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CHAPTER 5

Effects of early visual deprivation on perceptual and cognitive development

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Abstract: During early infancy, visual capabilities are quite limited. Nevertheless, patterned visual input during this period is necessary for the later development of normal vision for some, but not all, aspects of visual perception. The evidence comes from studies of children who missed early visual input because it was blocked by dense, central cataracts in both eyes. In this article, we review the effects of bilateral congenital cataracts on two aspects of low-level vision – acuity and contrast sensitivity, and on three aspects of higher-level processing of faces. We end by discussing the implications for understanding the developmental mechanisms underlying normal perceptual and cognitive development.

Keywords: visual deprivation; perceptual development; plasticity; acuity; face processing; contrast sensitivity

Newborns can see, but there are serious limitations on their visual perception: their visual acuity is 30–40 times worse than that of adults (Atkinson et al., 1977; Banks and Salapatek, 1978; Brown and Yamamoto, 1986; van Hof-van Duin and Mohn, 1986; Courage and Adams, 1990; reviewed in Maurer and Lewis, 2001a, b) and their processing of faces is very limited (e.g., de Haan et al., 2001; Cashon and Cohen, 2003, 2004; Bertin and Bhatt, 2004; Bhatt et al., 2005). There is rapid progress during infancy, such that by 6–8 months of age, visual acuity is only 6 times worse than that of adults (Mayer et al., 1995; reviewed in Maurer and Lewis, 2001a, b) and most types of face processing have emerged. By 4–6 years of age, acuity is adult-like (Mayer and Dobson, 1982; Ellemberg t al., 1999a), but some types of face processing continue to improve into adolescence (Carey et al., 1980; Bruce et al., 2000; Mondloch et al., 2002, 2003b). In this chapter, we will evaluate the role of visual input in driving the postnatal changes in acuity and in face processing by contrasting the perceptual development of children with normal eyes to that of children who were deprived of patterned visual input at birth because they were born with dense, central cataracts in both eyes.

Children treated for congenital cataract

In the patients we selected for our studies, the cataracts were central and so dense that they blocked all patterned visual input to the retina. Inclusion criteria included that the infant did not

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Children treated for bilateral congenital cataract afford an opportunity to evaluate the role of visual input in driving the postnatal perceptual changes seen in normal development. However, there are limitations to this natural experiment that must be kept in mind when interpreting any deficits. First, before treatment, the retina may not be completely deprived of visual input because changes from bright light to complete darkness may be transmitted through the cataractous lens sufficiently well to cause small changes in the illumination of the retina. Second, after treatment, the contact lenses provide a fixed focus, such that objects at some specific distance are in perfect focus, but objects closer to the child, or farther away, are increasingly out of focus. Typically, the contact lenses are fit to give the child perfect focus at arms' length until the child begins to walk, at which point the contact lens for one eye is changed to focus perfectly farther from the child. In addition, children treated for bilateral congenital cataract often develop secondary eye problems such as nystagmus (small, jiggly eye movements) or strabismus (misaligned eyes). As a result of the fixed focus and such secondary eye problems, children treated for bilateral congenital cataract do not receive completely normal visual input at any point in their lives. Thus, any deficits may arise from the initial complete deprivation of patterned visual input and/or from the continuing milder alterations of visual input. In fact, however, control experiments suggest that the deficits we have found arise from the original deprivation caused by the cataracts and not from later perturbations.

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Visual acuity

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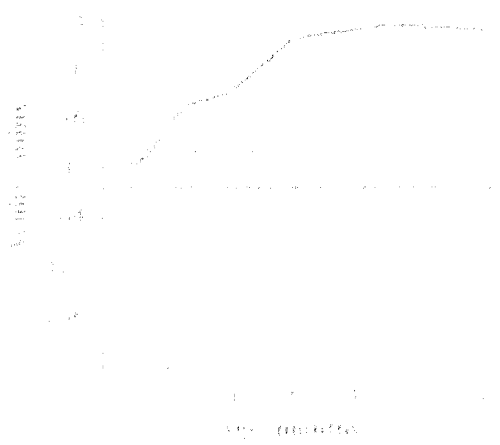
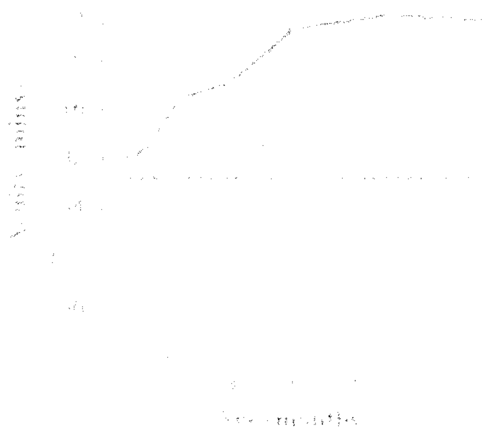




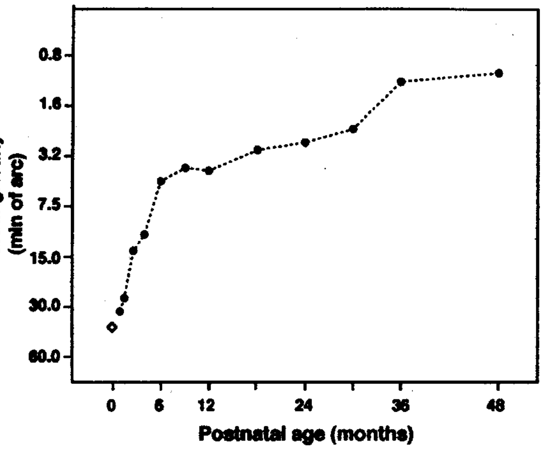


Fig. 1. Grating acuity from birth to 4 years of age. Shown are the normative values from the Teller Acuity Card procedure described in the text (Mayer et al., 1995). Each dot represents the smallest stripe size, in minutes of arc, for which infants at a particular age showed a reliable looking preference. Adapted with permission from Maurer and Lewis (2001b).

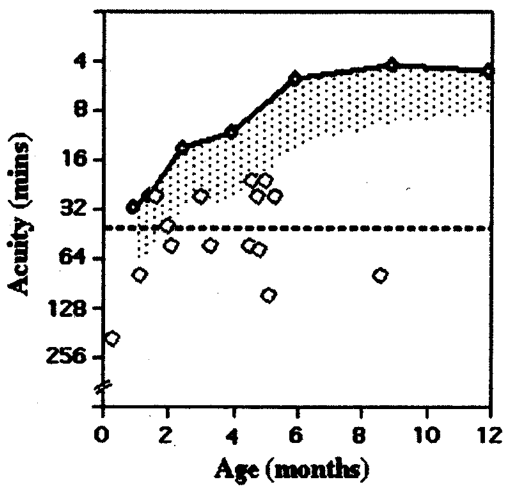


Fig. 2. Grating acuity of the right eye on the immediate test of children treated for bilateral congenital cataract. Each dot represents the acuity of a treated eye plotted at the age when contact lenses first allowed patterned visual input after surgery. The solid line and stippled area represent the mean acuity and lower 95% prediction limit (95% confidence that acuity will be at least as good as this value) for the normative group tested on Teller Acuity cards. The dotted line represents the geometric mean of the patients' acuity values. The data from the left eye are similar. Adapted with permission from Maurer et al. (1999).

newborns' acuity is more than 40 times worse that that of adults. Acuity improves rapidly over the first 6 months, followed by more gradual improvements over the next 4 years. Not until 4–6 years of age does grating acuity reach adult levels (Mayer and Dobson, 1982; Ellemberg et al., 1999a).

We have studied the acuity of children longitudinally after treatment for bilateral congenital cataracts (Lewis et al., 1995; Ellemberg et al., 1999b; Maurer et al., 1999; reviewed in Maurer and Lewis, 2001a, b). In one study, we measured the acuity of 12 patients on the day when they could first see — the day when they received their first contact lenses, which provided the first focused patterned visual input to the retina after removal of the cataracts (Maurer et al., 1999). The 1-week delay between surgery and the fitting of the first contact lenses was sufficient for the eyes to heal from the surgeries. On the first measurement, which occurred within 10 min of the end of visual deprivation, acuity in each eye was like that of newborns, regardless of the patient's age, which ranged from 1 to 9 months. As a result, those treated later had a larger deficit in acuity compared to children with normal eyes (see Fig. 2). These results indicate that patterned visual input drives the rapid improvement in acuity evident during the first 6 months of normal development (see Fig. 1). However, the visual system of the cataract patients was not dormant during the period of visual deprivation. This was evident when we retested their visual acuity after just 1 h of visual input: there was an improvement in almost every case (see Fig. 3), such that the mean acuity increased over the hour of visual experience to that of a typical 6-week-old with normal eyes. No such change occurred in an age-matched control group. Patients continued to improve faster than normal over the next week and month (see Fig. 4).

A control experiment with six additional infants treated for bilateral congenital cataract confirmed that the rapid improvement after treatment was driven by visual input and not by non-visual factors such as adjusting to the contact lens. For the control experiment, the immediate test occurred, as before, within 10 min of the infant receiving the contact lenses. Then, one eye was patched while the other eye received 1 h of visual input, after which both eyes received the usual retest of acuity.

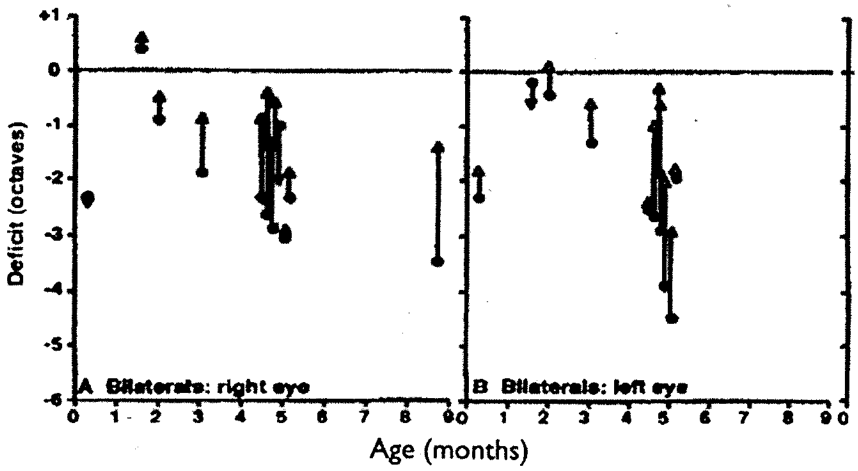


Fig. 3. Change in grating acuity after the first hour of visual input for children treated for bilateral congenital cataract. Each connected set of points represents the acuity deficit in octaves for one eye on the immediate test and the test after 1 h of visual input, plotted at the age when contact lenses first allowed patterned visual input after surgery. The dotted line at zero represents no deficit, and negative values represent deficits, with larger numbers representing larger deficits. Data for the right eyes are shown in Panel A and data for the left eyes in Panel B. Adapted with permission from Maurer et al. (1999).

