Deficits in Sensitivity to Spacing After Early Visual Deprivation in Humans: A Comparison of Human Faces, Monkey Faces, and Houses

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ABSTRACT: Early visual deprivation caused by bilateral congenital cataracts produces deficits in discriminating faces that differ in the spacing of features, but not in feature shape (Le Grand et al. [2001] Nature 410: 810). We investigated whether these deficits are specific to human faces by testing patients’ ability to discriminate between stimuli differing only in feature spacing in human and monkey faces (Experiment 1) and in houses (Experiment 2). Patients, as a group, showed deficits on only one task: they had lower accuracy than normal in discriminating feature spacing in human faces. In contrast, they were normal in discriminating feature spacing in monkey faces and in houses. The results suggest that early visual experience is necessary to set up (or preserve) the neural architecture used for processing human faces, but not for processing objects in general. © 2010 Wiley Periodicals, Inc. Dev Psychobiol 52: 775–781, 2010.

Keywords: sensitive periods; visual deprivation; face recognition; object recognition; spacing discrimination

INTRODUCTION

Patients born with dense bilateral congenital cataracts provide a natural experiment to investigate the effects of early visual deprivation in humans. Such patients later develop normal sensitivity to low spatial frequencies and high rates of flicker, but have deficits at low temporal frequencies and high spatial frequencies, including abnormal acuity (Ellemberg, Lewis, Maurer, Liu, & Brent, 1999), and deficits in global processing of shape and motion (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; Lewis et al., 2002). Additionally, they show a particular pattern of deficit in processing faces. They are normal at processing facial features and at tasks that can be performed with this skill (e.g., matching facial expression despite changes in identity; Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002; Le Grand, Mondloch, Maurer, & Brent, 2001; Le Grand, Mondloch, Maurer, & Brent, 2003; Mondloch, Robbins, & Maurer, 2010), but unlike adults with normal visual experience, they are impaired at discriminating faces that differ only in spacing of features (e.g., distance between the eyes; Le Grand et al., 2001) and at matching faces across changes in point of view (Geldart et al., 2002). Good performance on these tasks may depend on holistic processing involving integration of information across the face, a skill at which patients are also abnormal (they fail to integrate information across the top and bottom halves of a face; Le Grand, Mondloch, Maurer, & Brent, 2004). These studies suggest that the development of normal face processing is dependent on visual input and/or normal access to faces during the first few months of life.
The previous systematic set of studies suggests that patients treated for bilateral congenital cataract have deficits only in the types of processing that visually normal adults use specifically with human faces, namely holistic processing and sensitivity to spacing of features. For example, visually normal adults demonstrate holistic integration of features across faces (Le Grand et al., 2004; Young, Hellawell, & Hay, 1987) but not other categories (e.g., cars; Cassia, Piccozzi, Kuefner, Bricolo, & Turati, 2009), not even categories for which the observer has many years of experience making discriminations at the individual level (e.g., dog experts; Robbins & McKone, 2007). Similarly, visually normal adults’ sensitivity to small differences in the spacing between features (a configurational cue sometimes referred to as second-order relations) is high for human faces (e.g., Mondloch, Le Grand, & Maurer, 2002) but not for monkey faces (Mondloch, Maurer, & Ahola, 2006). What remains to be determined is whether the observed deficits after early visual deprivation are specific to human faces. Here, we addressed that question by examining whether the deficit in discriminating spacing differences between stimuli is specific to human faces or extends to other categories for which visually normal adults have some, albeit less, competence. To that end, we compared the sensitivity of patients and controls to spacing differences in human faces, monkey faces, and houses.

In Experiment 1, patients were tested on their ability to discriminate differences in the spacing between features in human faces and in monkey faces. Absolute spacing differences were identical for the two types of faces (Mondloch et al., 2006). The comparison allowed us to assess whether early visual deprivation damages the processing only of faces from the category for which visually normal adults develop expertise or generalizes to faces even from a category rarely experienced.

In Experiment 2, we extended the assessment to a nonface object, namely houses. Visually normal adults are much less sensitive to spacing differences in houses than in faces; for that reason, the spacing differences in the house stimuli had been increased until pilot data indicated that accuracy for human faces and houses was matched in visually normal adults. Across the two experiments, we therefore tested patients with stimulus sets matched both for absolute spacing changes (monkey and human faces, Experiment 1) and performance in visually normal adults (human faces and houses, Experiments 1 and 2).

