaptability seen here is selective for faces. Nor do any functional consequences of reduced identity adaptation, such as reduced face recognition ability (Rhodes *et al.*, 2014b).

Several higher-level face-processing deficits have been identified in cataract-reversal patients. These include poorer matching of faces across views, reduced sensitivity to feature spacing, and delayed onset of holistic coding (de Heering & Maurer, 2014). These deficits could all potentially contribute to their face recognition difficulties. The present results have identified a further perceptual deficit: reduced adaptability of norm-based face-coding mechanisms. We suggest that this deficit may also contribute to their face recognition difficulties, given the importance of efficient calibration of face-coding mechanisms by our diet of faces for face expertise (Rhodes & Leopold, 2011; Webster & MacLeod, 2011).

Reduced adaptability of face-coding mechanisms is also seen in cognitively able children with autism (Ewing, Leach, Pellicano, Jeffery & Rhodes, 2013a; Ewing, Pellicano & Rhodes, 2013b; Pellicano *et al.*, 2007; Pellicano, Rhodes & Calder, 2013; Rhodes *et al.*, 2014a). Autism is a developmental disorder characterized by reduced social interest (Chevallier, Kohls, Troiani, Brodkin & Schultz, 2012; Dawson, Webb & McPartland, 2005; Grelotti, Gauthier & Schultz, 2002; Schultz, 2005) that is apparent even within the first year of life. For example, infants later diagnosed with autism look less at other people at 1 year of age (Osterling & Dawson, 1994) and show a decline in attention to the eyes between 2 and 6 months of age (Jones & Klin, 2013). The present results raise the possibility that reduced visual experience with faces in the first year of life could contribute to reduced adaptability of later face-coding mechanisms in autism.

The present results raise some interesting questions for future research. One is whether the reduced adaptability seen here is selective for the coding of face identity. Does it extend to other aspects of face coding (e.g. expression, gaze)? Could it reflect a more pervasive problem in calibrating perceptual coding mechanisms to experience? To the extent that adaptability plays a functional role in perception, we suggest that it may be reduced for any attributes whose perception is impaired. Future studies measuring aftereffects for a range of visual attributes will be needed to answer these questions. Another interesting question is whether it is the loss of patterned visual input to the *right* hemisphere that produces the deficits seen here, as found for other face processing deficits (Le Grand, Mondloch, Maurer & Brent, 2003). Studies with unilateral congenital cataract patients should be able to answer this question.

Our results add to the evidence that early experience plays an important role in the development of face expertise (for a recent review, see Maurer & Werker, 2014). Adults who suffered visual deprivation in the first few months of life because of congenital cataracts experience a range of face processing problems, despite early removal of the cataracts. Here we found that identity-related face adaptation is also reduced in these patients. We conclude that early exposure to faces is important in setting up the neural architecture of adaptive coding mechanisms that support mature face recognition ability.

Acknowledgements

This research was supported by the Australian Research Council (ARC) Centre of Excellence in Cognition and its Disorders (CE110001021), an ARC Professorial Fellowship to Rhodes (DP0877379), an ARC Discovery Outstanding Researcher Award to Rhodes (DP130102300), a (Canadian) Natural Sciences and Engineering Council grant to Maurer, and a James S. McDonnell collaborative activity grant to Maurer. We thank Sally Stafford for assistance with data processing and analysis for Experiment 2. Ethical clearance was granted by the Ethics Boards of McMaster University and the Hospital for Sick Children.

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Received: 19 May 2015
Accepted: 23 October 2015