Acuity improved in the eye that received visual input but not in the fellow patched eye that did not (see Fig. 5), a result indicating that visual input caused the rapid improvement in acuity. The amount of improvement in the experienced eye was similar to that observed in the main experiment. Combined, the results indicate that patterned visual input during infancy not only drives the initial rapid improvement seen in infants with normal eyes, but that it also allows accelerated recovery after visual deprivation.

Despite the accelerated recovery immediately after treatment, children treated for bilateral congenital cataract do not develop normal visual acuity. The developmental progression is well illustrated by our longitudinal studies of contrast sensitivity (Maurer et al., 2006). The contrast sensitivity function represents the amount of contrast needed to see stripes of various size, or spatial frequency — the greater the sensitivity, the less contrast needed to see the stripes. As shown in Fig. 6, adults are most sensitive to mid spatial frequencies (i.e., 3–5 cycles per degree of visual angle): for those frequencies they can still see the stripes when the contrast is low. There is a decrease in sensitivity for higher spatial frequencies up to the acuity cutoff, above which adults cannot see stripes even of maximum contrast (black and white). There is a smaller drop-off for low spatial frequencies (wide stripes). As shown in Fig. 6, contrast sensitivity is quite good by 4 years of age and reaches adult levels by age 7 (Ellemberg et al., 1999a).

The pattern was quite different in children treated during infancy for bilateral congenital cataract whose contrast sensitivity we measured longitudinally beginning between 5 and 8 years of age. As shown in Figs. 7 and 8, 1–2 years after the initial test, contrast sensitivity for low spatial frequencies (wide stripes) had improved more than in the control group so that an initial deficit had vanished or decreased dramatically. Some of the improvement occurred after 7 years of age, that is, after the age at which development is usually complete. Contrast sensitivity for mid spatial frequencies did not change between tests, while that of the control group increased, leading the patients to have an increased deficit. Contrast sensitivity for high spatial frequencies (10–20 cycles per degree) was not measurable because the patients could not see such thin stripes at any age. Thus, visual input during middle childhood allows partial recovery from the effects of early visual deprivation, but only at the low spatial frequencies where vision began to recover rapidly immediately after treatment. The asymptotic

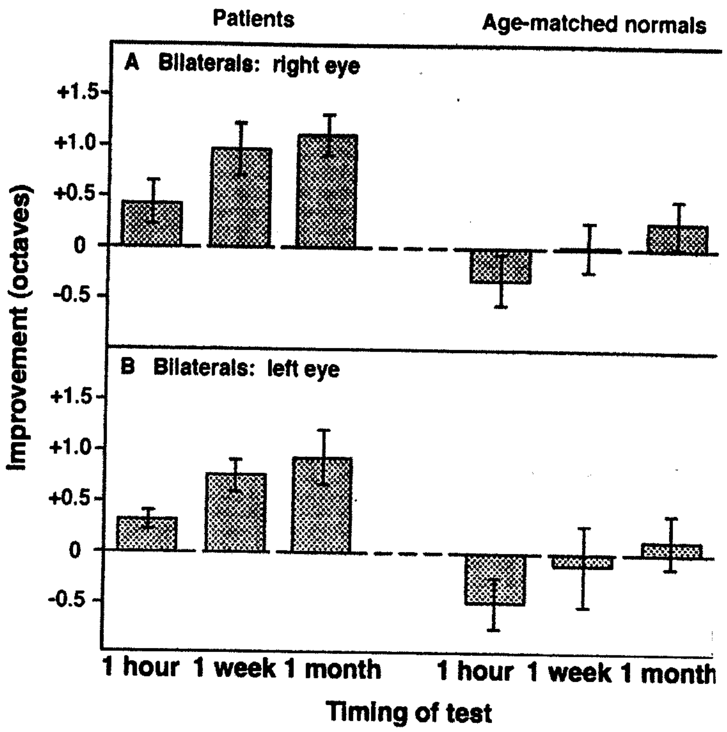


Fig. 4. Mean improvement in acuity in octaves (±1 s.e.) for children treated for bilateral congenital cataract from the immediate test to the test after the first hour of visual input, 1 week later, and 1 month later (left side) and for children in the age-matched control group (right side). Data for the right eye are shown in Panel A and data for the left eye in Panel B. Adapted with permission from Maurer et al. (1999).

sensitivity leaves the patient treated for bilateral congenital cataract with the contrast sensitivity of a typical toddler with normal eyes (Gwiazda et al., 1997). Complete recovery at higher spatial frequencies may be possible if the deprivation is especially short: a few patients treated at 6–8 days of age have achieved normal letter acuity (Kugelberg, 1992), as did 1 of 13 cases treated before 7 weeks of age in another cohort (Magnusson et al., 2002).

In sum, visual deprivation prevents the normal development of spatial vision. Although sensitivity to low spatial frequencies (wide stripes) can recover to normal levels, beginning with rapid improvement immediately after treatment, sensitivity to mid and high spatial frequencies does not. For those high spatial frequencies, there is a sleeper effect: visual deprivation during the first few months of life prevents the development of normal sensitivity to high spatial frequencies (10–20 cycles per degree) that infants with normal eyes typically do not begin to perceive until 2 years of age (Mayer et al., 1995). Studies of binocularly deprived monkeys suggest that the deficits are likely to arise at the level of the primary visual cortex, V1, where cells are sluggish, have abnormally large receptive fields, and reduced acuity, unlike cells in the retina and lateral geniculate nucleus, which respond normally (Crawford et al., 1975; Hendrickson and Boothe, 1976; Blakemore and Vital-Durand, 1983, 1986; Crawford et al., 1991).

Face processing

The poor contrast sensitivity of infants with normal eyes limits the information that they can perceive in faces: they can readily see the oval contour, the hair, and the basic layout of features but not the details of the internal features. Nevertheless, our

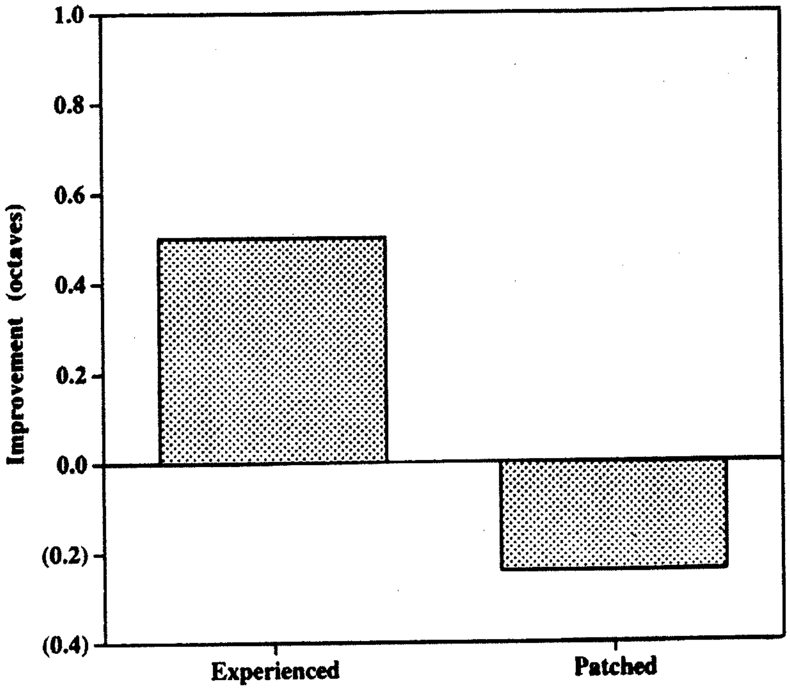


Fig. 5. Mean improvement in acuity in octaves between the immediate and 1 h tests for the six children treated for bilateral congenital cataract in the control experiment. Shown are the results for the eye that received visual experience (left side) and the fellow eye that was patched (right side).

studies of children treated for bilateral congenital cataract indicate that visual deprivation during this period when input is normally so limited prevents the later development of some, but not all, aspects of face processing (reviewed in Mondloch et al., 2003a). Here we report the ultimate deficit or ability in such patients: what they were able to achieve after removal of the cataract and contact lens fitting, followed by many years of (nearly) normal visual input (range 9 years to more than 20 years). In each case, the results from patients ($n = 11$–17 depending on task) were compared to those from controls matched on age, sex, handedness, and race/ethnic group.

Face detection

Adults can readily detect that a stimulus is a face based on its first-order relations (the ordinal relations that position two eyes above a nose, which is in turn above a mouth) (Diamond and Carey, 1986). They do so rapidly even when some of the individual features are missing (e.g., a line drawing with eyes and nose but no mouth) and even when the normal facial features are replaced by an arrangement of fruit or vegetables forming the correct first-order relations for a face (Moscovitch et al., 1997). Similarly, they can detect a face in an upright two-tone Mooney face (see Fig. 9) in which the perception of individual features has been degraded by transforming all luminance values to black or white (Kanwisher et al., 1998).

