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PAPER

Effects of normal and abnormal visual experience on the development of opposing aftereffects for upright and inverted faces

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Abstract

We used opposing figural aftereffects to investigate whether there are at least partially separable representations of upright and inverted faces in patients who missed early visual experience because of bilateral congenital cataracts (mean age at test 19.5 years). Visually normal adults and 10-year-olds were tested for comparison. Adults showed the expected opposing aftereffects for upright and inverted faces. Ten-year-olds showed an adultlike aftereffect for upright faces but, unlike the adult group, no aftereffect for inverted faces. Patients failed to show an aftereffect for either upright or inverted faces. Overall, the results suggest that early visual input is necessary for the later development of (at least partially) separable representations of upright and inverted faces, a developmental process that takes many years to reach an adult-like refinement.

Introduction

Adults are experts at face processing: they can recognize the identity of thousands of faces despite changes in age, viewpoint, expression, and lighting, while at the same time decoding direction of eye-gaze and emotional expression. Adults also differentiate faces into different categories, such as male/female, old/young, own/other race, human/monkey and upright/upside-down. The separability of such categories has been revealed by contingent or opposing aftereffects. In a simple aftereffect, adaptation to a distorted face (e.g. compressed or eyes moved up the head) leads to a shift in perception in the opposite direction, such that an unaltered face now appears distorted in the other direction (e.g. expanded or eyes moved down), and the face that now looks most normal or attractive is actually slightly distorted in the same direction as the adaptor (Rhodes, Jeffery, Watson, Clifford & Nakayama, 2003; Robbins, McKone & Edwards, 2007; Webster & MacLin, 1999). In contingent or opposing aftereffects, adaptation occurs simultaneously in opposite directions for different face categories at the same time. For example, after adaptation to expanded upright faces and compressed inverted (upside-down) faces, adults judge slightly expanded upright faces to be more attractive than undistorted faces and judge slightly compressed inverted faces to be more attractive than undistorted faces (Rhodes, Jeffery, Watson, Jaquet, Winkler & Clifford, 2004). If categories were not processed at least somewhat separably, effects of adapting to simultaneous opposite distortions should cancel out, leaving no aftereffect or simply increasing the range of faces seen as normal. Opposing aftereffects have been induced in adults for faces of different races (Jaquet, Rhodes & Hayward, 2007; Little, DeBruine, Jones & Waitt, 2008), species (Little *et al*., 2008), ages (Little *et al*., 2008; Schweinberger, Zäske, Walther, Golle, Kovács & Wiese, 2010) and sexes (Jaquet *et al*., 2007; Little, DeBruine & Jones, 2005, Little *et al*., 2008; Schweinberger *et al*., 2010; Watson & Clifford, 2006). No such opposing aftereffects can be induced by categories that are as physically distinct but not socially meaningful, such as female and hyperfemale (Bestelmeyer, Jones, DeBruine, Little, Perrett, Schneider, Welling & Conway, 2008) and Chinese and hyperChinese for Caucasian adults (Jaquet *et al*., 2007; see also Little, DeBruine & Jones, 2011) or for faces that belong to distinct social categories but that do not differ in physiognomy (Short & Mondloch, 2010). Thus, separable coding appears to occur only for categories that have some useful basis in experience.

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In this study, we investigated whether early visual experience is necessary to develop normal separable categories for upright and inverted faces. Specifically, we tested for opposing aftereffects between upright and inverted faces in patients who were born with dense bilateral cataracts that were removed during infancy and who were at least 12 years old at the time of the study. For comparison, we tested visually normal adults and 10-year-olds.

Relatively little is known about the development of separable face categories. During infancy, children begin to differentiate among face categories. For example, by 3 months of age, the event-related potentials evoked by faces differ for human and monkey faces (Halit, de Haan & Johnson, 2003) and, by 6 months, for upright and inverted faces (de Haan, Pascalis & Johnson, 2002). Infants also prefer own-race to other-race faces from 3 months of age (e.g. Kelly, Quinn, Slater, Lee, Gibson, Smith, Ge & Pascalis, 2005) and Caucasian 9-month-olds show an asymmetrical pop-out effect in that they look longer at a display containing a single Asian face among Caucasian distracters than at a display containing a single Caucasian face among Asian distracters (Hayden, Bhatt, Zieber & Kangas, 2009). By 5 years of age, Caucasian children show opposing aftereffects for Caucasian versus Chinese faces, but these seem to be mainly based on aftereffects for Caucasian faces without a simultaneous shift for Chinese faces (Short, Hatry & Mondloch, 2011).

In the current study, we examined the role of early visual experience in the development of separable categories for upright and inverted faces. Specifically, patients, adults, and children rated attractiveness before and after being simultaneously adapted to compressed upright faces and expanded inverted faces. We used the same task for all three groups so that we could compare performance directly without changes to stimuli or procedure (cf. Jeffery, McKone, Haynes, Firth, Pellicano & Rhodes, 2010). The method was based on that previously used for testing aftereffects in visually normal 5-year-olds (Short *et al.*, 2011), 8-year-olds (Anzures, Mondloch & Lackner, 2009), and adults (Anzures *et al.*, 2009; Short *et al.*, 2011). Although adults are often asked to rate facial normality in studies investigating aftereffects, we opted to ask participants to rate the attractiveness of faces pre- and post-adaptation. Aftereffects based on adults' judgments of facial attractiveness parallel those based on their judgments of normality, suggesting that the same underlying representation is accessed (Rhodes *et al.*, 2003), but pilot work indicated that children find the concept of attractiveness easier to understand than the concept of normality.

