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PAPER

# The role of early visual input in the development of contour interpolation: the case of subjective contours

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## Abstract

*We tested the effect of early monocular and binocular deprivation of normal visual input on the development of contour interpolation. Patients deprived from birth by dense central cataracts in one or both eyes, and age-matched controls, discriminated between fat and thin shapes formed by either illusory or luminance-defined contours. Thresholds indicated the minimum amount of curvature (the fatness or thinness) required for discrimination of the illusory shape, providing a measure of the precision of interpolation. The results show that individuals deprived of visual input in one eye, but not those deprived in both eyes, later show deficits in perceptual interpolation. The deficits were shown mostly for weakly supported contours in which interpolation of contours between the inducers was over a large distance relative to the size of the inducers. Deficits shown for the unilateral but not for the bilateral patients point to the detrimental effect of unequal competition between the eyes for cortical connections on the later development of the mechanisms underlying contour interpolation.*

## Research highlights

- Early monocular deprivation is more detrimental to later sensitivity to illusory contours than comparable binocular deprivation.
- The results imply that immediately after birth, binocular input plays a critical role in the construction and/or preservation of the neural architecture that will later mediate contour interpolation.

## Introduction

Early visual input during infancy is necessary for the normal development of many aspects of vision, including those maturing much later in childhood (e.g. Maurer, Mondloch & Lewis, 2007). Humans deprived of pattern vision from birth by dense central cataracts in one or both eyes later show losses in visual acuity, spatial and temporal contrast sensitivity, stereovision, and sensitivity in the peripheral visual field, with larger impairments after early monocular than after early binocular deprivation (Birch, Stager, Leffler & Weakley, 1998; Bowering, Maurer, Lewis & Brent, 1993; Ellemberg, Lewis, Maurer & Brent, 2000; Ellemberg, Lewis, Maurer, Liu & Brent, 1999; Lewis, Maurer & Brent, 1995; Mioche & Perenin, 1986; Tytla, Maurer, Lewis & Brent, 1988; Tytla, Lewis, Maurer & Brent, 1993). Deficits are also shown in higher-level perceptual functions such as the perception of global form and motion (Hadad, Maurer & Lewis, 2012; Lewis, Ellemberg, Maurer, Wilkinson, Wilson *et al.*, 2002), as well as some aspects of face processing (de Heering & Maurer, 2014). In contrast to the lower-level visual skills, impairments in the higher-level skills are considerably worse after early binocular deprivation than after early monocular deprivation (e.g. Lewis *et al.*, 2002). These higher-level perceptual deficiencies do not appear to result from losses in visual acuity (e.g. Hadad *et al.*, 2012; Lewis *et al.*, 2002).

Here we tested the effect of early monocular and binocular deprivation of normal visual input on contour interpolation, a basic perceptual process mediating the perception of completed contours. Organizing the retinal image into meaningful and coherent objects involves

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locating boundaries between objects and their surroundings. Inferring these boundaries, perceptually separating one object from another, entails edge detection – places in which there is a large and abrupt change in some low-level image features such as luminance, color, or texture (e.g. Bennett, Sekuler & Sekuer, 2007; Nothdurft, 1992, 1993). Individuals with a normal visual history, however, can perceive bounded objects even when local image information fails to provide cues to physically specify their edges (e.g. Ginsburg, 1975; Petry & Meyer, 1987). In some cases, such as in the case of the Kanizsa figure shown in Figure 1A, interpolation between isolated image parts leads to the perception of an object with edges where there is no physical change (e.g. Kanizsa, 1976, 1979). A bright square figure is perceived in this case in front of four disks despite the fact that luminance-defined edges of the square figure are present only at the positions of the four inducers. These illusory contours often reflect real-world surface boundaries: in natural environments of heterogeneous reflectance, illusory contours are often formed when luminance contours composing a real object are camouflaged by the luminance of the surrounding field. Interpolation of these contours allows edge detection and completion of boundaries between real objects and their background.

Research in adults with a normal visual history shows that although perceptual completion of illusory contours seems effortless, the mechanism underlying their interpolation is not instantaneous and requires a measurable amount of time (75–200 msec; e.g. Guttman & Kellman, 2004; Imber, Shapley & Rubin, 2005; Murray, Sekuler & Bennett, 2001). Perceptual completion is also limited by spatial constraints. Specifically, it is mostly tied to support ratio, the ratio of the length of contour specified physically by a luminance gradient (i.e. the physically present inducers) to the total length of contour (i.e. physically specified plus interpolated contour between the inducers; see Figure 1B; e.g. Banton & Levi, 1992; Kojo, Liinasuo & Rovamo, 1993; Maertens & Shapley, 2008; Pillow & Rubin, 2002; Shipley & Kellman, 1992).

Despite the early appearance of sensitivity to illusory contours during the first few months after birth (Ghim, 1990; Hayden, Bhatt & Quinn, 2008, Johnson & Aslin, 1998; Kavšsek, 2002; Kavsek & Yonas, 2006; Treiber & Wilcox, 1980; and Sireteanu, 2000, for vernier offset lines), this perceptual skill of completion, particularly in the case of illusory contours, has been shown to improve during infancy (e.g. Bertenthal, Campos & Haith, 1980; Condry, Smith & Spelke, 2001; Csibra, 2001; Csibra, Davis, Spratling & Johnson, 2000), and later childhood (Abravanel, 1982; Hadad, Maurer & Lewis, 2010). Interpolation during infancy and childhood is attenuated by stimuli with low-support ratio (Hadad *et al.*, 2010; Otsuka, Kanazawa & Yamaguchi, 2004), large displays