Patients treated for bilateral congenital cataract develop normal face detection (Mondloch et al., 2003a). To test face detection, we gave them a task consisting of brief presentations (100 ms) of either a Mooney face or a scrambled Mooney face (see Fig. 9 for examples) and asked them to indicate whether the stimulus was a face or nonface. We chose Mooney faces because they cannot be classified as faces based on individual features. As shown in Fig. 10, patients' accuracy and reactions times were normal. Thus, early visual deprivation does not prevent the later development of normal

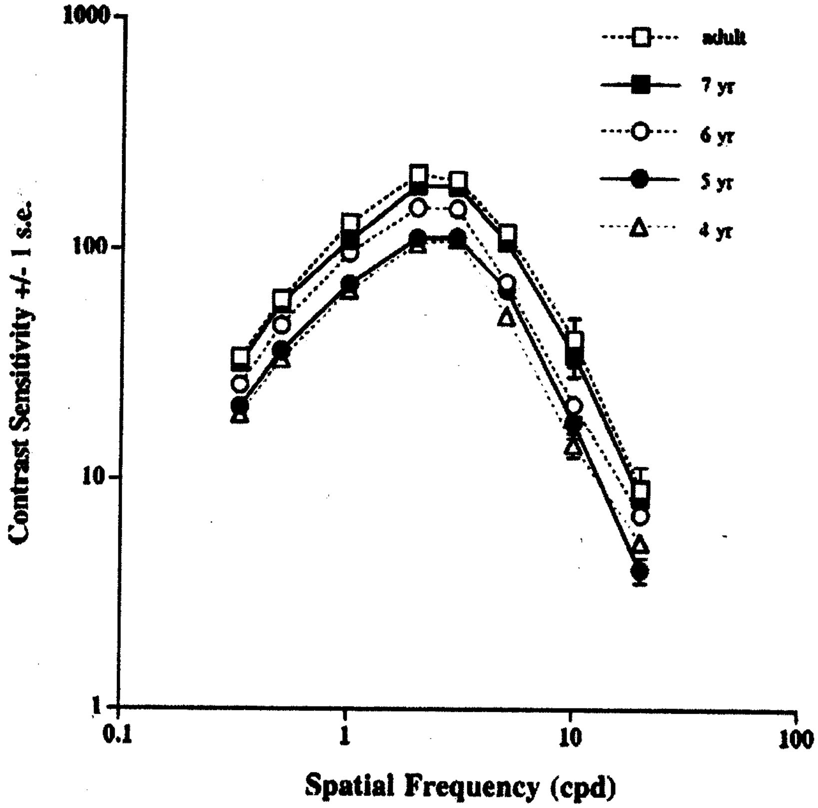


Fig. 6. Development of normal contrast sensitivity. Shown is the mean contrast sensitivity (±1 s.e.) of adults and four age groups of children for various spatial frequencies. When not shown, standard error bars are smaller than the symbols. Adapted with permission from Ellemberg et al. (1999a).

sensitivity to the first-order relations that underlie face detection. Preliminary data from longitudinal studies using a simpler task during infancy suggest that the ultimately normal performance may represent recovery from an earlier deficit (Mondloch et al., 1998). We are currently using ERP and fMRI to determine whether patients treated for bilateral congenital cataract use the normal neural networks for face detection or whether the plasticity extends to the recruitment of a different system that can, nevertheless, achieve normal accuracy and reaction time.

Recognition of facial identity

Adults can recognize thousands of individual faces rapidly and accurately and do so despite changes in the appearance of individual features caused by alterations in other cues that they must monitor such as head and eye orientation, emotional expression, or sound being spoken (Bahrick et al., 1975; see Bruce and Young, 1998, for a review). The reliable cues to individual identity (those that do not change with a trip to the hairdresser) are the shape of the head contour, the shape of individual internal features (e.g., eyes, nose, mouth, eyebrows), and the metric distances among the features, a configural cue called second-order relations. Although adults use all of these cues to decode facial identity, there is considerable evidence that their expertise in face recognition comes primarily from exquisite sensitivity to second-order relations (reviewed in Maurer et al., 2002). For example, adults are better at recognizing individual upright faces than at recognizing individual objects, but the superiority diminishes if

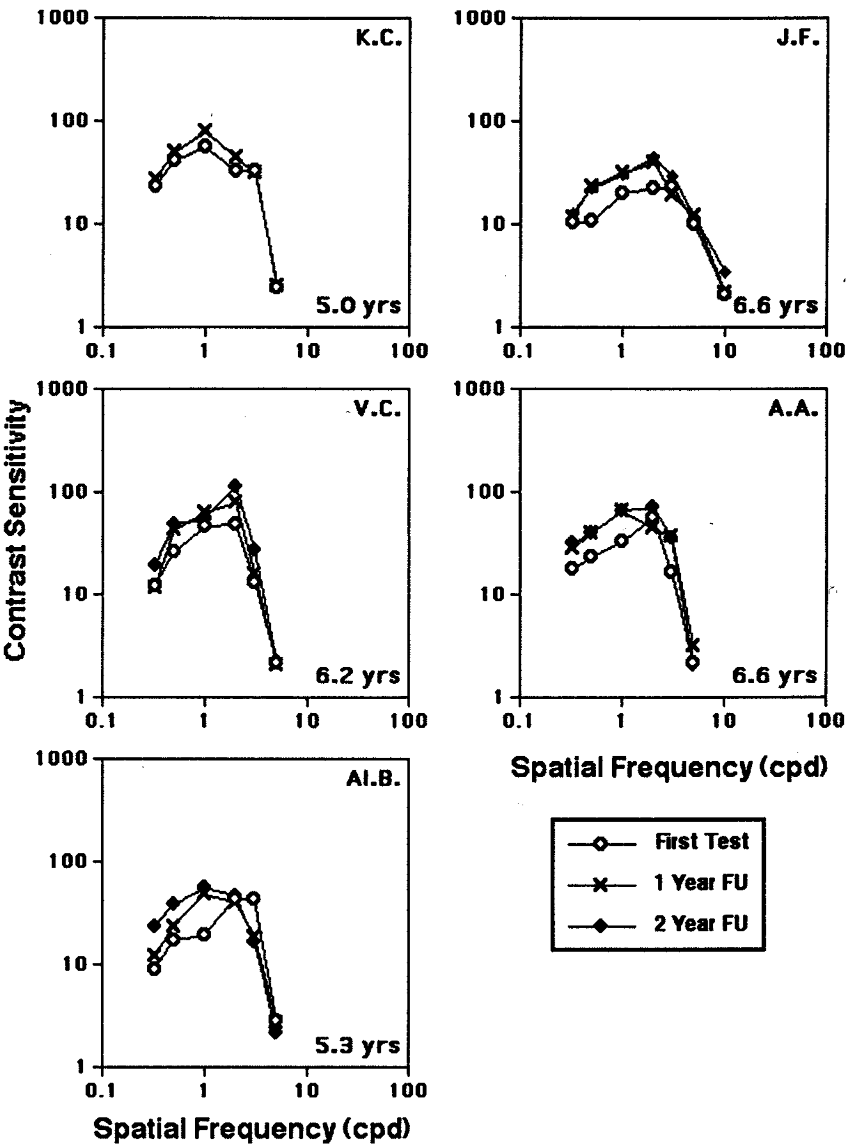


Fig. 7. Contrast sensitivity of children treated for bilateral congenital cataract who were first tested between age 5 and 8 years (○) and then retested 1 year (×) and/or 2 years (◇) later. Repeat tests from two older children are also shown. The age at the first test is indicated in the bottom right corner of the box for each patient. Adapted with permission from Maurer et al. (2006).

the stimuli are inverted (Yin, 1969), just as their sensitivity to second-order relations in faces plummets with inversion, much more than their sensitivity to facial features (Leder and Bruce, 1998; Freire et al., 2000; Mondloch et al., 2002; Malcolm et al., 2005; Leder and Carbon, 2006; Rhodes et al. 2006; but see Riesenhuber et al., 2004; Sekuler et al., 2004; Yovel and Kanwisher, 2004, 2005; see also Collishaw and Hole, 2000).

Our first study of face processing in children treated for bilateral congenital cataract indicated that they have deficits in recognizing the identity of a face they saw about one-half second earlier if the orientation of the head changed (e.g., from