If deficits are specific to human faces, then patients should show deficits with human faces but not monkey faces or houses. In contrast, if deficits are more general, then patients should show deficits with human faces, monkey faces, and houses. Assessing the ability of patients treated for cataract to discriminate spacing differences in these three types of stimuli will increase understanding of the importance of early visual input to face versus object recognition. This in turn has implications for understanding the plasticity of face and object processing during development.

**EXPERIMENT 1—FEATURE SPACING IN HUMAN AND MONKEY FACES**

Experiment 1 compared performance on a same-different task for detecting spacing changes in the human faces and monkey faces used previously with visually normal adults and children (Mondloch et al., 2006). Importantly, the human faces were those on which patients have been shown previously to have a deficit (Le Grand et al., 2001). Patient results were compared to those collected previously from visually normal adults (Mondloch et al., 2002, 2006).

**Methods**

**Participants.** The participants were 10 patients who had been diagnosed with dense central cataracts in each eye that blocked all patterned vision. The cataracts were diagnosed on the first eye exam, with no sign of an earlier period of patterned visual input. The cataractous lenses were removed surgically during infancy and the eyes given a compensatory optical correction, usually contact lenses. Details about the patients are presented in Table 1. Seven of the patients had completed the spacing task with human faces as part of one or more previous studies (including Le Grand et al., 2001). The research was approved by ethics committees at McMaster University and The Hospital for Sick Children, Toronto. All patients provided informed consent (for those younger than 17, the patient provided informed assent and a parent provided consent).

**Stimuli.** The stimuli were presented with SuperLab Pro (version 177) on an Hp p1130 Trinitron Cathode Ray Tube monitor (21 inches diagonally) connected to a PowerMac G4 cube.

Photographs of human faces contained variations in the spacing of the eyes and mouth and were identical to those used previously in studies of patients and normally developing children (Le Grand et al., 2001; Mondloch et al., 2002, 2006). The variations used are within normal limits for human faces. Monkey faces had been created so that the spacing positions matched exactly those in the human faces, after matching the height of the monkey’s inner face to the height of the human’s face (Mondloch et al., 2006). The spacing changes involved moving the eyes in/out and up/down, and moving the mouth up and down (for a total of five arrangements, with...
counterbalanced pairings for 15 same and 15 different trials for each stimulus type). The faces were 10.2 cm wide by 15.2 cm high, or 57° by 91° at the 100 cm viewing distance. Example stimuli, at the extremes of those used, are shown in Figure 1.

Procedure. The procedure was the same as that used previously to test sensitivity to human and monkey faces in visually normal children and adults (Mondloch et al., 2006) and to human faces in patients treated for cataract (except for the addition of a mask between presentations; Le Grand et al., 2001). Briefly, faces were presented sequentially: the first face was presented for 200 ms, followed by a mask for 300 ms, and then the second face remained on the screen until patients indicated whether the face was the same as, or different from, the first. A fixation cross was presented between trials. Stimuli were viewed binocularly. The type of face was blocked, with human faces presented first. Each stimulus type (monkey or human) was preceded by a presentation of all five spacing arrangements of that type, so that patients could see the range of similarity among the faces. The nature of the changes was not explicitly mentioned.

Patient results were compared to previously collected norms by calculating a z-score for each patient for each condition (human and monkey faces). To evaluate whether there was a significant deficit, z-scores were compared to zero using one-tailed t-tests.

For monkey faces, results were compared to adult norms collected previously (N = 24; Mondloch et al., 2006). As shown in Figure 2, patients generally performed in the normal range. A one-tailed t-test confirmed that the mean z-score (−.24) was not significantly different from zero, t(9) = 0.88, p = .20, despite the fact that more than half the patients were under 16 years of age and all were compared to adult norms.

For human faces, results were first compared to adult norms and the z-scores were low for the group as a whole (M = −0.81). A t-test comparing the z-scores to zero confirmed that the patients, as a group, were below normal, t(9) = 3.77, p = .002. To verify that the deficit was not caused by the younger age of the patients, we also compared their accuracy to age-matched norms (N = 36/age) for the same faces tested with a similar method (Mondloch et al., 2002; Mondloch, Le Grand, & Maurer, 2003). These results are shown in Figure 2. Patients’ accuracy for human faces was also abnormal in this comparison (M = −1.19, t(9) = 3.64, p = .003), replicating the previous finding (Le Grand et al., 2001).