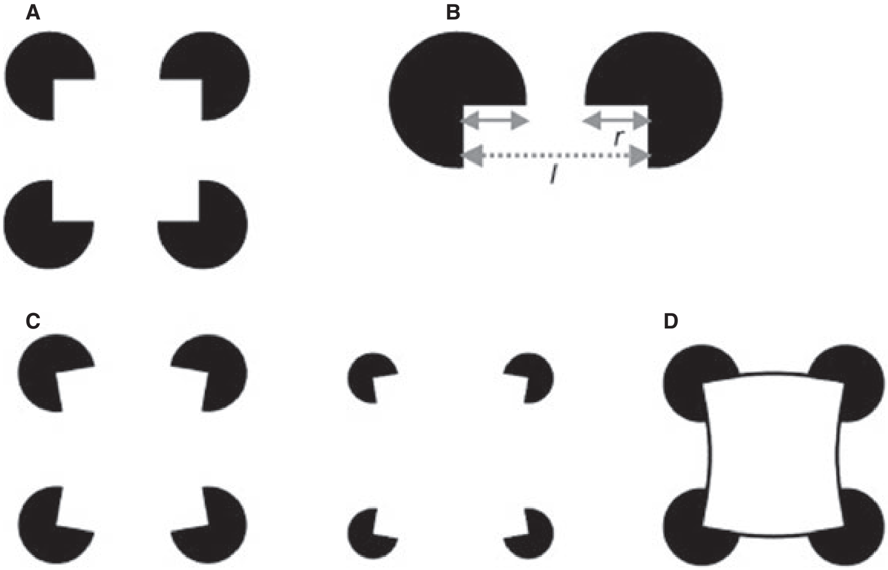

**Figure 1** *Manipulation of the support ratio and its effect on the perception of illusory contours (adapted from Hadad et al., 2010). (A) A Kanizsa illusory figure. (B) The support ratio denotes the ratio of the two radii of the inducers (2r) to the length of the side of the illusory square (l). (C) Examples of shapes with 50 and 30% contour support. The illusory square size (l) is constant across the two support ratios. When interpolation of contours between the inducers is over a small distance relative to the size of the inducers (i.e. high-support ratio), a stronger representation of the interpolated contour is obtained. (D) An example of luminance-defined contours forming the same shape as in panel C.*

(Kavšsek, 2002), and slow moving illusory contours (e.g. Curran, Braddick, Atkinson, Wattam-Bell & Andrew, 1999). The behavioral evidence for protracted development is supported by neurophysiological data demonstrating an extended structural maturation of the human cortex, including the early visual areas (Shankle, Romney, Landing & Hara, 1998), showing, among other changes, a significant increase in the number of cortical cells between birth and 6 years of age (Shankle *et al.*, 1998). Furthermore, neural circuits within the visual cortex mature postnatally. For example, whereas vertical connections within visual cortical areas V1 and V2 begin to develop prenatally, horizontal connections within cortical layers show a much more protracted development, not reaching maturity until 15 months of age (Burkhalter, 1993; Burkhalter, Bernardo & Charles, 1993).

Infants' sensitivity to illusory contours may thus reflect some rudimentary perceptual skill that is refined over many years as cortical circuitry develops. Given the known effects of visual deprivation on cortical development in animals and humans (e.g. Barlow, 1975; Greenough, Black & Wallace, 1987), it is possible that the postnatal changes in sensitivity to illusory contours are also shaped by visual experience. Some evidence for the detrimental effect of a period of visual deprivation starting in early childhood on the interpolation of illusory contours comes from the case of M.M. (Fine, Wade, Brewer, May, Goodman *et al.*, 2003), who had been blind from the age of 3 until the age of 43. Two years after having received a corneal transplant, M.M. was still unable to extract a shape formed by illusory contours. This patient, however, lost sight relatively late and remained blind for about 40 years. More relevant evidence for the effects of *early* experience comes from patients visually deprived during the first months of their lives (Putzar, Hötting, Rösler & Röder, 2007). These findings show that compared to individuals with normal visual history, binocular cataract patients treated after the age of 5–6 months take relatively longer to detect illusory figures in a visual search task, and have higher miss rates. These results imply that early visual input during infancy is necessary for the normal development of interpolation.

The present study further explores the way early visual experience shapes the development of this mechanism of perceptual completion. Specifically, we tested patients treated for dense congenital bilateral cataracts, which exemplifies the effects of visual deprivation per se and compared their results to those of patients treated for dense congenital unilateral cataract, which exemplifies the consequences not only of deprivation per se but also of unbalanced competition between the eyes. We used a task that allowed us to quantify differences in interpolation between these two groups of patients and participants with a normal visual history. Furthermore, we varied support ratio in order to determine whether early deprivation alters the geometrical constraints on contour interpolation.

To quantify interpolation, we used the shape discrimination task originally developed by Ringach and Shapley (1996). Observers were asked to indicate on each trial whether a shape formed by illusory contours was 'skinny' or 'fat'. The shapes were created by rotating the inducers (corners) of a Kanizsa square toward the center, as shown in Figure 2B. We used a staircase procedure to vary, over trials, the angle of rotation of the inducing elements (designated as alpha in Figure 2B). Thresholds were defined as the minimum angle of rotation for which the observer could identify the shapes accurately as fat or skinny. These thresholds indicated the minimum amount of the curvature (the fatness or thinness) required for discrimination of the illusory shape, and thus provide a measure of the precision of interpolation.

Interpolation between the inducers in the illusory contour conditions was supported either strongly (interpolation of contours between the inducers was over a small distance relative to the size of the inducers) or weakly (interpolation of contours was over a larger distance; Figure 1C). In order to measure the strength of interpolation, discrimination in these two conditions was compared with the discrimination of shape formed by luminance-defined contours. Stimuli in the luminance-defined condition had parabolic contours joining adjacent inducers to form the same shapes as in the illusory contour conditions (Figure 1D). Stimuli in the illusory contour conditions consisted of only the inducers, so that observers needed to perceive illusory luminance edges between the inducers to perform the task. We examined whether there were differences between patients and controls in the cost of interpolation (decreased sensitivity when contours are interpolated rather than luminance defined) for the two levels of support ratio. Although unlikely (e.g. Hadad *et al.*, 2010; Ringach & Shapley, 1996), it is possible, in theory, to solve the fat/skinny task by judging the orientation of a single inducer rather than interpolating between inducers; thus, differences in sensitivity to orientation between patients and controls might lead to changes in apparent interpolation. Our patients were therefore tested on a second control condition in which only one inducer was presented at a time and observers were asked to judge the orientation of this single inducer. As in the other conditions, thresholds were measured using a staircase procedure. Substantially different thresholds in the *single inducer* condition