Although opposing aftereffects have been observed for a range of categories, we used upright and inverted faces because of the well-documented tuning of adults' processing of faces to upright faces (e.g. Yin, 1969; Young, Hellawell & Hay, 1987) and because all groups would have a similar low level of experience with inverted faces. To offset any own-age advantages that might be stronger in adults, we used faces that would be relatively unfamiliar to all groups, namely the faces of 4-year-olds (cf. Anzures *et al.*, 2009). Ten-year-olds were tested as a second comparison group, both because little is known about opposing aftereffects at this age and because this was slightly younger than our youngest patients (aged 12). If patients were worse than adults only because of maturational changes (rather than their abnormal visual experience), then they should still be better than 10-year-olds.

Previous studies of our patient cohort indicate that some aspects of face processing develop normally despite early visual deprivation: discrimination of facial identity based on differences in the shape of the external contour (e.g. jaw shape; Le Grand, Mondloch, Maurer & Brent, 2001, 2003) or the shape of the internal features (e.g. shape of the eyes; Le Grand *et al.*, 2001, 2003; Mondloch, Robbins & Maurer, 2010). However, early visual deprivation prevents the normal later development of holistic face processing (Le Grand, Mondloch, Maurer & Brent, 2004), discrimination of facial identity based on feature spacing (e.g. the distance between the eyes; Le Grand *et al.*, 2001, 2003), and recognition of facial identity despite a change in point of view (Geldart, Mondloch, Maurer, de Schonen & Brent, 2002). The deficit in feature spacing is specific to the upright human face category for which normal adults have especially acute sensitivity: it does not extend to inverted faces, monkey faces, or houses (Le Grand *et al.*, 2001, 2003; Robbins, Nishimura, Mondloch, Lewis & Maurer, 2010). As a result, patients have a smaller-than-normal inversion deficit for feature spacing in upright faces. Combined, the data indicate that patterned visual input is necessary to set up, or preserve, the neural architecture that will later be tuned by experience to upright human faces. The pattern of patients' deficits raises the possibility that they fail to develop well-differentiated processing for upright versus inverted human faces.

We can make predictions based on previous research about the expected effect of adaptation to compressed upright faces and expanded inverted faces. For adults, evidence of separable categories would be provided by global shifts in judgments of attractiveness (cf. Robbins *et al.*, 2007) in opposite directions for upright and inverted faces, replicating previous opposing aftereffects for upright and inverted faces shown for judgments of normality (Rhodes *et al.*, 2004). Because 8-year-olds have been shown to have separable coding of own- versus other-race faces (Short *et al.*, 2011), we expected that 10-year-olds would, like adults, provide evidence of separable categories for upright and inverted faces by shifting their judgments of the attractiveness of altered faces after adaptation in opposite directions such that compressed upright faces and expanded inverted faces would look more attractive. If patients do not have separable coding for upright and inverted faces, the aftereffects should largely cancel each other out and/or expand the range of faces seen as normal, yielding little post-adaptation shift for either category.

Method

Participants

The participants were 32 visually normal adults (half male; 17–26, mean = 18.7 years; all Caucasian), 22 visually normal 10-year-olds (15 male; age range = 9:9 to 10:3; all Caucasian) and 10 patients treated for bilateral congenital cataract (six males; 12–27 years at test, mean = 19.5 years, not significantly different from adult group in age, $t(40) = .57$, $p = .58$). Adults were undergraduate students at McMaster who participated for course credit. Ten-year-olds were recruited from a database of child participants at Brock University. Visually normal adults and children had far vision of at least 20/20-2 on a standard linear acuity chart, as well as showing worse vision with +3 diopter lens (to rule out farsightedness). They also had normal stereopsis as tested by the Titmus test. Patients treated for cataract were from a group who had been followed longitudinally, and participated as part of a larger testing battery. They were diagnosed with dense central cataracts in both eyes, on the first eye exam (before 6 months of age), that blocked all patterned vision with no sign of an earlier period of patterned visual input. The cataractous lenses were removed surgically and the eyes given a compensatory optical correction, usually contact lenses, at between 9 and 294 days of age (mean 116 days, median 98 days). Their acuity in their better eye on the day of test was between 20/25 and 20/160 (median = 20/32). Details for each patient can be found in Table 1. When necessary, during the test, patients wore an optical correction to focus their eyes at the testing distance of 60 cm.

Stimuli and design

The experiment consisted of three phases: pre-adaptation ratings, adaptation, and post-adaptation ratings, all presented in the context of a story about a surprise birthday party, modelled on Anzures *et al.* (2009). Participants were told that the birthday party took place in Topsy-Turvy land ‘where sometimes things are upside-down’, and every second adaptation slide was completely inverted (see Figure 1).

Pictures of 20 4-year-old children were used to create the stimuli for pre- and post-adaptation (five faces for each orientation for each phase). Within each set of five faces, one was undistorted, two were compressed (−60%, −40%), and two were expanded (+40%, +60%; see Figure 1). The set of faces to be rated pre- versus post-adaptation was counterbalanced across participants and all were approximately 20 cm × 19 cm (or 18.9° × 18° at the 60 cm viewing distance). The faces appeared on a computer monitor in front of the participant.