The size of the patients’ deficit (based on age-norms) was not correlated with the duration of deprivation after

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**Table 1. Details of the 10 Patients Treated for Bilateral Congenital Cataract**

<table>
<thead>
<tr>
<th>Patient</th>
<th>Age at Test (years)</th>
<th>Binocularity</th>
<th>Stereoaucity (sec of arc)</th>
<th>Linear Letter Acuity</th>
<th>Duration of Deprivation (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>11.1</td>
<td>Suppress right eye</td>
<td>Not tested</td>
<td>20/200 20/40</td>
<td>61 61</td>
</tr>
<tr>
<td>M2</td>
<td>12.2</td>
<td>Diplopia</td>
<td>None</td>
<td>&lt;20/200 20/25</td>
<td>65 9</td>
</tr>
<tr>
<td>F1</td>
<td>13.2</td>
<td>Diplopia</td>
<td>None</td>
<td>20/63 20/63</td>
<td>98 98</td>
</tr>
<tr>
<td>F2</td>
<td>13.3</td>
<td>Diplopia</td>
<td>400</td>
<td>20/30 20/40</td>
<td>34 34</td>
</tr>
<tr>
<td>F3</td>
<td>13.6</td>
<td>Diplopia</td>
<td>None</td>
<td>20/125 20/50</td>
<td>92 92</td>
</tr>
<tr>
<td>F4</td>
<td>15.9</td>
<td>Not tested</td>
<td>Not tested</td>
<td>20/32 20/50</td>
<td>152 152</td>
</tr>
<tr>
<td>F5</td>
<td>23.0</td>
<td>Diplopia</td>
<td>None</td>
<td>20/25 20/70</td>
<td>91 91</td>
</tr>
<tr>
<td>M3</td>
<td>23.0</td>
<td>Diplopia</td>
<td>400</td>
<td>20/80 20/125</td>
<td>97 97</td>
</tr>
<tr>
<td>M4</td>
<td>27.5</td>
<td>Diplopia</td>
<td>140</td>
<td>20/50 20/60</td>
<td>161 196</td>
</tr>
<tr>
<td>M5</td>
<td>27.4</td>
<td>Diplopia</td>
<td>None</td>
<td>20/125 20/25</td>
<td>294 181</td>
</tr>
</tbody>
</table>

aAs measured by the Worth 4 Dot Test (measured within 1 year of testing).
bDiplopia refers to double vision.
cAs measured by the Titmus test (measured within 1 year of testing).
dBest corrected linear letter acuity on the day of testing.
eFrom birth until the fitting of a compensatory contact lens after surgical removal of the cataract.
birth (9–294 days between birth and the fitting of the contact lens) for either the better or worse eye, with age at test, or with acuity, all ps > .10, one-tailed. Thus, it seems that visual input during the first 0–10 months is especially important for the later development of normal face processing.

The patients’ difficulty in processing spacing in human faces is likely to be related to the early visual deprivation, rather than ongoing problems after treatment, such as having a fixed focus, misaligned eyes, nystagmus, or poor acuity. In visually normal adults, holistic face processing and sensitivity to spacing seem to rely on low-spatial frequency information much more than high-spatial frequency information (Goffaux & Rossion, 2006; Mondloch, Dobson, Parsons, & Maurer, 2004). Patients, as noted in the Introduction Section, have continuing deficits with high-spatial frequencies, not low-spatial frequencies (Ellemberg et al., 1999). Not surprisingly then, as indicated above, the size of their deficits was not correlated with their acuity at the time of the test. Moreover, any such visual deficits at the time of test cannot account for worse performance with human faces because the spacing differences to be discriminated were identical for human and monkey faces.

Overall, the results suggest that early visual deprivation damages something that is critical to the processing of human faces. However, there are two possible concerns with this conclusion. One is that patients showed a range of performance on monkey faces (see Fig. 2). This may have been because some processed the monkey faces (poorly) as “faces,” while some processed them (well) as “objects.” Another possible concern is that visually normal adults are less accurate for the monkey faces than the human faces (69% vs. 78%; Mondloch et al., 2006) such that low values on the monkey norms may account for the patients’ scoring in the normal range with monkey faces (although 8-year olds performed worse than adults on both face sets). To address both these concerns, we tested patients on a class of nonface stimuli (houses) where performance for the spacing stimuli had been matched to that with human faces in visually normal adults.