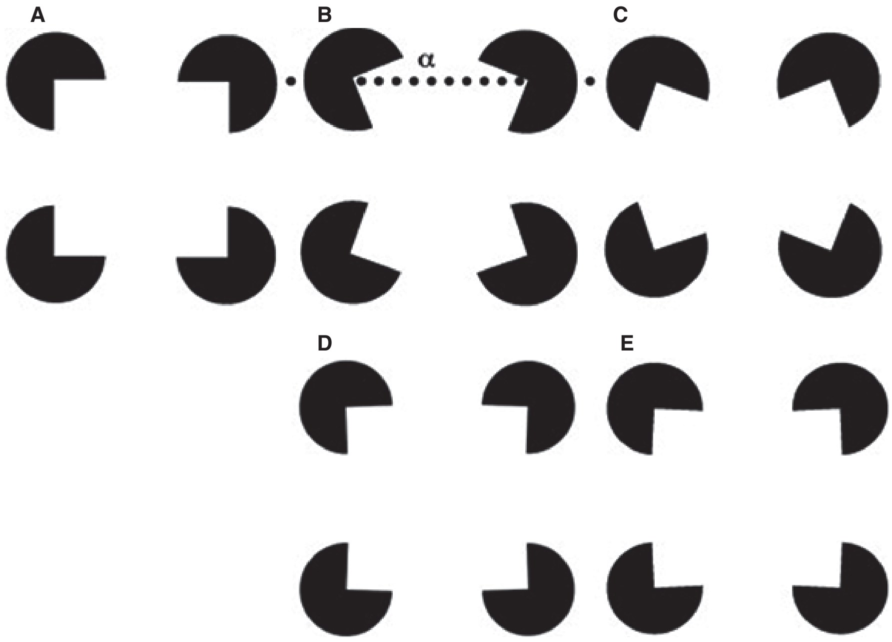

**Figure 2** *Rotation of the inducers to produce fat or skinny shapes (adapted from Hadad et al., 2010). Panel A shows an illusory square with no rotation (α = 0), with α corresponding to the rotation of the upper left inducer around its center. In panel B, α > 0 produces skinny shapes. In panel C, α < 0 produces fat shapes, with α varying over trials according to a staircase. Panels D and E show skinny and fat shapes, respectively, with small angles of rotation.*

compared to the *interpolated* conditions would indicate that performance in the experimental conditions could not be based solely on local orientation cues. In such a case, differences between groups in the interpolated conditions would be taken to reflect differences in the mechanism of interpolation.

## Methods

### *Participants*

### Visually deprived subjects

Visually deprived subjects were 16 patients treated for bilateral congenital cataract (duration of deprivation = 14–197 days; mean = 81 days), and 12 patients treated for unilateral congenital cataract (duration of deprivation = 19–183 days; mean = 86 days), who had followed a patching regimen of their non-deprived eye throughout early childhood. All patients were at least 10 years old at the time of the tests (bilateral: mean age = 19.7; range = 12.1–30.7; unilateral: mean age = 18.8; range = 9.8–29.1). Clinical details for each patient are presented in Table 1. All patients included in the study were born with dense central cataracts in one or both eyes with no other abnormalities in the ocular media or the retina, no evidence of persistent hyperplastic primary vitreous, and no ocular disease such as glaucoma. However, patients with common associated abnormalities such as strabismus, nystagmus, or microcornea were included. All patients had worn their optical correction regularly after treatment (at least 75% of the time).

Diagnosis of congenital cataracts was based on the first eye exam carried out within the first 6 months of age. As in previous studies (e.g. Ellemberg, Lewis, Maurer, Brar & Brent, 2002; Ellemberg *et al*., 2000), we assumed that these patients had been deprived from birth because it would be rare to have dense cataracts develop rapidly between birth and 6 months. Duration of deprivation was thus calculated as the period extending from birth until the age of first optical correction after surgery to remove the cataract. Patients treated for unilateral congenital cataract were all instructed by their ophthalmologist to patch their non-deprived eye. Occlusion therapy was initiated shortly after the time of the first optical correction and continued through at least 5 years of age. However, because of variation in instructions and compliance, the mean amount of patching from the time of the first optical correction until 5.0 years of age ranged from 2.8 to 10.4 waking hours per day (see Lewis *et al*., 1995, for details of these calculations).

**Table 1** *Clinical details and raw thresholds of patients in the bilateral and the unilateral cataracts groups*

| Patient/Age (years) | Refraction[a] | Surgery/CL (days) | Snellen acuity[a] | Nystagmus[b] | Additional details | Interpolation Cost (deg) High support/ Low support |
|---|---|---|---|---|---|---|
| Bilateral patients | | | | | | |
| DO (12.1) | OD +13.00<br>OS +17.00 | (OD: 56, OS: 57)/OU: 61 | 20/200<br>20/63 | Fine horizontal | Strabismus surgery OU at 7 years | 0.78/3.48 |
| JB (13.3) | OU: +27.00 | (OD: 84, OS: 85)/OU: 98 | 20/80<br>20/80 | Pendular nystagmus | Strabismus surgery OU at 5 years | −.11/4.65* |
| RC (13.5) | OD:<br>OS: | (OD: 112, OS: 113)/OU: 121 | $20/40^{+1}$<br>$20/32^{-2}$ | – | Strabismus surgery OU at 1.04 years | 1.37/4.33* |
| TA (13.47) | OU: +23.00 | (OD: 43, OS: 45)/OU: 50 | $20/40^{+1}$<br>$20/32^{-2}$ | – | – | 0.33/0.25 |
| BB (14.93) | OD: +24.5 OS: +27 | (OD: 14, OS: 15)/(OU: 28) | 20/80<br>20/80 | – | – | −.05/2.17 |
| RA (17.45) | OD: +25.0<br>OS: +20.5 | (OD: 47; OS: 52)/OU: 102 | 20/40<br>20/80 | Fine Vertical Pendular OU | – | 0.88/3.23 |
| MM (18.27) | | (OD: 21, OS: 24)/OU: 48 | 20/40<br>20/40 | – | – | −.31/2.2 |
| JS (18.1) | OD: +12.5<br>OS: +14.5 | (OD: 65, OS: 68)/OU: 92 | 20/63<br>20/25 | Horizontal nystagmus | Strab surgery OU @ 1.5 & 3 yrs | −.05/1.99 |
| JF (18.2) | OU: +14 | (OD: 79; OS: 80)/OU: 100 | 20/30<br>20/60 | Latent OU | Strab surgeries @ 1.3 (OS), 1.8 (OD) & 4.8 (OU) yrs | 0.75/4.25 |
| AB (19.17) | OD: +20.0 OS: +18.5 | (OD: 71, OS: 74)/OU: 91 | 20/60<br>$20/50^{-2}$ | Latent OU | Membrane surgery OD @ 0.8 yrs | 0.78/1.24 |
| CR (20.3) | OD: +14.5<br>OS: +15.5 | (OD: 197, OS: 202/OU: 238) | 20/20<br>20/80 | Fine Latent OU | Strab surgery OU @ 0.75 yrs | 1.37/1.99 |
| SA (22.22) | OD: +13.0 OS: +14.0 | (OD: 118, OS: 120)/OU: 147 | 20/32<br>20/32 | – | – | 1.37/−.04 |
| CB (25.72) | OD +7.50<br>OS +5.50 | (OD: 55; OS:47)/91 | 20/25<br>20/64 | Strong latent, horizontal nystagmus OS and fine nystagmus OD | Strab surgery OU at 1.5 years | 0/−.01 |
| CP (28.67) | OD: +16 OS: +15 | (OD: 149; OS: 143)/OU: 187 | 20/25<br>20/80 | Latent OU | LET surgery @ 1.8 years | 0.42/3.22 |
| IW (29.45) | OD +14.5<br>OS +16.5 | (OD: 133, OS:223)/(OD: 181, OS: 294) | 20/100<br>20/40 | Horizontal manifest nystagmus with latent component | Strab surgeries @ 3.2, 5.8 & 10 years | 1.67/2.76 |
| MD (30.68) | OD: +9.00<br>OS: +7.50 | (OD: 44, OS: 93)/OU: 129 | 20/50<br>20/63 | Manifest + latent OU | Capsular membrane needling @ 0.3 yrs, Secondary membrane & Elsching's pearl removal @ 0.8 yrs | 0.6/7.56* |
| Unilateral patients | | | | | | |
| EH (18.07) | OD: +8.5 | 40/56 | 20/40−2<br>20/32 | Latent | – | 1.24/4.65* |
| MC (18.11) | OS: +21 | 35/55 | 20/20−2<br>20/50−2 | Latent | Strab surgery @ 0.6 yrs. | −.37/.68 |
| RR (19) | OS: +11 | 57/97 | 20/40−1<br>20/63−3 | Latent | – | 1.37/0.99 |
| RB (17) | OD: +22.5 | 42/55 | 20/25−2<br>20/25−2 | Latent | Strab surgery OU @ 5.2 yrs. | 0.68/0.88 |
| TB (18) | OS: +25.00 | 45/80 | 20/25−2<br>20/40 | Manifest | Strab surgery @ 1.08 yrs | 1.66/6.55* |
| AT (24.11) | OS: +19.5 | 169/245 | 20/20−1<br>20/200 | Latent | Strab surgery OS @ 1 & 1.8 yrs. | −.47/6.55* |
| SD (20.02) | OS: +14.50 | 150/176 | 20/20−1<br>20/63−3 | – | Strab surgery @ 3.9 yrs. | 0.58/10.31* |
| AC (16.01) | | 154/165 | 20/63−2<br>20/20+1 | – | – | 0.58/4.65* |
| GW (9.8) | OS: +14.25 | 19/26 | 20/25−1<br>20/40+1 | – | Alternating exotropia with OD hyperdeviation | 0.41/2.77 |
| VL (17.3) | OS: +23 | 183/196 | 20/16−2<br>CF at 1m | – | Strab surgery @ 6.1 yrs. | −.55/0.19 |