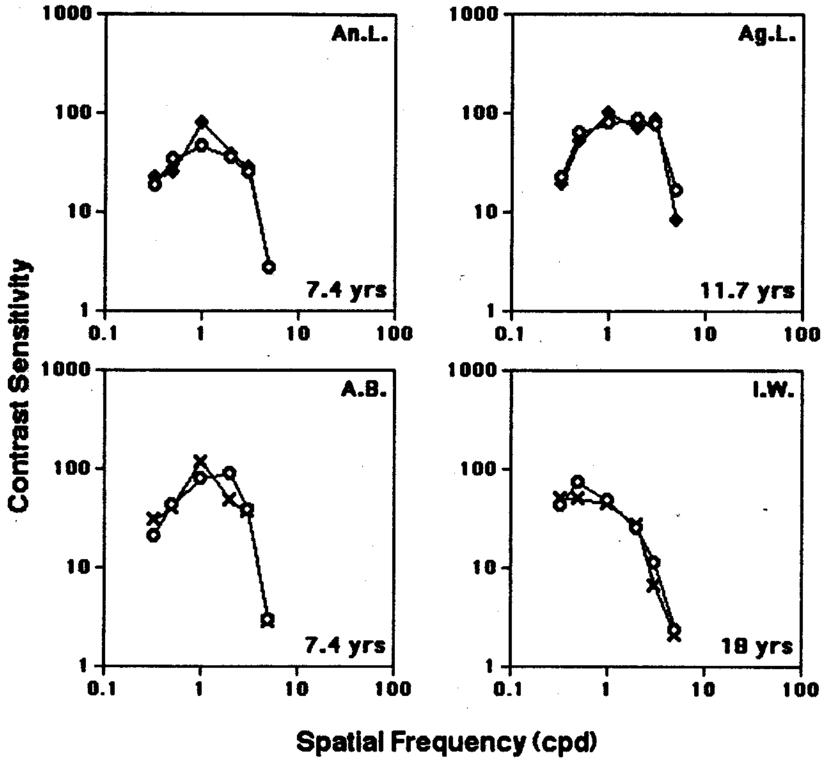
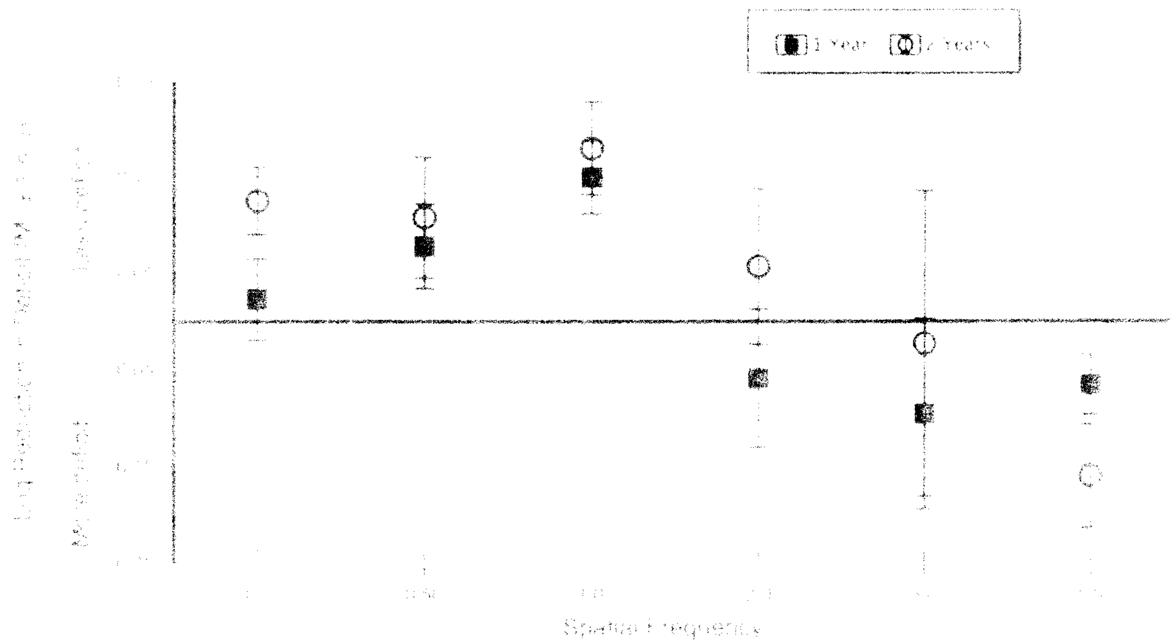


Fig. 7. *Continued.*

looking up to turned 45° toward the side) (Geldart et al., 2002). Good performance on this task depends on sensitivity to second-order relations because as the head is rotated, the shape of features and the external contour appear to change or are occluded, but the basic layout of the face determined by bone structure — the second-order relations — remains constant. As would be expected, the accuracy of adults with normal eyes on this task drops dramatically if the stimuli are inverted (Mondloch et al., 2003b). Therefore, we suspected that early visual deprivation might interfere with the development of sensitivity to second-order relations. Because the patients were normal on our measures of lip-reading, matching emotional expression, and matching direction of eye gaze (Geldart et al., 2002) — all of which could be solved by attending to specific features and none of which were impaired by inversion (Mondloch et al., 2003b) — we suspected that the patients might have normal featural processing.

To test these predictions directly, we created a task (which has come to be called the "Jane" test of facial identity) in which subjects make same/different judgments about pairs of faces presented sequentially that differ only in the shape of the external contour, only in the shape of the eyes and mouth, or only in the spacing between the eyes and between the eyes and mouth (Mondloch et al., 2002). Figure 11 illustrates the faces used. Changes of each type are presented in separate blocks in order to encourage reliance on contour processing, featural processing, and processing of second-order relations, respectively. Control experiments with normal adults confirmed that, as expected if it is a valid measure of sensitivity to second-order relations, inversion decreased accuracy for the spacing set much more than it did for the other two sets (Mondloch et al., 2002). Studies of children with normal eyes indicate that accuracy for the feature and contour sets is (nearly) adult-like by 6 years of age but that accuracy for the spacing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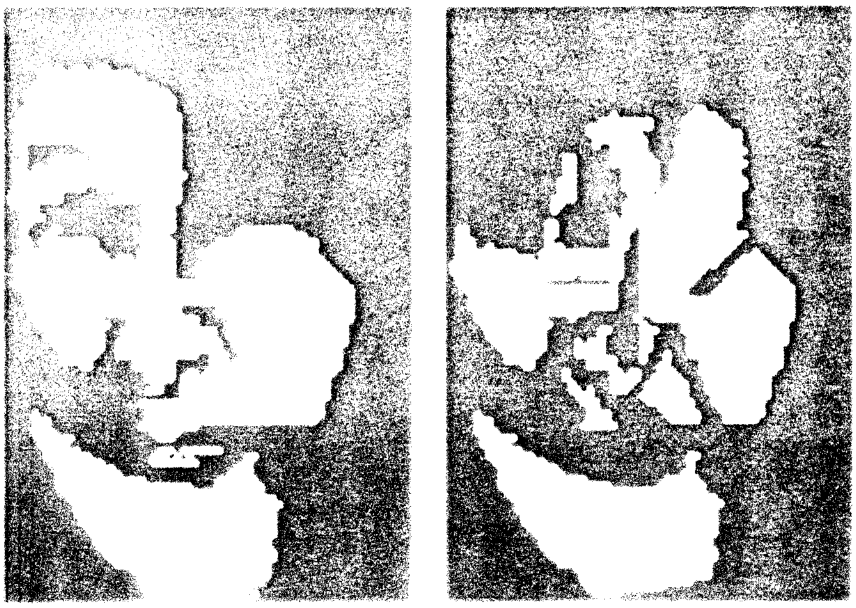

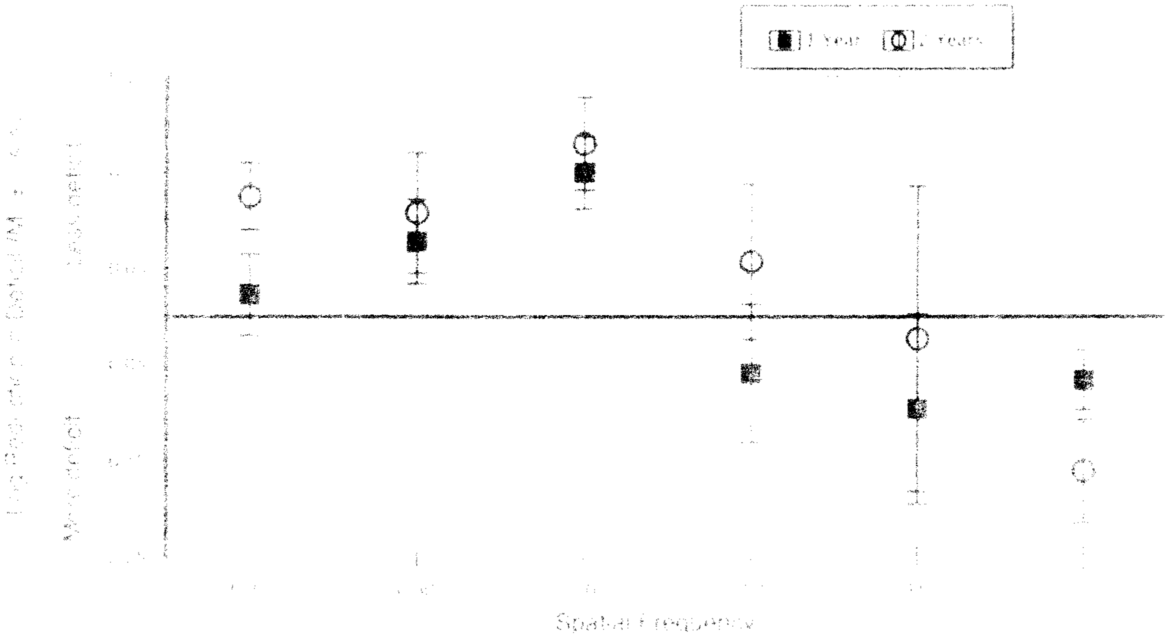
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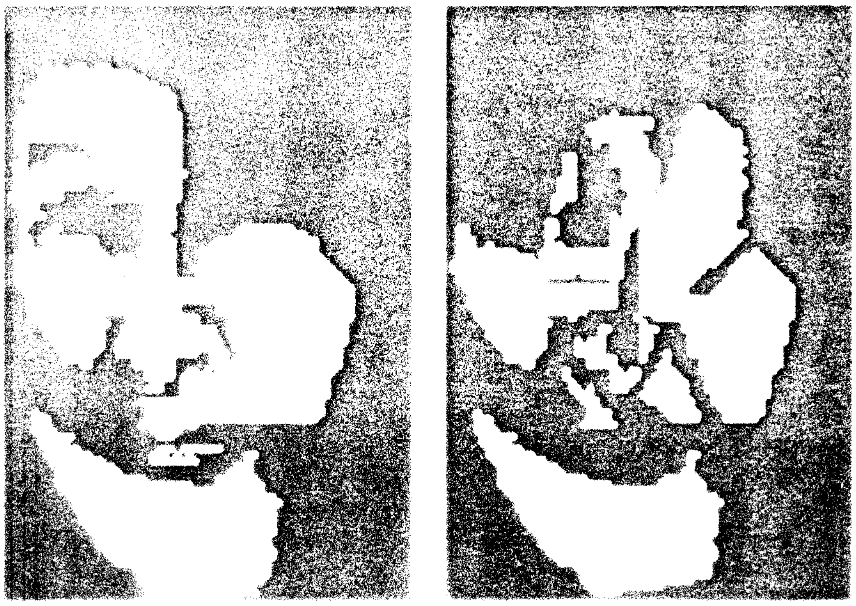