FIGURE 1 Examples of the spacing stimuli used in Experiment 1 (Panel a) and in Experiment 2 (Panel b). Shown are the two items with the largest difference in spacing within each set.

FIGURE 2 z-Scores for each patient, in order of age at test, for spacing discrimination in human faces, monkey faces, and houses. z-Scores were calculated compared to age-norms for human faces and adult norms for monkey faces and houses. Patients M1, F2, F4, F5, and M3–M5 had completed a version of the human face spacing task as part of previous experiments. The group means for all patients are shown at the far right. Negative values indicate deficits compared to the norm.

EXPERIMENT 2—FEATURE SPACING IN HOUSES

We tested patients’ discrimination of houses that differed only in spacing between features. We used a match-to-sample task and larger spacing differences in the house stimuli than face stimuli so as to equate visually normal adults’ accuracy on the house task and the human face task used in Experiment 1.
Methods

Participants. The participants were the same 10 patients tested in Experiment 1. Six patients completed Experiment 2 first, and four completed Experiment 1 first. Patients completed both experiments on the same day.

Apparatus and Stimuli. The apparatus was identical to that described in Experiment 1. The stimuli consisted of 10 pictures in each of three conditions, in which houses differed only in the spacing between features, only in feature shape, or were completely different control houses. These two latter conditions were tested because we had reason to believe that patients might show a general deficit in the processing of houses (Grady et al., 2006).

The spacing changes included moving the upper windows in and out, the bottom window up and down and the door left and right (for a total of 10 arrangements, made into 25 possible pairs by combining each of 5 houses in “Set A” with each of 5 houses in “Set B”). A similar process was used for the feature and control houses. Examples of the houses with the most extreme differences are shown in Figure 1b.

Houses were matched for spatial frequency amplitude by applying the average amplitude spectra for all sets to each house (c.f., Husk, Bennett, & Sekuler, 2007). The houses were 12 cm wide by 18 cm high, or 13.7° by 20.4° at the 50 cm viewing distance. Spacing changes in the houses, as well as presentation times and task, had been adjusted during a pilot study so that visually normal adults achieved 77% accuracy (Robbins, Shergill, Maurer, & Lewis, unpublished work), which matches the 78% accuracy for visually normal adults on the human faces task from Experiment 1, t(58) = 0.242, p = .81 (two-tailed).

Procedure. The procedure for the house task was a delayed match-to-sample task. On each trial, a fixation cross was presented followed by a single house presented for 1,000 ms, immediately followed by a pair of houses, which remained on the screen until the patient indicated which of the pair matched the first house by pressing a button corresponding to the left or right house. Each house pair was presented twice, once with the correct answer on the left and once with the correct answer on the right, making a total of 50 trials per house condition. Each set was preceded by an untimed presentation of all 10 houses in that set, so that patients could see the range of similarity among the houses. The differences in each set were not explicitly pointed out. Patients were instructed orally and by written instructions on the screen. Stimuli were viewed binocularly. Patients were tested first on the feature set, then the spacing set, and then the set containing completely different houses.

Results and Discussion

Every patient was above 90% correct on the feature shape and control conditions (M = 97% for each condition), a pattern suggesting no general deficit at house processing. However, visually normal adults were at ceiling for the feature shape and control tasks, a pattern making interpretation of patients’ normal performance problematic. For that reason, these two conditions were not analyzed further.

Patients’ accuracy on the spacing set of houses was converted to z-scores based on norms from a control group of 36 adults (18 males and 18 females) with normal vision tested previously on the same task (Robbins et al., unpublished work). All patients’ z-scores on the spacing task clustered around zero (see Fig. 2), and a one-sample t-test confirmed that the patients as a group were normal: M = −0.12, t(9) = 0.61, p = .28 (one-tailed). Age-norms are not available, but normal performance in comparison to adults provides a conservative test of our hypothesis.