The faces in the adaptation phase of the experiment were of seven 4-year-olds who did not appear in pre- or post-adaptation phases. All were shown compressed (−60%) in the upright pictures and expanded (+60%) in the inverted pictures. A total of 10 pages, each with 1–7 faces, were shown in each orientation during the adaptation phase. Adaptor faces within the story ranged from 5 × 5 cm to 15 × 11 cm (or 4.8° × 4.8° to 14.3° × 10.5°); substantially smaller than the test faces. Distorted faces were all created using the spherize function in Photoshop.

Procedure

Each participant was tested binocularly. During the pre- and post-adaptation phases they were asked to rate the attractiveness of the faces using a 5-point scale illustrated with different sized cups or boxes. Prior to the task, participants were trained to use the scale by rating the

Table 1 *Details of the 10 patients treated for bilateral congenital cataract*

				Linear letter acuity[c]		Duration of deprivation (days)[d]	
Patient	Age at test (years)	Binocularity[a]	Stereoacuity (sec of arc)[b]	Right	Left	Right	Left
M1	12.2	Diplopia[e]	None	< 20/200	20/25	65	9
F1	13.6	Diplopia	None	20/125	20/32	92	92
F2	15.9	Not tested	Not tested	20/32	20/50	152	152
M2	18	Fuses	None	20/32	20/32	48	48
M3	18.5	Fuses	None	20/40	20/70	100	100
F3	19.4	Diplopia	None	20/60	20/63	134	134
F4	23.0	Diplopia	None	20/25	20/70	91	91
M4	23.0	Diplopia	400	20/80	20/125	97	97
M5	25	Diplopia	None	20/160	20/25	294	181
M6	27.5	Diplopia	140	20/50	20/63	161	196

[a] as measured by the Worth 4 Dot Test (measured within one year of testing).
[b] as measured by the Titmus test (measured within one year of testing).
[c] best corrected linear letter acuity on the day of testing.
[d] from birth until the fitting of a compensatory contact lens after surgical removal of the cataract.
[e] Diplopia refers to double-vision.

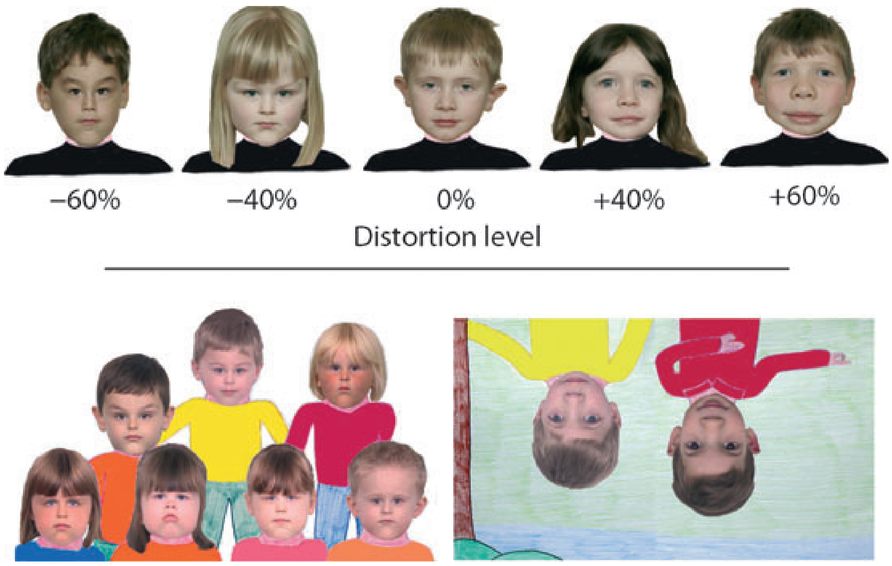

Figure 1 *Examples of pre-/post-adaptation faces at each level of distortion (−60%, −40%, 0%, +40%, +60%) are shown in the top panel. Two of the adapting pages, one in each orientation, are shown in the bottom panel. The upright adapting pages showed faces with a −60% (compressed) distortion, whereas inverted adapting pages showed faces with a +60% (expanded) distortion.*

attractiveness of three presents and three balloons that differed systematically in attractiveness (see Anzures *et al.*, 2009). Participants were then asked to rate the 10 pre-adaptation faces one at a time (one set of five different upright faces was shown intermixed with a second set of five different inverted faces) for how 'pretty or handsome they looked' (each face was introduced as a child coming to the party, who wanted to look his/her best). Participants were given as long as they needed to rate each face, with responses recorded by the experimenter. The story then continued into the adaptation phase, with participants reminded to continue looking at the screen throughout. The adaptation phase took approximately 4 mins to read (giving approximately 2 mins of adaptation in each orientation). The post-adaptation phase was also part of the story with 10 new people introduced (five upright intermixed with five inverted) and participants were again asked to rate each face. Top-up adaptation was given before each face to-be-rated by showing faces that had appeared in the adaptation phase in the orientation about to be tested. Thus, each participant rated 10 faces during pre-adaptation (five upright) and 10 different faces during post-adaptation; which set of faces was presented pre-adaptation was counterbalanced across subjects. In between, they were adapted to completely different faces of a smaller size. Story pages appeared on a colour monitor, while the experimenter read from a paper copy. The experimenter provided general encouragement but no specific feedback.

Results

Each participant provided one rating for each of the five distortion levels (−60%, −40%, 0%, +40% and +60%) for each orientation pre- and post-adaptation. The means for each group are shown in Figure 2. Overall, adults' ratings of upright versus inverted faces appear to have shifted in opposite directions post-adaptation and ratings of visually normal 10-year-olds appear to have shifted in the expected direction for upright faces, with no effect of distortion for inverted faces either pre- or post-adaptation. In contrast, patients' ratings of both upright and inverted faces failed to shift following adaptation; instead, there is some suggestion of the flattening of both curves after adaptation.