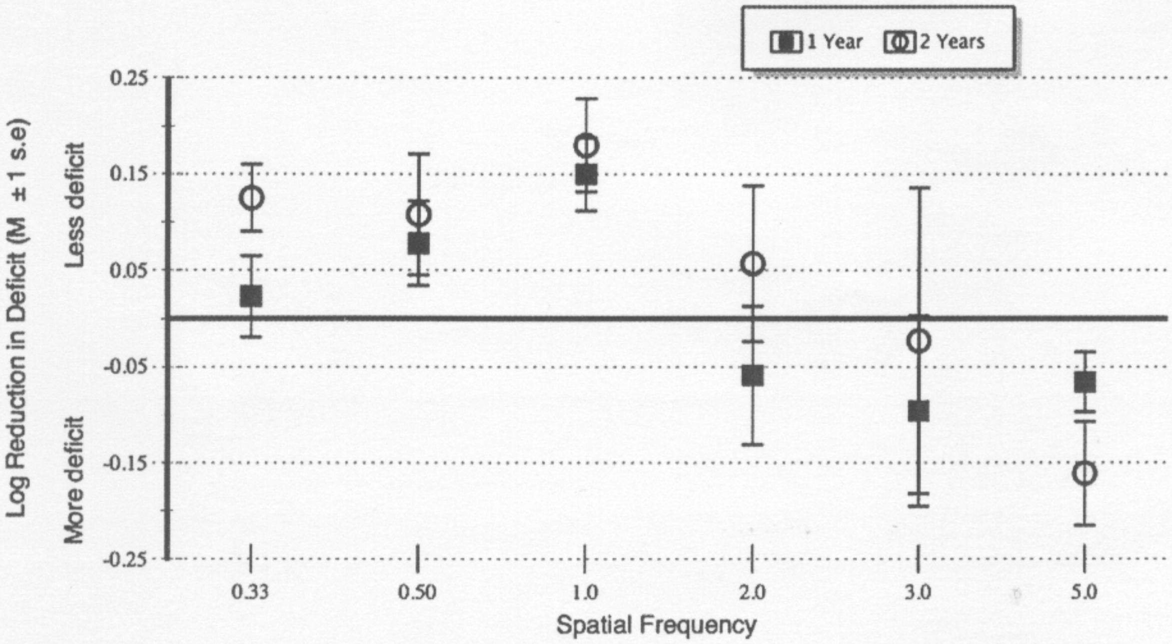


Fig. 8. Change in contrast sensitivity deficit in log units for the patients shown in Fig. 7 who were first tested before 8 years of age. Each point represents the mean change in deficit (±1 s.e.) after 1 year (closed symbols) or after 2 years (open symbols). Positive values represent a reduction in the size of the deficit (i.e., normalization) and negative values represent an increase in the size of the deficit (i.e., greater deviation from normal). Adapted with permission from Maurer et al. (2006).

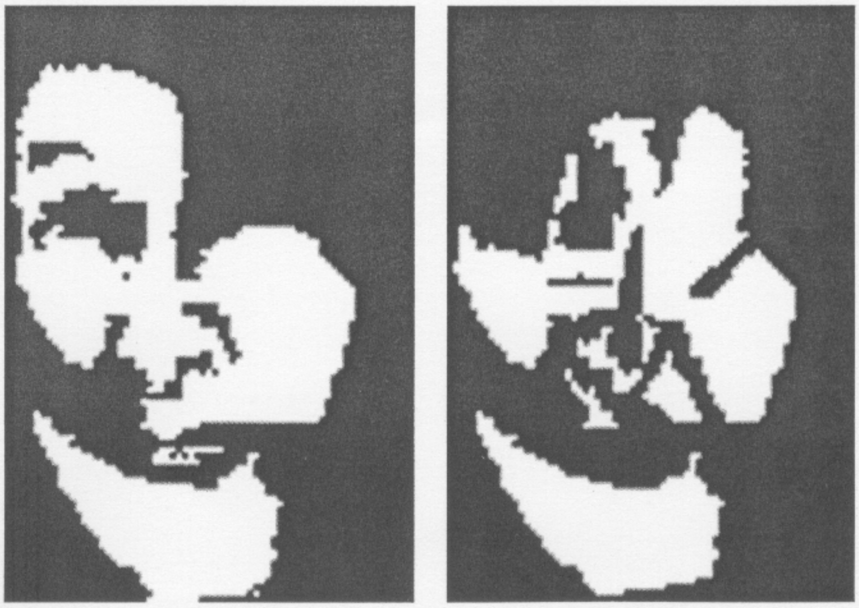


Fig. 9. An example of a Mooney face (A) and a scrambled Mooney face (B) of the type used to test face detection in children treated for bilateral congenital cataract. All luminance values are set to white and black, a manipulation that eliminates veridical facial features. Nevertheless, adults can detect the first-order relations that define a face when the stimuli are upright.

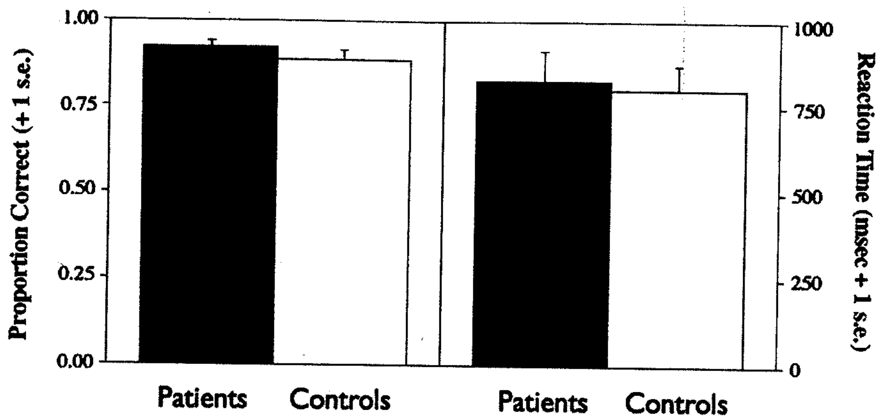


Fig. 10. Mean accuracy (± 1 s.e.) (left panel) and mean reaction time (right panel) for determining whether a Mooney image was a face or non-face in patients treated for bilateral congenital cataract and in the age-matched control group.

set improves even after 14 years of age (Mondloch et al., 2002, 2003a). This is despite the fact that accuracy for the contour and spacing sets is identical in adults with normal eyes, that adults' accuracy for the featural set is in the typical range that we have found with a much larger set of faces (Mondloch et al., unpublished data), and that the spacing differences cover most of the variance in the normal population of adult Caucasian female faces (Farkas, 1981).

Sensitivity to second-order relations not only develops more slowly than sensitivity to other cues to facial identity, it also emerges later in development. A simpler version of the Jane task indicated that 4-year-olds are able to recognize the faces of children they learned from a storybook and a picture of their own face when tested with foils with contour or feature differences. In contrast, they perform at chance when tested with foils with spacing differences, even though the spacing differences captured most of the variability among children's faces (Mondloch et al., 2006b; but see McKone and Boyer, 2006, for evidence of earlier sensitivity to spacing differences as a cue to typicality). Note, however, that when the spacing differences exceed natural limits, sensitivity to spacing differences in faces is apparent in infants as young as 5 months (but not 3 months) of age (Bertin and Bhatt, 2004; Bhatt et al., 2005).

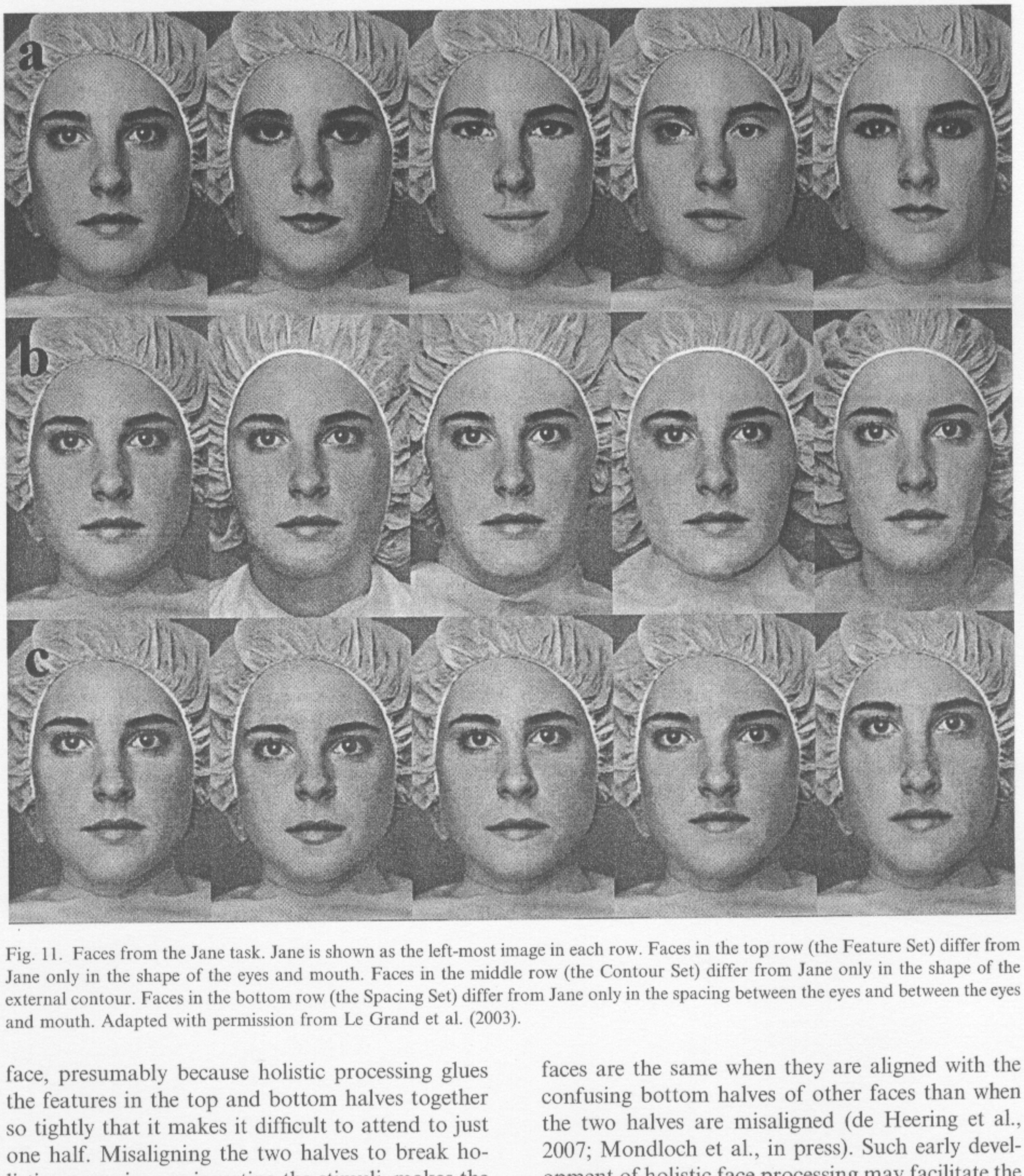
As indicated in Fig. 12, patients treated for bilateral congenital cataract performed normally on the contour and featural sets but had significant impairments on the spacing set, even when the initial deprivation had ended by 2 months of age (Le Grand et al., 2001, 2003; Mondloch et al., 2003a). Subsequent studies with children treated for unilateral cataract suggested that it is specifically input to the right hemisphere during early infancy that is necessary to set up the system so that it can later gain expertise in recognizing faces based on second-order relations (Le Grand et al., 2003). Thus, visual input during early infancy, at a time when the infant demonstrates no sensitivity to second-order relations, is necessary to set up the neural substrate — presumably in the right hemisphere — that will allow the later development of normal sensitivity to second-order relations.