**Table 1** *(Continued)*

| Patient/Age (years) | Refraction$^a$ | Surgery/CL (days) | Snellen acuity$^a$ | Nystagmus$^b$ | Additional details | Interpolation Cost (deg) High support/ Low support |
|---|---|---|---|---|---|---|
| JA (18.9) | OS: +17.0 | 42/66 | 20/25+1<br>20/63+2 | – | Secondary membrane removal @ 0.2 yrs. | 0.68/4.99* |
| NF (29.11) | OD:<br>OS: −3.5 | 92/124 | 20/50<br>20/25−1 | – | Membrane surgery @ 0.3 yrs, strab surgery for RET @ 2.3 yrs. Slight moderate RET with slight right hypertropia | 0.18/1.52 |

*Notes*: OD = right eye; OS = left eye; OU = both eyes; RET = right exotropia; LET = left esotropia; RXT = right exotropia; LXT = left esotropia. Asterisks in the Interpolation Cost column indicate that the threshold of the patient was found significantly higher than those of controls in Crawford's modified *t*-test for single case method (Crawford & Garthwaite, 2002).

## Visually normal controls

Results of patients were compared to those of visually normal control subjects in two age groups ($n$ = 12 per group) tested under the same conditions: 12- to 14-year-olds (mean age = 13.1; range = 12.1–14.1 years; 6 females), and 19- to 21-year-olds (mean age = 19.9; range = 18.1–21.1 years; 6 females). Although interpolation is adult-like by 10 years of age for binocular tests (Hadad *et al*., 2010), we chose to test both a younger and older control group because the monocular testing used here, unlike the binocular tests in our normative paper, might lead to poorer motivation or attention, especially in the younger patients.[1] All controls reported that they had no history of eye problems and all met our criteria on a visual-screening exam. Detailed criteria for visual screening for this group of controls are described in our previous work in which a different group of control participants aged 6 to 22 were tested (Hadad *et al*., 2010).

### *Apparatus and stimuli*

Stimuli were generated on an Apple Macintosh G5 computer using the MATLAB programming environment (Version 7.4.0.287, MathWorks) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The stimuli were presented on a 21-inch color CRT monitor (Dell P1130). The pixel resolution was 1600 × 1200, with one pixel corresponding to 0.021° at the testing distance of 50 cm, and the refresh rate was 85 Hz. A more detailed description of the stimuli is given in Hadad *et al*. (2010). The mean luminance was 90 cd/m$^2$, and the contrast between the black elements and the white background was 90%. Participants viewed the displays with their heads stabilized in a chin-and-forehead rest. Figure 2 depicts examples of the stimuli. The basic stimulus was an illusory square (Figure 2A) composed of four black circles, each missing a 90° notch. The four inducers (the Pacman-like shapes) were rotated in different directions to produce either skinny or fat shapes (Figures 2B and C; Ringach & Shapley, 1996).

Support ratio was manipulated by varying the ratio between the two radii of the inducers (2r) and the length of the side of the illusory square (l) (see Figure 1B), specifically, by changing the size of inducing elements while keeping the square size constant. The square in both support ratio conditions subtended 4.35° of visual angle. The total diameter of the inducers (2r) in the relatively high-support ratio subtended 2.17° of visual angle, producing a support ratio of approximately 50%, and their diameter in the low-support ratio subtended 1.37° of visual angle, producing a ratio of approximately 30% (Figure 1C).

Control displays containing luminance-defined contours (Figure 1D) matched those of the illusory contours except for containing a contour composed of an arc of 0.13° width with varying curvature, tangential to the black inducing edges. These displays were at the intermediate inducer size of 1.7°, between that of the high-support and the low-support conditions. The size was chosen based on pilot data in individuals with a normal visual history using the 'skinny–fat' task with luminance-defined displays with inducers size of 2.17° (equivalent to the high-support displays) and 1.37° (equivalent to the low-support displays). There was no

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[1] Comparing the monocular norms to our previously collected binocular norms (Hadad *et al*., 2010) suggests that monocular testing affects performance adversely, but only in children 12 to 14 years old. For that reason, we chose to use separate monocular norms for patients younger and older than 14.

effect of size of the luminance-defined contours on performance.