Pre-adaptation baseline

To see if groups differed before adaptation, we conducted a 3 × 2 × 5 mixed ANOVA with group (adult, 10-year-old, patients), orientation (upright/inverted) and distortion level as factors. There was a significant orientation by group by distortion interaction, $F(8, 244) = 2.72$, $p = .007$, partial $\eta^2 = .08$, as well as a group by distortion interaction, $F(8, 244) = 6.68$, $p < .001$, partial $\eta^2 = .18$, and main effects of orientation, $F(1, 61) = 93.70$, $p < .001$, partial $\eta^2 = .61$, distortion, $F(4, 244) = 31.18$, $p < .001$, partial $\eta^2 = .34$, and group, $F(2, 61) = 3.69$, $p = .031$, partial $\eta^2 = .11$. However, these results must be interpreted with caution because of the homogeneity of variance violation and unequal group sizes. Based on the interactions with group, and the problem of unequal group size, we conducted a 2 (orientation) × 5 (distortion level) ANOVA for each group.

For adults, there were significant main effects of orientation, $F(1, 31) = 103.45$, $p < .001$, partial $\eta^2 = .77$, and distortion, $F(4, 124) = 41.99$, $p < .001$, partial

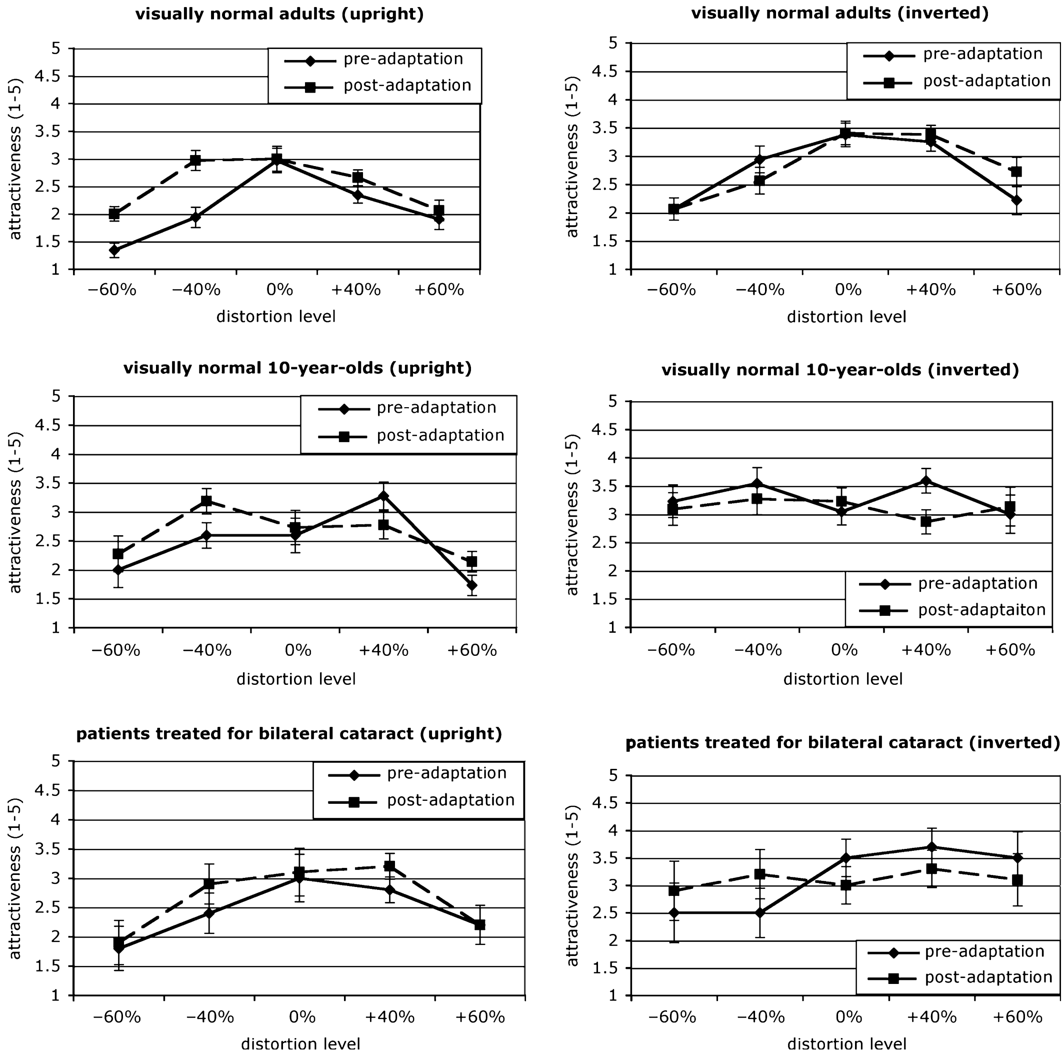

Figure 2 *Attractiveness ratings for each of the five distortion levels, for upright (left column) and inverted (right column) faces, for each of the three groups: visually normal adults (top row), visually normal 10-year-olds (middle row) and patients treated for bilateral congenital cataract (bottom row). Negative face distortions are for compressed faces, positive distortions are for expanded faces. During adaptation, upright faces were compressed (−60%) and inverted faces were expanded (+60%). Error bars show ± 1 SEM for the differences scores between pre- and post-adaptation ratings.*

η^2 = .58, but no interaction, Wilks' lambda = .79,[1] F(4, 28) = 1.89, p = .140, partial η^2 = .21. Thus, adults produced different ratings for upright and inverted faces (lower ratings for upright faces), but the shapes of the curves are similar. The main effect of distortion is because of significantly higher attractiveness ratings for less distorted faces, both for upright, Wilks' lambda = .087, F(4, 28) = 73.31, p < .001, partial η^2 = .91 and inverted faces, F(4, 124) = 17.93, p < .001, partial η^2 = .37.