Holistic face processing

One reason for the patients' deficit in processing second-order relations might be that they never learned to process faces holistically. Unlike objects, adults process faces as a holistic Gestalt, gluing the features together into a whole that is difficult to parse into individual features. One measure of holistic processing is the composite face effect (e.g., Young et al., 1987; Hole, 1994). When adults are asked to judge the identity of faces from just the top half, they have difficulty doing so if the top half is aligned with the bottom half of another person's

Fig. 11. Faces from the Jane task. Jane is shown as the left-most image in each row. Faces in the top row (the Feature Set) differ from Jane only in the shape of the eyes and mouth. Faces in the middle row (the Contour Set) differ from Jane only in the shape of the external contour. Faces in the bottom row (the Spacing Set) differ from Jane only in the spacing between the eyes and between the eyes and mouth. Adapted with permission from Le Grand et al. (2003).

face, presumably because holistic processing glues the features in the top and bottom halves together so tightly that it makes it difficult to attend to just one half. Misaligning the two halves to break holistic processing, or inverting the stimuli, makes the task much easier (see Fig. 13). Children as young as 4–6 years of age show an adult-like composite face effect: just like adults, they are 20–25% less accurate in seeing that the top halves of two unfamiliar faces are the same when they are aligned with the confusing bottom halves of other faces than when the two halves are misaligned (de Heering et al., 2007; Mondloch et al., in press). Such early development of holistic face processing may facilitate the development of sensitivity to second-order relations by forcing the child to pay attention to the proportions of the face and to relate them to the proportions of an average face at the center of an



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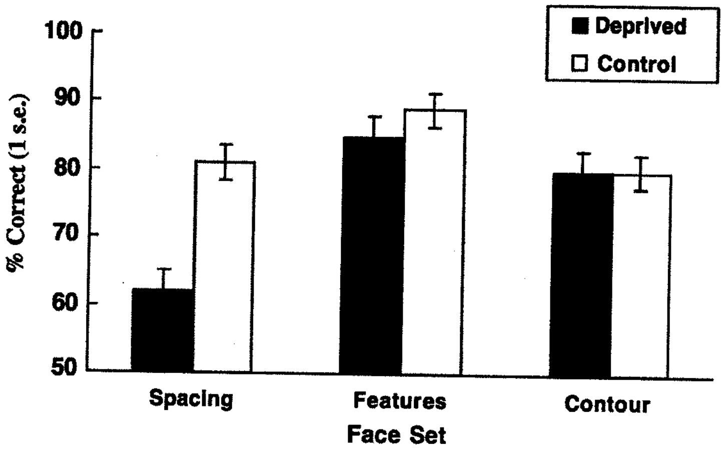

Fig. 12. Mean accuracy (±1 s.e.) for the Spacing, Feature, and Contour Sets of the Jane task (see Fig. 11). Shown are the results for children treated for bilateral congenital cataracts and for age-matched controls.

n-dimensional face space (Rhodes et al., 1987, 2003; Valentine, 1991; Rhodes and Jeffery, 2006).

Patients treated for bilateral congenital cataract do not show normal holistic processing of faces, even when the deprivation ended by 3 months of age (Le Grand et al., 2004). Importantly, they demonstrated this deficit by *superior* performance on the composite face task. Unlike the control group, their accuracy in judging that the top halves of the two sequential faces were the same was as high when the two tops were aligned with different bottom halves as when they were misaligned. In fact, their accuracy in the critical condition (same/aligned) where holistic processing impairs normal performance was significantly *higher* than that of the control group.

Cashon and Cohen (2003, 2004) have tested for the first signs of holistic processing during infancy by testing whether babies treat a switched face with the internal features of one familiar face and the external features of another familiar face like a novel face (as it would be if the internal and external features are integrated holistically) or as a familiar face (as it would be if the features are processed separately). The results indicate that 4-month-olds, but not 3-month-olds, process the internal and external features holistically. Combined, the results indicate that visual input during the first 3 months of life — before the first manifestations of holistic processing — is necessary to set up the system for its later development.

Summary and developmental implications

In summary, early visual deprivation from congenital cataract prevents the later development of normal visual acuity, contrast sensitivity for mid and high spatial frequencies, and two aspects of configural face processing: holistic face processing and decoding of identity based on second-order relations. It does not prevent the development (or more, likely, allows recovery) of normal contrast sensitivity for low spatial frequencies, normal face detection, and normal featural processing. The deficits described here are all examples of sleeper effects: visual deprivation during a period in normal infancy before the first manifestations of functional ability prevents their later development (Maurer et al., 2007).

Because the cataracts blocked all patterned visual input to the retina, we do not know if specific types of input are necessary for each visual capability; for example, whether it is specifically input from faces that is necessary for the normal development of face processing. However, the fact that holistic processing and sensitivity to second-order relations later become refined for the types of faces

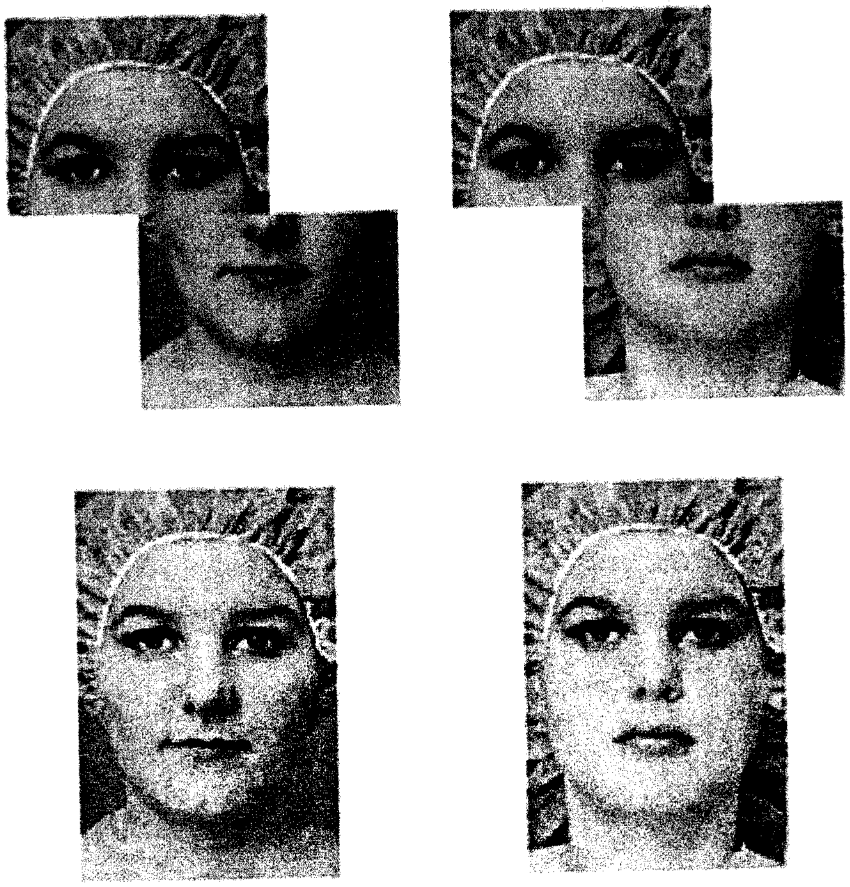

Fig. 13. Examples of faces used on same trials in the composite face task. Subjects are asked to indicate whether the top halves of the two faces are the same when the bottom half is different and misaligned (top panel) or aligned (bottom panel). Holistic processing makes the top halves of the aligned faces look different. Adapted with permission from Le Grand et al. (2004).

the individual typically observes (own race; own species) indicates that it is likely that face input *per se* plays some role (Michel et al., 2006; Mondloch et al., 2006a; Rhodes et al., 2006).

One possible explanation of such sleeper effects is that visual input during early infancy is necessary to set up or preserve the optimal neural architecture for the visual capability. In the absence of visual input, the requisite cells and/or connections may fail to develop or be lost through competitive interactions from inputs from other sensory modalities, as suggested by the specialization of the visual cortex, including the primary visual cortex, for touch, hearing, and perhaps even language in the congenitally blind (Kujala et al., 1995; Cohen et al., 1999; Röder et al., 2000; Bavelier and Neville, 2002; Burton et al., 2002a, b; Sadato et al., 2002; Amedi et al., 2003; Burton et al., 2003; Gizewski et al., 2003; reviewed in Maurer et al., 2005). By this account, the visual capability cannot develop normally at a later point in development because the optimal neural architecture to support it is not available.