### Design

The experiment employed an orthogonal combination of three factors: group (unilateral, bilateral, and controls), stimulus (fat or skinny), and contour type (luminance defined, high support, or low support). Stimulus, contour type, and eye tested were manipulated within participants.

### Procedure

The procedure was identical to that described in Hadad *et al*. (2010). The study was conducted in accordance with the code of ethics of the World Medical Association (Declaration of Helsinki), and ethics clearance was given by the Research Ethics Boards of McMaster University and the Hospital for Sick Children, Toronto. Briefly, participants were tested monocularly while viewing the stimuli from a distance of 50 cm. Half of the participants in each group were tested with the left eye first, whilst the remaining half were tested with the right eye first. The eye not being tested was patched with 3M Micropore$^{\mathrm{TM}}$ tape. Each participant completed three sets of tests: luminance defined, high support, and low support, with each condition preceded by demonstration trials, criterion trials, and a practice run with the same type of stimulus that was to be tested. Four demonstration trials with stimuli rotated 10° were first presented to familiarize participants with the stimuli to be shown in that run. Criterion trials were then presented to verify that participants understood the task. Criterion trials consisted of three blocks of four trials, each trial of which had stimuli with 10° of rotation. Skinny and fat shapes were presented in a random order. Participants needed to judge the shape correctly as skinny or fat on all four trials within a block and had three chances to meet this criterion. The practice run consisted of one full staircase as described below with the type of stimuli to be used in the test run to follow. On each trial, observers were instructed to fixate on a 2.17° black circle in the center of the screen, which was removed after a variable interval. After a 250-ms delay, observers were shown the test stimulus for 1000 ms. The task on each trial was to indicate whether the shape was skinny or fat, and the experimenter pressed a corresponding key. Observers received visual and auditory feedback about their accuracy.

For each staircase, both skinny and fat shapes were presented on randomized trials, with equal probability to appear. A one-up, three-down staircase procedure, converging on a correct response rate equivalent to 79.4% accuracy (Levitt, 1971), determined the amount of rotation of the inducers (and the resulting curvature of the figure) for each trial. In the first display, the four inducers were rotated 10°. The angle of rotation was reduced by one octave (where an octave is a halving of a value) to 5° in case three consecutive correct responses occurred. Step size remained at one octave until an error was made, at which point step size was reduced to half-octave intervals. Following an error, the staircase reversed direction and a stimulus with a larger rotation angle was presented until three consecutive correct responses were made, after which the direction of the staircase reversed again to present successively smaller angles. Each staircase terminated either after 10 changes in the direction of the staircase ('reversals'), or after a maximum of 80 trials, whichever came first. The threshold for each condition, defined as the minimum angle of rotation needed to accurately discriminate the shape, was based on the geometrical mean of the rotation angle of the final six reversals. The actual test run was identical to the practice run except that now the experimenter was unaware of the stimulus presented on each trial. This procedure including demonstration trials, criterion trials, practice run, and test run was repeated for each type of stimulus (illusory contours with high-support ratio, illusory contours with low-support ratio, or luminance-defined contours). Half of each group was tested first with luminance-defined stimuli, and half was tested first with the illusory contours. Within the illusory contour blocks, the order of support ratio (high or low) was counterbalanced across participants in each group. This whole testing protocol was completed in a single session that lasted no longer than half an hour, including breaks.

The analysis compared thresholds for one eye of each of the participants: the worse eye (as determined from the most recent assessment of Snellen acuity test) of patients treated for bilateral cataracts, and the deprived eye of patients treated for unilateral cataracts. Because contour interpolation is a basic visual skill that depends mainly on lower cortical areas including area V1 and feedback to it from area V2 (e.g. Bullier, Hupé, James & Girard, 2001), we expected worse outcomes after unilateral than after bilateral deprivation, as shown for other basic visual skills (e.g. Bowering *et al*., 1993; Ellemberg *et al*., 2000). Thus, we took the conservative approach of comparing the worse eyes of bilaterally deprived patients to the deprived eye of unilaterally deprived patients. To equate testing condition to that of patients, testing was monocular also for the control participants with the eye to be tested selected randomly for each individual. As described above, none of the control participants had a history of eye problems, and all met our criteria for normal vision in each eye on a visual screening exam. There is then no reason to assume any difference in vision between the eyes for this control group of participants.

## Results

Patients' thresholds for each task were converted into *z*-scores based on the mean and standard deviation of the age-matched controls (mean and standard deviation for controls are summarized in Table 2; thresholds were quite similar to those we obtained earlier in a different group of controls tested binocularly (Hadad *et al*., 2010). Patients less than 14 years old were compared to the control group aged 12–14 years; all other patients were compared to the adult control group. Negative *z*-scores indicate a deficit compared to normal, and positive *z*-scores reflect above-average performance. Figure 3 presents individual *z*-scores for each eye of the participants in the bilateral group (Panel b; 16 bilateral patients were tested on their worse eye to allow the conservative comparison; however, when allowed, we also measured thresholds for the better eye of these patients (Panel a; $n = 12$)), and for the deprived eye of unilateral patients (Panel c; $n = 12$). Thresholds in the bilateral group, even those collected from the patients' worse eye, were mostly within the normal range (only 3 out of the 16 patients tested with their worse eye showed values outside the normal range). For the unilateral patients, on the contrary, thresholds were outside the normal range for every subject in at least one of the conditions tested (even when the non-deprived eye of these patients was tested).

Because some patients had negative *z*-scores for real contours, indicating deficits even in the control condition in which no interpolation is required, an index for *interpolation cost* was calculated for each subject in each condition of support ratio. This index estimates the precision of the representation emerging from interpolation when luminance-defined contours are not physically specified (Hadad *et al*., 2010). Specifically, the cost associated with interpolation was computed as the ratio of the interpolated threshold (high support, low support) and the luminance-defined threshold (see Equation 1). Higher values indicate a larger cost associated with interpolation, whereas lower values indicate a more precise interpolation process. Values statistically equal to 1 indicate no cost for the interpolation of the contours into a shape.