For 10-year-olds, there were significant main effects of orientation, F(1, 21) = 27.72, p < .001, partial η^2 = .57, and distortion, F(4, 84) = 10.95, p < .001, partial η^2 = .34, and a significant interaction, Wilks' lambda = .42, F(4, 18) = 6.21, p = .003, partial η^2 = .58. Thus, 10-year-olds showed overall differences between upright and inverted ratings (upright slightly lower) and there were differences in the shape of the curves. There was a significant effect of distortion (higher ratings for less distorted faces), for upright, F(4, 84) = 11.99, p < .001, partial η^2 = .36, but not inverted faces, F(4, 84) = 2.13, p = .084, partial η^2 = .09.

For patients, there were again significant main effects of orientation, F(1, 9) = 23.71, p = .001, partial η^2 = .73, and distortion, F(4, 36) = 7.03, p < .001, partial η^2 = .44, but no interaction, F(4, 36) = 1.35, p = .27, partial η^2 = .13. Similar to the other groups, ratings for inverted faces were somewhat higher than for upright faces. Although ratings for inverted faces appear fairly flat, the effect of distortion was significant for both upright, F(4, 36) = 3.25, p = .023, partial η^2 = .27, and inverted faces, F(4, 36) = 4.88, p = .003, partial η^2 = .35.

Overall, it appears that there are some baseline differences between groups. These will be taken into

[1] Where sphericity is violated, Wilks' lambda is used.

account in our second analysis of adaptation. However, it should also be noted that there were no ceiling or floor effects for either orientation in any group, leaving room for post-adaptation shifts to be found.

Adaptation

We analysed the adaptation results in two ways. First, we compared the results of all groups, for both orientations, pre- and post-adaptation across all distortion levels (a $3 \times 2 \times 2 \times 5$ ANOVA). We then followed this up with $2 \times 2 \times 5$ ANOVAs for each group, such that opposing aftereffects would be manifested as three-way interactions between orientation, pre- and post-adaptation trials, and distortion level.

Second, we analysed the effects of adaptation by calculating change scores for each individual between their pre-adaptation and post-adaptation ratings. This set of analyses was performed to account for the baseline differences between groups and homogeneity of variance violations. To increase the sensitivity of the measurements from the small number of trials, we averaged each participant's ratings separately for the two compressed and for the two expanded faces for pre-adaptation ratings and then calculated the same averages for post-adaptation ratings. We omitted ratings of the undistorted faces because there was no sign of adaptation in the upright orientation for the undistorted faces for any of the groups. We then quantified the size of the aftereffect for each orientation for each participant by calculating change scores (a common practice in adaptation studies; e.g. Jeffery *et al.*, 2010; Robbins *et al.*, 2007). Specifically, we subtracted pre-adaptation ratings from post-adaptation ratings for compressed faces and for expanded faces, and then subtracted those two numbers from each other (difference for compressed minus difference for expanded). Because all upright faces were compressed during adaptation and all inverted faces were expanded, simultaneous aftereffects would be expected to yield positive change scores for upright faces and negative change scores for inverted faces. In addition to comparing these scores in an ANOVA with orientation and group as factors, we compared each group's mean change scores for each orientation to a chance value of zero. The individual scores and means are shown in Figure 3.

Analysis of pre- and post-adaptation raw scores

There were significant three-way interactions between group, pre-post and distortion level, $F(8, 244) = 2.45$, $p = .015$, partial $\eta^2 = .07$, and group, orientation and distortion, $F(8, 244) = 3.49$, $p = .005$, partial $\eta^2 = .10$, as well as two-way interactions between group and distortion, $F(8, 244) = 6.55$, $p < .001$, partial $\eta^2 = .18$, pre–post and distortion, $F(4, 244) = 3.41$, $p = .010$, partial $\eta^2 = .05$, pre–post and orientation, $F(1, 61) = 17.39$, $p < .001$, partial $\eta^2 = .22$, and orientation and distortion, $F(4, 244) = 3.22$, $p < .001$, partial $\eta^2 = .09$, and

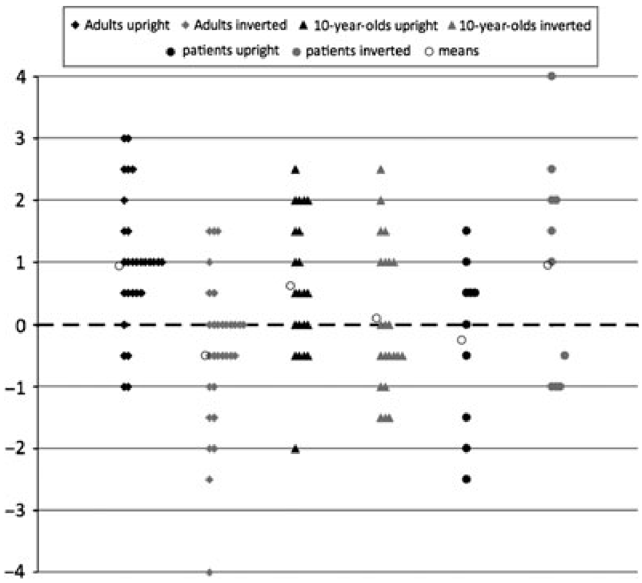

Figure 3 *Individual adaptation scores (change in compressed − change in expanded) for each individual in each of the three groups, upright and inverted. Tied scores are shown offset. Means for each group are shown as black unfilled circles. Aftereffects in the expected direction are shown by positive scores for upright faces and negative scores for inverted faces.*