Alternatively, the optimal architecture may be preserved and the needed connections formed, but those connections may be silenced or visual neuronal responses may be actively inhibited because of stronger input from other modalities during the initial deprivation and perhaps even subsequently. This possibility is suggested by evidence that the visual cortex can become responsive to tactile and auditory inputs even when blindness begins as late as adolescence (Cohen et al., 1999; Sadato et al.,

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2002) and, to a lesser extent, even in adulthood (Burton et al., 2002a, 2004). Further support comes from evidence that a blind adult, who had been born without natural lenses, slowly became able to perceive unified objects when he was first given compensatory glasses at age 29 (Mandavilli, 2006; but see Fine et al., 2003). Such evidence suggests that there are multimodal connections to the visual cortex that can develop or be preserved even in the absence of sensory input and that can be revealed in adulthood.

A third — and not mutually exclusive — possibility is that early visual deprivation leads to the recruitment of alternative pathways to support vision that bypass the primary visual cortex and that send input to higher visual centers via the superior colliculus, pretectum, and pulvinar. That possibility is suggested by evidence from cats that were deprived of early visual input by hoods covering their heads who later are able to learn to make visual discriminations, although it takes much more than the normal number of trials (Zablocka et al., 1976, 1980; Zernicki, 1979; Zablocka and Zernicki, 1996). Subsequent selective lesions indicate that the deprived cats use an alternative pathway to perform the task: lesions to the primary visual cortex impaired the performance of the normal cats in the control group but not the deprived group, whereas lesions of the pretectum or superior colliculus impaired performance of the deprived group but not the normal group. If children treated for bilateral congenital cataract use such an alternative pathway, then the pattern of recovery and deficit may simply reflect the limits on the functions that the alternative pathway can support.

Future research using neuroimaging techniques may help to distinguish among these hypotheses. It is also possible that training with feedback in the areas of deficit might lead to improved or even normal visual capabilities, as it has for contrast sensitivity deficits in adults with anisometropic amblyopia, a reduction in vision caused by unequal refractive errors in the two eyes during early childhood (Zhou et al., 2006). Additional evidence for the likely benefit of training comes from studies indicating that the vision of adults with normal eyes improves after playing action video games (Green and Bavelier, 2003, 2006, 2007) and from studies that have effectively trained adults to reduce the other-race disadvantage in face recognition (Elliott et al., 1973; Goldstein and Chance, 1985). Training studies with adults and children with a history of early visual deprivation from bilateral cataracts may help to elucidate whether the deficits reflect permanent changes in the neural architecture or whether there is sufficient residual plasticity to allow additional recovery. Whatever the outcome, our results indicate that early visual input shapes the nervous system of the infant with normal eyes in ways that permit the child to later develop the acute sensitivity to the details of pattern that is needed for reading and sensitivity to the configural properties of faces that is vital to social interactions.

Acknowledgments

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References

Amedi, A., Raz, N., Pianka, P., Malach, R. and Zohary, E. (2003) Early 'visual' cortex activation correlates with superior verbal memory performance in the blind. Nat. Neurosci., 6(7): 758–766.

Atkinson, J., Braddick, O. and Moar, K. (1977) Contrast sensitivity of the human infant for moving and static patterns. Vis. Res., 17(9): 1045–1047.

Bahrick, H.P., Bahrick, P.O. and Wittlinger, R.P. (1975) Fifty years of memory for names and faces: a cross-sectional approach. J. Exp. Psychol. Gen., 104(1): 54–75.

Banks, M.S. and Salapatek, P. (1978) Acuity and contrast sensitivity in 1-, 2-, and 3-month-old human infants. Invest. Ophthalmol. Vis. Sci., 17(4): 361–365.

Bavelier, D., and Neville, H. (2002) Cross-modal plasticity: where and how? Nat. Rev. Neurosci., 3 (6): 443–452.

Bertin, E. and Bhatt, R.S. (2004) The Thatcher illusion and face processing in infancy. Dev. Sci., 7(4): 431–436.

Bhatt, R.S., Bertin, E., Hayden, A. and Reed, A. (2005) Face processing in infancy: developmental changes in the use of different kinds of relational information. Child Dev., 76(1): 169–181.

Blakemore, B. and Vital-Durand, F. (1983) Visual deprivation prevents the postnatal maturation of spatial contrast sensitivity neurons of the monkey's striate cortex. J. Physiol., 345: 45.

Blakemore, B. and Vital-Durand, F. (1986) Effects of visual deprivation on the development of the monkey's lateral geniculate nucleus. J. Physiol., 380(1): 493–511.

Brown, A.M. and Yamamoto, M. (1986) Visual acuity in newborn and preterm infants measured with grating acuity cards. Am. J. Opthamol., 102(2): 245–253.

Bruce, V., Campbell, R.N., Doherty-Sneddon, G., Import, A., Langton, S., McAuley, S. and Wright, R. (2000) Testing face processing skills in children. Br. J. Dev. Psychol., 18(3): 319–333.

Bruce, V. and Young, A.W. (1998) In the Eye of the Beholder: The Science of Face Perception. Oxford University Press, Oxford.

Burton, H., Diamond, J. and McDermott, K. (2003) Dissociating cortical regions activated by semantic and phonological tasks: a fMRI study in blind and sighted people. J. Neurophysiol., 90(3): 1965–1982.

Burton, H., Sinclair, R. and McLaren, D. (2004) Cortical activity to vibrotactile stimulation: An fMRI study in blind and sighted individuals. Hum. Brain Mapp., 23(4): 210–238.

Burton, H., Snyder, A., Conturo, T., Akbudak, E., Ollinger, J. and Raichle, M. (2002a) Adaptive changes in early and late blind: a fMRI study of Braille reading. J. Neurophysiol., 87(1): 589–607.

Burton, H., Snyder, A., Diamond, J. and Raichle, M. (2002b) Adaptive changes in early and late blind: an fMRI study of verb generation to heard nouns. J. Neurophysiol., 88(6): 3359–3371.

Carey, S., Diamond, R. and Woods, B. (1980) Development of face recognition: a maturational component? Dev. Psychol., 16(4): 257–269.

Cashon, C.H. and Cohen, L.B. (2003) The construction, deconstruction, and reconstruction of infant face perception. In: Pascalis O. and Slater A. (Eds.), The Development of Face Processing in Infancy and Early Childhood: Current Perspectives. NOVA Science Publishers, New York, pp. 55–68.

Cashon, C.H. and Cohen, L.B. (2004) Beyond U-shaped development in infants' processing of faces: an information-processing account. J. Cogn. Dev., 5(1): 59–80.

Cohen, L., Weeks, R., Sadato, N., Celnik, P., Ishii, K. and Hallett, M. (1999) Period of susceptibility for cross-modal plasticity in the blind. Ann. Neurol., 45(4): 451–460.

Collishaw, S.M. and Hole, G.J. (2000) Featural and configural processes in the recognition of faces of different familiarity. Perception, 29(8): 893–909.

Courage, M. and Adams, R. (1990) Visual acuity assessment from birth to three years using the acuity card procedure: cross-sectional and longitudinal samples. Optom. Vis. Sci., 67(9): 713–718.

Crawford, M.L., Blake, R., Cool, S. and von Noorden, G. (1975) Physiological consequences of unilateral and bilateral eye closure in macaque: some further observations. Brain Res., 85(1): 150–154.

Crawford, M.L.J., Pesch, T.W., von Noorden, G.K., Harwerth, R.S. and Smith, E.L. (1991) Bilateral form deprivation in monkeys: electrophysiologic and anatomic consequences. Invest. Ophthalmol. Vis. Sci., 32(8): 2328–2336.

De Haan, M., Johnson, M., Maurer, D. and Perrett, D. (2001) Recognition of individual faces and average face prototypes by 1- and 3-month-old infants. Cogn. Dev., 16(2): 659–678.

De Heering, A., Houthuys, S. and Rossion, B. (2007) Holistic face processing is mature at 4 years of age: evidence from the composite face effect. J. Exp. Child Psychol., 96(1): 57–70.

Diamond, R. and Carey, S. (1986) Why faces are and are not special: an effect of expertise. J. Exp. Psychol. Gen., 115(2): 107–117.

Ellemberg, D., Lewis, T.L., Liu, C.H. and Maurer, D. (1999a) The development of spatial and temporal vision during childhood. Vis. Res., 39(14): 2325–2333.

Ellemberg, D., Lewis, T.L., Maurer, D., Liu, C.H. and Brent, H.P. (1999b) Spatial and temporal vision in patients treated for bilateral congenital cataracts. Vis. Res., 39(20): 3480–3489.

Elliott, E., Wills, E. and Goldstein, A. (1973) The effects of discrimination training on the recognition of white and oriental faces. Bull. Psychon. Soc., 2: 71–73.

Farkas, L. (1981) Anthropometry of the Head and Face in Medicine. Elsevier, New York.

Fine, I., Wade, A.R., May, M.G., Goodman, D.F., Boynton, G.M. and Wandell, B.A. (2003) Long-term visual deprivation affects visual perception and cortex. Nat. Neurosci., 6(9): 915–916.

Freire, A., Lee, K. and Symons, L.A. (2000) The face-inversion effect as a deficit in the encoding of configural information: direct evidence. Perception, 29(2): 159–170.

Geldart, S., Mondloch, C., Maurer, D., de Schonen, S. and Brent, H. (2002) The effects of early visual deprivation on the development of face processing. Dev. Sci., 5(4): 490–501.

Gizewski, E., Gasser, T., de Greiff, A., Boehm, A. and Forsting, M. (2003) Cross-modal plasticity for sensory and motor activation patterns in blind subjects. Neuroimage, 19(3): 968–975.

Goldstein, A. and Chance, J. (1985) Effects of training on Japanese face recognition: reduction of the other-race effect. Bull. Psychon. Soc., 23: 211–214.

Green, C. and Bavelier, D. (2003) Action video game modifies visual selective attention. Nature, 423(6939): 534–537.

Green, C.S. and Bavelier, D. (2006) Effect of action video games on the spatial distribution of visuo-spatial attention. J. Exp. Psychol. Hum. Percept. Perform., 32(6): 1465–1478.

Green, C.S. and Bavelier, D. (2007) Action video game experience alters the spatial resolution of vision. Psychol. Sci., 18(1): 88–94.

Gwiazda, J., Bauer, J., Thorn, F. and Held, R. (1997) Development of spatial contrast sensitivity from infancy to adulthood: psychophysical data. Optom. Vis. Sci., 74(10): 785–789.