As noted in the Methods Section, the spacing changes in houses had been adjusted during a pilot study so that visually normal adults achieved 77% accuracy, approximately the same as the 78% accuracy found previously for spacing discrimination in human faces as tested in Experiment 1. (Patients’ mean accuracy was also 77% on the house task.) To achieve this level of accuracy in visually normal adults with houses, the spacing changes needed to be physically larger than those previously used for faces. Indeed, for the most direct comparison (in/out distance of windows vs. eyes) the spacing changes in the houses (55–1,168 arc min of visual angle) were over four times larger than those in the faces (128–276 arc min of visual angle) in absolute terms, or about twice as large if the size of the stimuli is taken into account (a change of about 38% in the face stimuli vs. 67% in the houses). The house stimuli also needed to be presented longer and as a two-alternative forced choice matching-to-sample procedure. For visually normal adults, the face task was as easy or even easier than the houses task, despite shorter, sequential presentations and smaller spacing changes, reflecting their face expertise. It is this expertise that patients appear to lack, with 9 of 10 patients having lower accuracy and lower z-scores for human faces than houses.

GENERAL DISCUSSION

The results suggest that deficits in sensitivity to spacing after early visual deprivation are specific to human faces. Patients have deficits in processing the spacing of features in human faces (Le Grand et al., 2001), a deficit replicated in this study, but not in geometric shapes (Geldart, 2000, unpublished thesis) or houses (this study). They also seem
to be normal at processing monkey faces: their z-scores for the monkey spacing task was not different from that of normal adults and 7 of 10 patients actually had higher z-scores for spacing in monkey than in human faces, with the overall group score also better for monkey faces, \(t(9) = 3.42, p = .008\) (two-tailed), the opposite pattern from that observed for visually normal adults. The face system narrows during normal infant development to exclude monkey faces: 6-month olds can discriminate both individual human and individual monkey faces but, without training, 9-month olds and adults pass the same test only for human faces (Pascalis, De Hann, & Nelson, 2002). By 8 years of age, children are more sensitive to spacing changes in human than monkey faces (Mondloch et al., 2006). Patients’ face processing appears not to have undergone that perceptual narrowing in favor of human faces. Similarly, patients appear to be normal at discriminating inverted faces but this must be interpreted with some caution as visually normal adults are already close to floor (Le Grand et al., 2001). Collectively, the results suggest a general spacing discrimination mechanism that can be applied to houses (or monkey faces) and that develops slowly and normally even in patients who missed early visual experience. In addition, adults have a more specific mechanism that is tuned to familiar categories of faces (e.g., upright, own species, own race; Mondloch et al., 2006; Rhodes, Hayward, & Winkler, 2006) and that depends on early visual experience. The application of the specific mechanism may be facilitated by holistic processing of faces (integration across the face)—a process that emerges early and that is also impaired after early visual deprivation (Le Grand et al., 2004).

A recent study with monkeys suggests that it may be the lack of patterned visual input in general, rather than the lack of face input in particular, that leads to deficits in face perception after early visual deprivation (Sugita, 2008). Sugita showed that monkeys that had had normal visual experience other than never seeing faces (human or monkey) for the first 2 years of life could nevertheless discriminate spacing and feature changes in both human and monkey faces. After 1 month of exposure to one class of face (human or monkey), the discrimination ability remained for the exposed class but was no longer manifested for the unexposed class. Thus, in visually normal human infants, early patterned visual input may set up or preserve the neural architecture that will be tuned later by experience for holistic processing of faces of one’s own race and species, and (perhaps as a consequence) face-specific sensitivity to the spacing of features. However, such early patterned input appears not to be necessary for discriminating among other objects such as houses, even when the only differences are feature spacing within such objects.

Overall, the current results are consistent with other studies showing that faces are processed differently from other objects. They also suggest that the face system may be less plastic, or at least less resistant to damage, than the object system.

NOTES

We thank Jesse Husk for providing houses used to create the stimuli and for helping to match the amplitude spectra across house sets. We thank an anonymous reviewer of a previous version for pointing out the differences in spacing between houses and faces relative to stimulus size. Some of these data were presented at the annual meeting of Cognitive Neuroscience, San Francisco, April 2008, and at the Australasian Experimental Psychology Conference, Perth, March 2008. The work was supported by grants to Daphne Maurer from the Natural Sciences and Engineering Research Council (9797; Experiment 1) and to Daphne Maurer and Terri Lewis by the Canadian Institute of Health Research (MOP-36430; Experiment 2). The authors declare they have no conflict of interests.

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