main effects of orientation, $F(1, 61) = 66.73$, $p < .001$, partial $\eta^2 = .52$, and distortion, $F(4, 244) = 38.08$, $p < .001$, partial $\eta^2 = .38$, all other *p*s > .085. As for the baseline analysis, homogeneity of variance was violated, so caution is needed in interpreting the results. Given that there were again several relevant interactions with group, and problems with homogeneity for unequal groups, we conducted separate 2 (orientation) × 2 (pre–post) × 5 (distortion) ANOVAs for each group.

For visually normal adults, there was a significant three-way interaction, Wilks' lambda = .45, $F(4, 28) = 8.55$, $p < .001$, partial $\eta^2 = .55$, showing different effects of adaptation for the two orientations. There were also significant two-way interactions between pre–post and orientation, $F(1, 31) = 21.48$, $p < .001$, partial $\eta^2 = .41$, and orientation and distortion, $F(4, 124) = 2.59$, $p = .040$, partial $\eta^2 = .08$, and main effects of pre–post, $F(1, 31) = 11.18$, $p = .002$, partial $\eta^2 = .27$, orientation, $F(1, 31) = 59.62$, $p < .001$, partial $\eta^2 = .66$, and distortion, $F(4, 124) = 55.54$, $p < .001$, partial $\eta^2 = .64$. The pre–post by distortion interaction was not significant, $p = .55$.

For visually normal 10-year-olds, the expected three-way interaction between distortion level, pre–post, and orientation was not significant, $F(4, 84) < 1$, $p = .682$, partial $\eta^2 = .03$, but a significant interaction between pre–post and orientation nevertheless suggests some differences in adaptation between the two orientations, $F(1, 21) = 5.78$, $p = .025$, partial $\eta^2 = .22$. The remaining two-way interactions were also significant: pre–post by distortion, $F(4, 84) = 6.70$, $p < .001$, partial $\eta^2 = .24$, and orientation by distortion, Wilks' lambda = .38, $F(4, 18) = 7.35$, $p = .001$, partial $\eta^2 = .62$. There were also main effects of orientation, $F(1, 21) = 21.42$, $p < .001$, partial $\eta^2 = .51$, and distortion, $F(4, 84) = 8.71$, $p < .001$, partial $\eta^2 = .29$. The main effect of pre–post was not significant, $F(1, 21) < 1$, $p = .941$, partial $\eta^2 = .00$.

For patients treated for cataracts, only the orientation by distortion interaction, $F(4, 36) = 3.12$, $p = .027$, partial $\eta^2 = .26$, and main effects of orientation, $F(1, 9) = 16.25$, $p = .003$, partial $\eta^2 = .65$, and distortion, $F(4, 36) = 8.19$, $p < .001$, partial $\eta^2 = .48$ were significant, all other *p*s > .196, partial η^2s < .178. Thus, patients did not show the interactions of orientation with pre- versus post-adaptation that were shown by the other two groups.

Analysis of change scores

As noted above, because of the differences between groups in pre-adaptation baselines, we also conducted analysis on the change scores, which should have more power, take baseline differences into account, and remove the homogeneity of variance violation. A 3 (group) × 2 (orientation) ANOVA showed a significant group by orientation interaction, $F(1, 2) = 5.60$, $p = .006$, partial $\eta^2 = .16$, and no main effects, *p*s > .414. For adults, this effect was driven by adaptation to both upright, $M = 0.94$, $t(31) = 5.07$, $p < .001$, and inverted faces, $M = -0.50$, $t(31) = 2.35$, $p = .025$, in opposite directions. For 10-year-olds, this effect was driven only by adaptation to upright faces, $M = 0.61$, $t(21) = 2.56$, $p = .018$, with no change found for inverted, $M = 0.09$, $t(21) = 0.36$, $p = .72$. For patients, the mean difference scores were not significantly different from chance for either orientation (upright, $p = .569$ or inverted, $p = .121$) and the means were actually in the opposite direction from adults and 10-year-olds ($M = -0.25$ upright, $M = 0.95$ inverted).[2]

Overall, our two sets of analyses converge to suggest opposing aftereffects to upright and inverted faces in visually normal adults on this task. Results also suggest an aftereffect for upright faces in visually normal 10-year-olds, although this was not found to be significant for inverted faces. Patients treated for cataract show a different pattern from either visually normal adults or 10-year-olds, by failing to show aftereffects for upright or inverted faces.