**Table 2** *Mean and SDs of the raw thresholds in each of the conditions for the control participants*

| Age group | Real contour | High support | Low support |
|---|---|---|---|
| 12–14 ($n = 12$) | .53 (.32) | .76 (.38) | 1.31 (.64) |
| 19–21 ($n = 12$) | .46 (.24) | .64 (.38) | 1.01 (.58) |

$$\text{Interpolation cost} = \text{interpolation threshold}/\text{luminance defined threshold}$$

Figure 4 shows mean interpolation cost as a function of support ratio, for patients and controls. A mixed-designed ANOVA was carried out with group (normally sighted controls, bilateral deprivation [worse eye], unilateral deprivation) as a between-subject factor and contour type (highly-supported contours, weakly supported contours) as a within-subject factor. The analysis demonstrated a significant effect of support ratio on interpolation cost, $F(1, 49) = 53.94$, $p < .0001$, $\eta_p^2 = 0.52$, with much higher interpolation cost for the low-support contours ($M = 3.50$) than for the high-support contours ($M = 1.58$). More importantly, this effect of support ratio varied between the groups, $F(2, 49) = 4.32$, $p < .01$, $\eta_p^2 = 0.15$. Specific comparisons show that while no effect of group was observed for the highly supported contours, $F < 1$, a significant difference between groups was seen in interpolation cost for the weakly supported contours, $F(2, 49) = 3.83$, $p < .02$, $\eta_p^2 = 0.14$. Post-hoc comparisons indicated differences in interpolation cost between the unilateral patients ($M = 4.73$) and the control group ($M = 2.75$), $p < .05$, but not between the bilateral patients ($M = 3.69$) and the control group (see Figure 4). In the unilateral cases, the threshold for the non-deprived (better) eye was also significantly worse than controls ($p < .05$) and no better than that for the deprived eye ($p > .15$). This pattern of similar deficits for the deprived and non-deprived eyes of unilaterally deprived patients has been demonstrated for other visual skills (e.g. Ellemberg *et al*., 2002). Altogether, the results provide evidence for much larger interpolation deficits in the unilateral compared to the bilateral patients group. Individuals treated for bilateral deprivation seem normal in interpolation even when tested with their worse eye.

To examine whether deficits seen in the unilateral but not in the bilateral patients group can be explained by differences in duration of deprivation or in acuity, we ran an ANCOVA with group (bilateral and unilateral patients) as a between-subject factor, contour type (high- and low-support contours) as a within-subject factor, and duration of deprivation and visual acuity as covariates. The analysis reveals a marginally significant interaction between group and support ratio, $F(1, 24) = 3.57$, $p < .07$, $\eta_p^2 = 0.14$, indicating, again, a much more pronounced effect of support ratio for the unilateral patients.

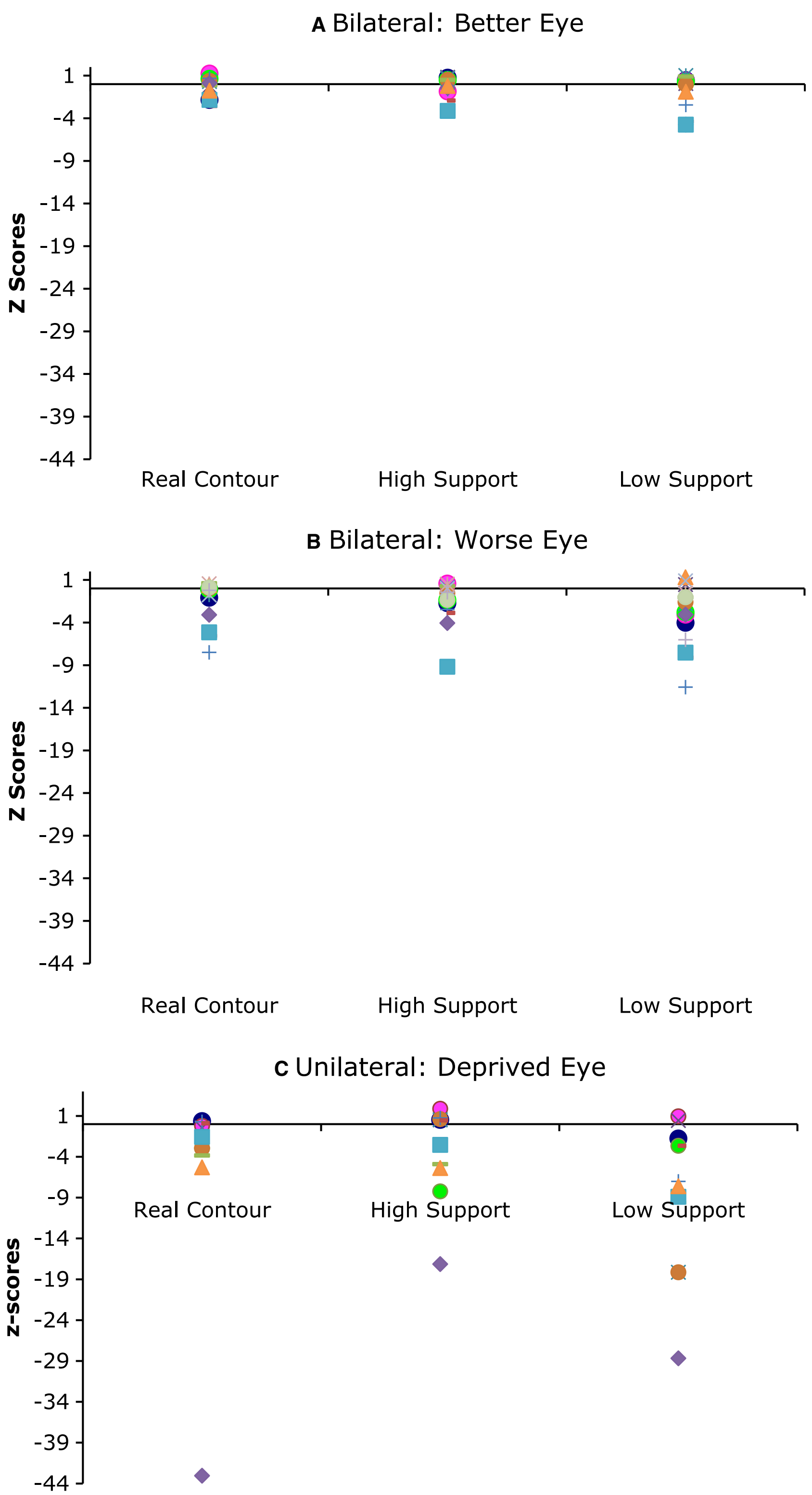

**Figure 3** *Z-scores as a function of contour type for (A) the better eye of 12 bilateral patients; (B) the worse eye of 16 bilateral patients; and (C) the deprived eye of 12 unilateral patients. Each dot represents the results for an individual patient tested with real contour, high-support condition, and low-support condition. Most thresholds for the bilateral patients were within the normal range even for those obtained from the worse eye.*