Hendrickson, A. and Boothe, R. (1976) Morphology of the retinal and dorsal lateral geniculate nucleus in dark-reared monkeys (*Maccaca nemestrina*). Vis. Res., 16(5): 517–521.

Hole, G. (1994) Configurational factors in the perception of unfamiliar faces. Perception, 23(1): 65–74.

Kanwisher, N., Tong, F. and Nakayama, K. (1998) The effect of face inversion on the human fusiform face area. Cognition, 68(1): B1–B11.

Kugelberg, U. (1992) Visual acuity following treatment of bilateral congenital cataracts. Doc. Ophthalmol., 82(3): 211–215.

Kujala, T., Huotilainen, M., Sinkkonen, J., Ahonen, A., Alho, K., Hamalainen, M., Ilmoniemo, R.S., Kajola, M., Knuutila, J.E., Lavikainen, J., Salonen, O., Simola, J., Standerskjold-Nordenstam, C.-G., Tiitinen, H., Tissari, S.O. and Naatanen, R. (1995) Visual cortex activation in blind humans during sound discrimination. Neurosci. Lett., 183(1–2): 143–146.

Leder, H. and Bruce, V. (1998) Local and relational aspects of face distinctiveness. Q. J. Exp. Psychol., 51(3): 449–473.

Leder, H. and Carbon, C. (2006) Face-specific configural processing of relational information. Br. J. Psychol., 97(part 1): 19–29.

Le Grand, R., Mondloch, C., Maurer, D. and Brent, H.P. (2001) Early visual experience and face processing. Nature, 410(6831): 890 Correction: 2001, 412 (6849) p. 786.

Le Grand, R., Mondloch, C., Maurer, D. and Brent, H. (2003) Expert face processing requires visual input to the right hemisphere during infancy. Nat. Neurosci., 6(10): 1108–1112 Erratum: 2003, 6 (12) 1329.

Le Grand, R., Mondloch, C., Maurer, D. and Brent, H. (2004) Impairment in holistic face processing following early visual deprivation. Psychol. Sci., 15(11): 762–768.

Lewis, T.L., Maurer, D. and Brent, H.P. (1995) The development of grating acuity in children treated for unilateral or bilateral congenital cataract. Invest. Ophthalmol. Vis. Sci., 36(10): 2080–2095.

Magnusson, G., Abrahamsson, M. and Sjöstrand, J. (2002) Changes in visual acuity from 4 to 12 years of age in children operated for bilateral congenital cataracts. Br. J. Ophthalmol., 86(12): 1385–1398.

Malcolm, G., Leung, C. and Barton, J.J.S. (2005) Regional variations in the inversion effect for faces: differential effects for feature shape, spatial relations, and external contour. Perception, 33(10): 1221–1231.

Mandavilli, A. (2006) Look and learn. Nature, 441(7091): 271–272 (News feature).

Maurer, D., Ellemberg, D. and Lewis, T.L. (2006) Repeated measures of contrast sensitivity reveal limits to visual plasticity after early binocular deprivation in humans. Neuropsychologica, 44(11): 2104–2112.

Maurer, D., Le Grand, R. and Mondloch, C. (2002) The many faces of configural processing. Trends Cong. Sci., 6(6): 255–260.

Maurer, D. and Lewis, T. (2001a) Visual acuity and spatial contrast sensitivity: normal development and underlying mechanisms. In: Nelson C. and Luciana M. (Eds.), Handbook of Developmental Cognitive Neuroscience. MIT Press, Cambridge, MA, pp. 237–250.

Maurer, D. and Lewis, T.L. (2001b) Visual acuity: the role of visual input in inducing postnatal change. Clin. Neurosci. Res., 1(1): 239–247.

Maurer, D., Lewis, T.L., Brent, H.P. and Levin, A.V. (1999) Rapid improvement in the acuity of infants after visual input. Science, 286(5437): 108–110.

Maurer, D., Lewis, T.L. and Mondloch, C. (2005) Missing sights: consequences for visual cognitive development. Trends Cogn. Sci., 9(3): 144–151.

Maurer, D., Mondloch, C.J. and Lewis, T.L. (2007) Sleeper effects. Dev. Sci., 10(1): 40–47.

Mayer, D.L., Beiser, A.S., Warner, A.F., Pratt, E.M., Raye, K.N. and Lang, J.M. (1995) Monocular acuity norms for the Teller acuity cards between ages one month and four years. Invest. Ophthalmol. Vis. Sci., 36(3): 671–685.

Mayer, D.L. and Dobson, V. (1982) Visual acuity development in infants and young children as assessed by operant preferential looking. Vis. Res., 22(9): 1141–1151.

McKone, E. and Boyer, B. (2006) Sensitivity of 4-year-olds to featural and second-order relational changes in face distinctiveness. J. Exp. Child Psychol., 94(2): 134–162.

Michel, C., Rossion, B., Han, J., Chung, C.-S. and Caldara, R. (2006) Holistic processing is finely tuned for faces of our own race. Psychol. Sci., 17(7): 608–615.

Mondloch, C.J., Geldart, S., Maurer, D. and Le Grand, R. (2003b) Developmental changes in face processing skills. J. Exp. Child Psychol., 86(1): 67–84.

Mondloch, C.J., Le Grand, R. and Maurer, D. (2002) Configural face processing develops more slowly than featural face processing. Perception, 31(5): 553–566.

Mondloch, C.J., Le Grand, R. and Maurer, D. (2003a) Early visual experience is necessary for the development of some–but not all–aspects of face processing. In: Pascalis O. and Slater A. (Eds.), The Development of Face Processing in Infancy and Early Childhood: Current Perspectives. Nova Science Publishers, New York, pp. 99–117.

Mondloch, C.J., Leis, A. and Maurer, D. (2006b) Recognizing the face of Johnny, Suzy, and me: insensitivity to the spacing among features at four years of age. Child Dev., 77(1): 234–243.

Mondloch, C.J., Lewis, T.L., Maurer, D. and Levin, A.V. (1998) The effects of visual experience on face preferences during infancy. Dev. Cognit. Neurosci., Tech. Rep. No. 98.4.

Mondloch, C.J., Maurer, D. and Ahola, S. (2006a) Becoming a face expert. Psychol. Sci., 17(11): 930–934.

Mondloch, C.J., Pathman, T., Maurer, D., Le Grand, R. and De Schonen, S. (in press) The composite face effect in six-year-old children: Evidence of adultlike holistic face processing. Vis. Cogn.

Moscovitch, M., Winocur, G. and Behrman, M. (1997) What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. J. Cogn. Neurosci., 9(5): 555–604.

Rhodes, G., Brennan, S. and Carey, S. (1987) Identification and ratings of caricatures: Implications for mental representations of faces. Cogn. Psychol., 19(4): 473–497.

Rhodes, G., Hayward, W. and Winkler, C. (2006) Expert face coding: configural and component coding of own-race and other-race faces. Psychon. Bull. Rev., 13(3): 499–505.

Rhodes, G. and Jeffery, L. (2006) Adaptive norm-based coding of facial identity. Vis. Res., 46(18): 2977–2987.

Rhodes, G., Jeffery, L., Watson, T.L., Clifford, C.W.G. and Nakayama, K. (2003) Fitting the mind to the world: face adaptation and attractiveness aftereffects. Psychol. Sci., 14(6): 558–566.

Riesenhuber, M., Jarudi, I., Gilad, S. and Sinha, P. (2004) Face processing in humans is compatible with a simple shape-based model of vision. Proc. Biol. Sci., 271(supplement 6): S448–S450.

Röder, B., Rösler, F. and Neville, H. (2000) Event-related potentials during auditory language processing in congenitally blind and sighted people. Neuropsychologia, 38(11): 1482–1502.

Sadato, N., Okada, T., Honda, M. and Yonekura, Y. (2002) Critical period for cross-modal plasticity in blind humans: a functional MRI study. Neuroimage, 16(2): 389–400.

Sekuler, A., Gaspar, C., Gold, J. and Bennett, P. (2004) Inversion leads to quantitative not qualitative changes in face processing. Curr. Biol., 14(5): 391–396.

Valentine, T. (1991) A unified account of the effects of distinctiveness, inversion, and race in face recognition. Q. J. Exp. Psychol. A, 43(2): 161–204.

Van Hof-van Duin, J. and Mohn, G. (1986) The development of visual acuity in normal fullterm and preterm infants. Vis. Res., 26(6): 909–916.

Yin, R.K. (1969) Looking at upside down faces. J. Exp. Psychol., 81: 141–145.

Young, A.W., Hellawell, D. and Hay, D.C. (1987) Configurational information in face perception. Perception, 16(6): 747–759.

Yovel, G. and Kanwisher, N. (2004) Face perception: domain specific, not process specific. Neuron, 44(5): 889–898.

Yovel, G. and Kanwisher, N. (2005) The neural basis of the behavioral face-inversion effect. Curr. Biol., 15(24): 2256–2262.

Zablocka, T. and Zernicki, B. (1996) Discrimination learning of grating orientation in visually deprived cats and the role of the superior colliculi. Behav. Neurosci., 110(3): 621–625.

Zablocka, T., Zernicki, B. and Kosmal, A. (1976) Visual cortex role in object discrimination in cats deprived of pattern vision from birth. Acta Neurobiol. Exp. (Wars), 36(1–2): 157–168.

Zablocka, T., Zernicki, B. and Kosmal, A. (1980) Loss of object discrimination after ablation of the superior colliculus-pretectum in binocularly deprived cats. Behav. Brain Res., 1(6): 521–531.

Zernicki, B. (1979) Effects of binocular deprivation and specific experience in cats: behavioral, electrophysiological, and biochemical analyses. In: Brazier M. (Ed.), Brain Mechanisms in Memory and Learning: From the Single Neuron to Man. Raven Press, New York, pp. 179–195.

Zhou, Y., Huang, C., Xu, P., Tao, L., Qiu, Z., Li, X. and Lu, Z.-L. (2006) Perceptual learning improves contrast sensitivity and visual acuity in adults with anisometropic amblyopia. Vis. Res., 46(5): 739–750.