Discussion

Adults and 10-year-olds showed the expected shift for upright faces, despite simultaneous adaptation in the opposite direction for the same faces inverted, replicating previous findings of aftereffects for upright faces in adults (e.g. Rhodes *et al.*, 2004; Robbins *et al.*, 2007; Watson & Clifford, 2003; Webster & Maclin, 1999) and children 5 to 8 years old (Anzures *et al.*, 2009; Jeffery *et al.*, 2010; Short *et al.*, 2011). Adults showed a simultaneous shift in the opposite direction for inverted faces, replicating previous findings of orientation-contingent aftereffects (Rhodes *et al.*, 2004; Watson & Clifford, 2006). However, for 10-year-olds, there was no evidence of any shift for inverted faces, a finding suggesting less separate processing for upright and inverted faces. Unlike the visually normal groups, patients treated for bilateral congenital cataract showed no systematic aftereffects for either upright or inverted faces. Combined, the results suggest that separable processing for upright and inverted faces requires early visual input to develop normally, a developmental process that continues past 10 years of age.

Opposing aftereffects in visually normal adults

The findings for adults are consistent with many previous studies showing contingent or opposing aftereffects for socially meaningful categories. In addition to upright and inverted faces, opposing aftereffects have been found for same- and other-race faces, male and female faces, infant and adult faces, and monkey and human faces (Bestelmeyer *et al.*, 2008; Jacquet *et al.*, 2007; Little *et al.*, 2005, 2008; Schweinberger *et al.*, 2010; Watson & Clifford, 2006). Such opposing aftereffects are mitigated or absent for categories that are as physically distinct but not socially meaningful (Bestelmeyer *et al.*, 2008; Jacquet *et al.*, 2007; see Rotshtein, Hensen, Treves, Driver & Dolan, 2005, for fMRI evidence at the level of the fusiform face area). The simultaneous opposing aftereffects indicate that, in adults, the neurons for coding upright/inverted, male/female, infant/adult, own/other-race, and monkey/human faces are at least partially non-overlapping, probably on a number of dimensions. Some overlap between the coding of face categories obviously still exists as can be seen by transfer between categories. For example, Schweinberger *et al.* (2010) showed transfer of age-specific adaptation across gender, but larger effects when the gender at adaptation and test was the same (see also Webster, Kaping, Mizokami & Duhamel, 2004). Overall then, in adults, different sub-categories of faces, including upright and inverted faces, are coded in partially separable systems.

Because size and identity differed between adapting and test faces, the opposing aftereffects reported here are not likely to have arisen at lower levels of cortical processing (e.g. V1) where coding is retinotopic (cf. Webster & MacLin, 1999; Yamashita, Hardy, De Valois & Webster, 2005). In previous studies, adaptation to inverted faces has been found to transfer weakly to upright faces, unlike the robust transfer of aftereffects from upright to inverted faces (Robbins *et al.*, 2007; Watson & Clifford,

[2] There was also no sign of adaptation when the scores of the two patients tested before age 16 were excluded: upright $M = -0.06$, $p = .888$; inverted $M = 0.81$, $p = .276$. There was also no correlation between the size of the effect and age at test, $r = .125$, $p = .365$ upright and $r = .077$, $p = .416$ inverted.

2003, 2006; Webster & MacLin, 1999). Watson and Clifford (2003, 2006) speculate that these patterns arise because adults process upright faces based on both individual parts/features and configural cues like feature spacing, while they use only part-based processing for inverted faces. Because there is some overlap in feature shape between upright and inverted faces, adaptation of the part-based system by upright faces transfers well to inverted faces. Because the configural system is used weakly, if at all, in processing inverted faces but plays a major role in processing upright faces, adaptation to inverted faces transfers poorly to upright faces, for which the unadapted configural system is still operative.

A related possibility is suggested by a recent study of transfer between a face with its eyes moved up and a T matched to the location of the eyes and mouth and with its crossbar moved by the comparable amount (Susilo, McKone & Edwards, 2010). Adaptation to an upright face with raised eyes, or a T with the crossbar raised by the same number of pixels, caused an average face or T, respectively, to appear to have lower-than-normal eyes/crossbar, with aftereffects of comparable size. Adaptation transfer between faces and Ts (or Ts and faces) was modest, but significantly above zero. Importantly, the pattern of adaptation for inverted Ts or faces was quite different with robust transfer in every case. Susilo and colleagues speculate that adaptation in all cases affected mid-level shape processing of global features but that only adaptation to the upright face caused adaptation, in addition, to a higher-level mechanism that is tuned to upright faces. By extension, simultaneous opposing aftereffects for upright and inverted faces may reflect the joint effect of (1) adaptation of the mid-level shape system that responds similarly to stimuli with similar visual features (e.g. the part-based processing in Watson and Clifford's account) and (2) adaptation of the higher-level system that is tuned only or mainly to upright faces (e.g. the configural processing system in Watson and Clifford's account). The simultaneous opposing adaptations may cancel out some of the effect of the first mechanism because the mid-level features in upright and inverted faces overlap partially but not completely (e.g. both contain ovoid shapes forming the eyes and mouth but in different locations and with eyebrow curvature in opposite directions). It may also expand the range of shapes that look normal. In contrast, the simultaneous opposing aftereffects will cancel out little of the effect of the second higher-level mechanism because it will be activated by the upright but not the inverted adapting faces. However, it is not possible to make definitive quantitative predictions about the relative size of the opposing aftereffects because it will depend on the tuning characteristics of neurons responsive to upright versus inverted faces, and there is evidence for narrower tuning for the upright population (e.g. Gilaie-Dotan, Gelbard-Sagiv & Malach, 2010; Robbins *et al.*, 2007; Watson & Clifford, 2006). In addition, quantitative predictions depend on the effectiveness of weak versus strong adaptors (e.g. inverted and upright faces) in altering the responses of weakly versus strongly responsive neurons, respectively (Guo, Oruc & Barton, 2009).