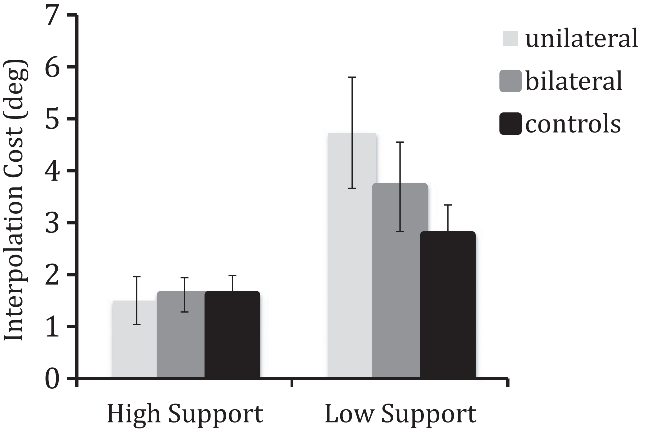

**Figure 4** *Mean interpolation cost as a function of support ratio for the deprived eye of unilateral patients (light grey), worse eye of the bilateral patients (dark grey) and for controls (black). Support ratios of 30% and 50% represents low- and high-support ratios, respectively.*

Consistent with the ANCOVA results, independent *t*-test comparisons showed no difference between acuities in these two groups, $t(21) = .76$, $p > .45$. We also calculated Pearson correlation coefficients between visual acuity (using the deprived eye of the unilateral patients and the worse eye of the bilateral patients) and thresholds in the high-support and low-support conditions. None of these correlations reached significance (all $r < .3$; all $p > .32$).[2] Differences between the two groups of patients cannot be explained by duration of deprivation either, as durations were comparable for the two groups of patients, $t(21) = .63$, $p > .64$. Pearson correlations between duration of deprivation and thresholds in the high-support and low-support conditions did not reach significance (all $r < .25$; all $p > .38$). Finally, the amount of patching was not correlated with the extent of the deficit in the unilateral group. In fact, the three unilateral patients who exhibited the worst outcomes (TB, AT, and SD), had been unilaterally deprived for the longest duration (> 6 months), suffered the most from unbalanced competition, and had the least patching of the non-deprived eye (3–4 h/day) throughout childhood. Thus, even if patching therapy in itself impairs vision to some extent, the deficits seen in this group of patients are more likely related to the unbalanced competition between the eyes caused by the unilateral cataract.

We also tested the statistical difference between each cataract patient and the control group using the Crawford's modified *t*-test for comparing performance on two tasks (Crawford & Garthwaite, 2005). The analysis on interpolation cost scores for the high- and the low-support ratio conditions show that only 3 out of 16 bilateral patients showed a statistically different effect of support ratio compared to controls. In contrast, 8 out of 12 in the unilateral group showed a statistically different effect of support ratio when compared to controls (see Table 1).

Finally, to ensure that the pattern of results cannot be attributed to differences in sensitivity to local orientation, we asked 12 of the bilateral and 9 of the unilateral patients to judge the orientation of a single inducer. Thresholds were obtained using a staircase procedure identical to that used in the other conditions in this study. Thresholds were derived after 10 reversals or after a maximum of 80 trials, whichever came first. The standard orientation was the orientation of the top left inducer, based on the possible non-interpolation strategy reported in Ringach and Shapley (1996) (i.e. subjects reported using a strategy that consisted of attending to only one inducer (usually the top left one) while fixating in the middle of the screen). We asked participants to judge whether the single inducer was rotated clockwise or counterclockwise. The standard orientation was displayed and defined verbally and participants were given four demonstration trials and 12 practice trials before the actual test to ensure that they understood the task and perceived the two possible orientations relative to the standard one. Two inducer sizes, equivalent to the inducer sizes of the high- and low-support ratio conditions, were used, counterbalanced across subjects. Thresholds in the single inducer conditions were overall lower than in the interpolated ones (illusory contours conditions). A mixed-design ANOVA was carried out on thresholds with group (the deprived eye of the unilateral patients and the worse eye of the bilateral patients) as a between-subject factor and inducer size (high-equivalent and low-equivalent) as a within-subject factor. Contrary to the results for the interpolated conditions, the interaction between the inducer size and group was not significant, $F < 1$, and thresholds did not differ between the two inducers size, $F(1, 20) = 2.98$, $p > .1$. Furthermore, for both groups of patients, thresholds of orientation discrimination of a single inducer at a size equivalent to the one used in the low-support illusory contours were better (1.85 and 3.02 for bilateral and unilateral patients, respectively) than in its counterpart interpolated condition (2.98 and 5.81 for bilateral and unilateral patients, respectively). This pattern of results for the single inducer condition confirms that the larger

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[2] To normalize for better-eye acuity, deprived and non-deprived acuity ratio was also computed showing no significant correlation with magnitude of deficits in the unilateral group, both for the highly supported contours ($r = .17$, $p > .05$) and for the weakly supported contours ($r =. 14$, $p > .05$).

deficits observed in the weakly supported contours compared to the strongly supported ones are a consequence of a deteriorated interpolation mechanism rather than differences in local orientation judgments.

Altogether the results suggest deficits in the interpolation of illusory contours after early monocular but not after binocular visual deprivation. The deficits are shown mainly in the most demanding condition of interpolation in which the contours are weakly supported, providing clear evidence that these deficits are more likely to result from an impaired interpolation mechanism rather than from any other factors that may differentiate the two groups.

## Discussion

The visual system ordinarily goes beyond the information present in the two eyes by actively connecting image regions that are physically disconnected on the retina. The present results show that normal early binocular input is necessary for this mechanism of perceptual completion to develop. Individuals deprived of visual input from birth by dense central cataracts in one eye, but not those deprived in both eyes, later show deficits in perceptual interpolation in each eye when tested monocularly.[3] The deficits are shown mostly for weakly supported contours, for which interpolation is more demanding, and thus confirm that it is impairment in the interpolation mechanism itself that underlies differences in performance rather than any other factors that may differentiate the two groups.

An additional control experiment confirmed that the 'within normal range' performance in the bilateral group should not be attributed to strategies of using local orientation cues that could, in theory, be used to perform the task. The results demonstrated that performance in the *single inducer* condition was better than that in the *interpolated* conditions, indicating that participants were not using local orientation cues in performing the skinny–fat task in the interpolated contours conditions. Furthermore, if performance in the interpolated contours was based solely on local orientation with no interpolation process involved, support ratio, similar to inducer size in the case of single inducer condition, should have yielded null results. The data, however, showed that contrary to the single inducer condition in which performance did not vary with inducer size (i.e. high- versus low-support size-equivalent inducer), performance in the interpolated conditions was tied to support ratio. The larger deficits observed in the weakly supported contours compared to the strongly supported ones is thus more likely to result from a deteriorated interpolation mechanism rather than from differences in local orientation judgments.