Overall, our results in adults replicate previous findings of opposing aftereffects for upright and inverted faces with the current child-friendly paradigm, despite the small number of trials. They indicate separable processing of these categories.

Aftereffects in 10-year-olds

Like adults, 10-year-olds showed some evidence of using separable processing for upright versus inverted faces; their ratings of compressed upright faces increased post-adaptation despite concurrent adaptation to expanded inverted faces. However, unlike adults, 10-year-olds' ratings of inverted faces did not change consistently following adaptation.

It is unlikely that the lack of an aftereffect for inverted faces in the current experiment was caused by lack of attention, because the upright and inverted pages of the story were intermixed and if anything children seemed more engaged with the inverted sections of the story. Simple and opposing aftereffects for other categories have also been shown in children as young as 5 using essentially the same paradigm (Short *et al.*, 2011). Ten-year-olds quite happily rated inverted, as well as upright, faces, in the pre- and post-adaptation phases and used the whole scale; however, they failed to systematically rate more distorted inverted faces as less attractive than undistorted faces even before adaptation, and this may have contributed to the lack of an aftereffect. This lack of consistent rating may also suggest that 10-year-olds are less sensitive than adults to differences among inverted faces, a pattern that has two implications: (a) the inverted adapting faces may have been perceptually less distorted than the upright adapting faces – a metric known to influence the magnitude of aftereffects (e.g. Robbins *et al.*, 2007); and (b) 10-year-olds' ratings of inverted faces may be less sensitive to differences in distortion than those of adults. These two hypotheses would be supported if significant opposite shifts for both upright and inverted faces were observed in a study in which the adapting inverted faces were more distorted (e.g. +80%) than the adapting upright faces (e.g. +40%).

The lack of aftereffects for inverted faces may also indicate that the separable tuning of upright and inverted face processing is still not complete at 10 years of age, an interpretation that is consistent with evidence that the inversion deficit for judging the distance between the eyes emerges between 9 and 11 years of age (Baudouin, Gallay, Durand & Robichon, 2010). There must be some separability because the expanded inverted adapting face did not cancel out the effect of the compressed upright adapting face. It is possible that 10-year-olds process both upright and inverted faces with reference to separable categories, but that these are not yet as well differentiated as they will become, much like young

Caucasian children whose coding for Caucasian and Chinese faces is less well differentiated than in older children and adults (Short *et al.*, 2011). Overall, it seems that the tuning of the face system to separably code upright and inverted faces may not be fully mature by age 10.

Aftereffects in patients treated for bilateral congenital cataract

Patients treated for bilateral congenital cataract failed to show opposing aftereffects. As a group, their adaptation change scores shifted in opposite directions to the visually normal adults: after adaptation to compressed upright faces and expanded inverted faces, patients' mean rating was higher for expanded upright faces and compressed inverted faces. If anything, in the raw data they showed a widening of the range of faces rated as attractive after adaptation for upright faces, and like 10-year-olds, did not show an aftereffect for inverted faces, although the statistics on the pre-adaptation scores indicate slightly more differentiation of different inverted distortions than shown by the 10-year-olds.

The negative results for patients are unlikely to be explained by poor motivation or attention to the faces. The procedure was short, with upright and inverted adapting faces interleaved, and a live experimenter reading the story and monitoring attention. The systematic effect of distortion level on patients' ratings of upright faces both pre- and post-adaptation also argues against non-visual explanations. The normal pre-adaptation baseline for upright faces also left scope to detect a change after adaptation, and showed that the lack of adaptation was not based on lack of power to detect any differences.

The absence of opposing aftereffects in the patients raises the possibility that they failed to develop separable coding for upright faces and that instead they use general shape processing mechanisms to process all classes of stimuli. Aspects of feature shape which overlap in upright and inverted faces would be processed by overlapping neuronal populations within the shape processing system, much like inverted faces and Ts for adults with normal vision (Susilo *et al.*, 2010). Because patients are less sensitive than normal controls to the exact location of facial features within the face contour (Le Grand *et al.*, 2001, 2003; Robbins *et al.*, 2010), the overlap might be even greater than normal. Opposing aftereffects would, as a result, cancel out for these overlapping shapes. Aspects of feature shape that do not overlap for upright and inverted faces could be simultaneously adapted, leading to a wider range of shapes that look normal or attractive after adaptation. This hypothesis, that patients treated for bilateral congenital cataract use general shape processing mechanisms for face recognition, is consistent with evidence that patients fail to develop markers of adult expertise for upright faces: they show no evidence of holistic processing of upright faces with the composite face task (Le Grand *et al.*, 2004) and they can process feature spacing normally in monkey faces and houses but they fail to show the normal greater sensitivity for upright human faces (Robbins *et al.*, 2010). It is also consistent with evidence of the patients' normal application of more general shape-processing mechanisms to upright faces: they are as accurate as visually normal adults in recognizing differences in the shape of the external contour or of internal features such as the eyes, even with pairings that adults with normal vision find relatively difficult (Le Grand *et al.*, 2001; Mondloch *et al.*, 2010). Combined, the evidence suggests that early visual input is necessary to set up or preserve the neural architecture that will later become specialized for holistic processing of upright human faces, separable from general shape processing.

Conclusion

In summary, by using opposing adaptation, we demonstrated that differentiated processing of upright and inverted faces continues to be fine-tuned after 10 years of age and fails to develop in the absence of early visual input.

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