The normal performance exhibited by the bilateral patients is inconsistent with the only published study that tested the perception of illusory contours in pattern-deprived patients. In that study, Putzar and colleagues (Putzar *et al.*, 2007) compared reaction times and error rates in a visual search task in patients treated for juvenile bilateral cataracts and in controls. Putzar and colleagues (2007) concluded that early bilateral visual deprivation caused deficits in perceiving illusory contours because patients treated after 6 months of age (but not those treated earlier) had longer detection times than controls. However, in a second experiment of that study, five cataract patients treated between 5 and 24 months of age did have higher miss rates but were able to identify the illusory shape as accurately as controls, once they had detected them. This indicates that interpolation processes could in fact be intact in visually deprived patients and that these processes may activate time-consuming controlled mechanisms rather than the fast, automatic ones used by controls. This alternative interpretation is supported further by the present data. Even when using a more sensitive task with demands for precise interpolation for the perception of subtle changes in shape curvature, thresholds in our bilateral patients were normal. Another possibility is that only binocular deprivation longer than 6 months interferes with the development of interpolation since most of our patients' deprivation ended before that age. In any event, the mere absence of patterned information to both eyes during the first few months after birth does not seem to prevent the normal development of perceptual interpolation.

Monocular deprivation for about the same durations in infancy, however, does affect the later development of perceptual completion. Unlike the bilateral patients, the unilaterally deprived patients show large and clear deficits, pointing to the detrimental effect of unequal competition between the eyes for cortical connections on the later development of the mechanisms underlying contour interpolation. These deficits cannot be explained by poor acuity because their extent was not correlated with acuity, and because acuity of the unilateral patients did not vary from those of the bilateral patients who did not show substantial deficits after about the same period of deprivation. Furthermore, if difference in acuity between the two groups of patients accounts for the results, a similar effect to that of support ratio should

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[3] Although we tested all patients monocularly, we assume (a) similar deficits in a deprived eye and fellow non-deprived eye of unilaterally deprived patients and that (b) any deficits in the better eye of bilaterally deprived cases would each result in comparable deficits when tested binocularly.

have been observed also for inducer size in the single inducer condition. The pattern of results for the control condition, however, was different, indicating neither an effect of inducer size nor an interaction between this factor and group. Greater deficits in interpolating weakly supported contours in the unilateral group are thus more likely to be attributed to a weakened mechanism of interpolation after monocular deprivation.

The lower sensitivity observed in the unilateral group is also unlikely to result from strabismus that commonly occurs in patients treated for cataracts. First, the incidence of strabismus was no different after unilateral (6/12) than after bilateral (8/16) deprivation. Second, within the unilaterally deprived group, the contour interpolation deficits were no greater in the patients who had strabismus than in those who did not (see Table 1). And third, the strabismus was secondary to the deprivation and therefore likely not the primary cause of amblyopia as supported by the fact that acuity is no different in those with versus without strabismus. Nor can differences in stereoacuity explain lower sensitivity in the unilaterally than in the bilaterally deprived group: poor stereo vision is common to both groups and is, if anything, worse in bilaterally deprived patients, who show no evidence of fusion. Moreover, there is little agreement about the relation between the ability to resolve depth relations and competency in interpolation and unit formation (cf. Anderson, Singh & Fleming, 2002; Kellman & Shipley, 1991; Shipley & Kellman, 1992).

Finally, the lower sensitivity observed in the unilateral group is unlikely to result from reduced ability to control and maintain fixation. Both manifest and latent nystagmus would result in nonstable fixation during monocular viewing conditions but the incidence of one or both types of nystagmus was no different in the unilateral and bilateral cases (see Table 1). Furthermore, illusory contours appear stronger when freely viewed than when a fixation target is imposed (e.g. Banton & Levi, 1992).

As in previous studies (e.g. Ellemberg *et al.*, 2000; Ellemberg *et al.*, 2002), we assumed that these patients had been deprived from birth because it would be rare to have dense cataracts develop rapidly between birth and 6 months. Duration of deprivation was thus calculated as the period extending from birth until the age of first optical correction after surgery to remove the cataract. There could, however, be errors in diagnosis as we cannot be certain that all of these patients had dense central cataracts at birth. Yet, such errors in diagnosis are as likely to have occurred in unilateral as in bilateral cases and thus would not explain differences in thresholds between these two groups of patients.

Our findings of a worse outcome after monocular than after binocular deprivation is reminiscent of previous findings for other relatively low-level aspects of vision such as acuity, spatial and temporal contrast sensitivity, stereovision, and vision in the peripheral visual field (Birch *et al.*, 1998; Bowering *et al.*, 1993; Lewis *et al.*, 1995; Mioche & Perenin, 1986; Tytla *et al.*, 1988; Tytla *et al.*, 1993; Ellemberg *et al.*, 2000; Ellemberg *et al.*, 1999). Such relatively low-level aspects of vision are mediated mainly by the primary visual cortex, an area of the visual pathway that is less severely affected by binocular deprivation (which exemplifies the effects of visual deprivation per se) than by monocular deprivation (which exemplifies the consequences not only of deprivation per se but also of unbalanced competition between the eyes). Specifically, neurons in the striate cortex of monocularly, compared to binocularly deprived monkeys, respond more sluggishly and have more abnormal spatial frequency tuning (Blakemore, 1990; Blakemore & Vital-Durand, 1983). Moreover, far more striate neurons are completely unresponsive to stimulation from the deprived eye after monocular than after binocular deprivation in monkeys (Crawford, Pesch, von Noorden, Harwerth & Smith, 1991; Horton & Hocking, 1998a, 1998b). The substantial deficits after monocular but not after binocular deprivation in perceptual interpolation may result, at least in part, from such deficits in lower cortical areas of the visual system. Indeed, neural evidence (e.g. Dresp & Bonnet, 1993; Pillow & Rubin, 2002) suggests that illusory contours may be built up by a fast, low-level system mediated by early visual area V1 as well as by feedback connections from V2 to V1.

The deficit in interpolation after monocular deprivation is an example of a sleeper effect (Maurer *et al.*, 2007): visual deprivation in the first few months of life prevents the development of the ability to interpolate fragmented contours into a shape, a perceptual skill that normally is not adult-like until after 9 years of age (Hadad *et al.*, 2010; Hadad, Maurer & Lewis, 2015). This sleeper effect indicates that, immediately after birth, coordinated binocular input plays a critical role in the construction and/or preservation of the neural architecture that will later mediate the mechanism of interpolation. The fact that the deficits were large even after short monocular deprivation further suggests that monocular deprivation for as little as the first 2–3 months of life is sufficient to compromise the necessary architecture.

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