THE ROLE OF EARLY VISUAL EXPERIENCE IN THE DEVELOPMENT OF EXPERT FACE PROCESSING

By

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PREFACE

This thesis is in part comprised of four manuscript chapters (Chapters 2-5). The chapters were a collaborative effort between myself, Daphne Maurer and Catherine Mondloch. For Chapters 2, 3, and 5, I was extensively involved in all aspects of the study including creating the stimuli, designing and programming the experiments, testing the participants, conducting the analyses, and preparing the manuscripts for publication. For Chapter 4, I was involved in testing the participants, conducting the analyses, and preparing the manuscript for publication. I was not involved in all aspects of the study reported in Chapter 4 because pilot testing had already commenced at the time that I began graduate school at McMaster University. The research reported in this thesis was conducted between October 1998 and May 2002.

ABSTRACT

I examined the role of early visual experience in the development of expert face processing by comparing individuals with normal visual histories to patients deprived of early visual experience because of congenital cataract. The patients were tested following treatment, and after several years of visual experience (at least 8 years), on three tasks that measured different aspects of face processing.

The first task measured face discrimination based on sensitivity to second-order relations (the spacing among facial features), and sensitivity to featural information (the shape of the features). The patients performed normally at discriminating faces based on featural processing, but were severely impaired at discriminating faces based on second-order relational processing. The second task used the Composite Face Effect (Hole, 1994) to measure holistic processing (gluing the features into a gestalt). Unlike normal controls, the patients showed no evidence of encoding faces holistically. The third task measured face detection based on sensitivity to the first-order relations (i.e., two eyes above a nose and mouth): classifying two-tone Mooney stimuli as either face-like or not. The patients were as fast and accurate as normal controls at detecting Mooney faces.

Because the right hemisphere plays an important role in face processing, I also used Task 1 to test patients who were treated for early visual deprivation that affected mainly the left hemisphere or the right hemisphere. Deprivation affecting mainly the right hemisphere caused impairment in second-order relational processing that was as severe

as deprivation affecting both hemispheres. Deprivation affecting mainly the left hemisphere had no apparent effects on face processing.

Together these findings indicate that the normal development of certain aspects of face processing require visual experience during infancy. Early visual input to the right hemisphere may be especially important for setting up the neural circuitry that will become responsible for expert face processing.

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CHAPTER 1

INTRODUCTION

The ability to recognize individual faces is a highly specialized skill that emerges during infancy, continues to develop throughout childhood, and becomes adult-like in adolescence. Although expertise in face recognition develops after years of experience differentiating faces, several theorists argue that exposure to faces during infancy is critical for various face processing skills to develop normally. This thesis examines the role of early visual experience in the development of expert face processing. The studies reported in Chapters 2-5 take advantage of a natural experiment: children and adults who were born with congenital cataract that deprived them of visual input during infancy. To determine whether early visual input is necessary for the development of expert face processing, the deprived patients (mean age = 14 years) were compared to visually normal control subjects on their ability to process various types of configural information, and the ability to process faces based on featural information.

Expertise in face recognition

Adults are experts at face processing. They recognize faces at the subordinate level (e.g., that's Wayne Gretzky) more often than at the basic level (i.e., that's a face), and can do so rapidly and accurately (Tanaka, 2001). This tendency to identify faces more often at the subordinate level is considered a marker of perceptual expertise (Tanaka & Gauthier, 1997). In fact, adults can recognize thousands of individual faces, even when the person is at a distance, in poor lighting, has a new hairdo, or is a former schoolmate who has not been seen for over 20 years (Bahrick, Bahrick, & Wittlinger, 1975). This proficiency in face recognition is remarkable considering that human faces share the same basic arrangement of features (two eyes above a nose, that is above a mouth), and those features are highly similar in all individuals.

Expertise in face recognition develops after years of experience in differentiating among upright faces. As a result of this experience, faces are processed differently than objects for which we are not experts (e.g., houses, landscapes, and animals) (e.g., Diamond & Carey, 1986; Scapinello & Yarmey, 1970; Valentine & Bruce, 1986; Yin, 1969), at least when faces are upright. A striking demonstration of adults' expertise in processing upright faces is the *face-inversion effect* – much poorer accuracy and longer reaction times when faces are presented upside-down versus upright. The magnitude of this inversion effect is much larger for faces than most non-face objects (for reviews see Maurer, Le Grand, & Mondloch, 2002; Rossion & Gauthier, 2002; Valentine, 1988). The face-inversion effect has been taken as evidence that adults process upright faces differently from inverted faces and non-face objects. Furthermore, adults' expertise in face recognition has been attributed to their reliance on processing configural information.

The many faces of configural processing

The term *configural processing* has been used to refer to any phenomenon that involves processing not just the individual features, but also the relations among them (for a review see Maurer et al., 2002). It is contrasted with *featural processing* –

processing information related to the individual features of the face such as the shape, color or size of the eyes. Configural processing of faces can be divided into three types (1) sensitivity to *first-order relations* – detecting that a stimulus is a face because of the basic arrangement of its features with two eyes above a nose, that is above a mouth; (2) *holistic processing* – integrating facial features into a whole or Gestalt, thus rendering individual features less accessible; and (3) sensitivity to *second-order relations* – encoding the spacing among facial features, like the distance between the eyes. Although all three components of configural processing are affected by inversion, they are distinguished by behavioral marker tasks and different developmental trajectories. While face processing relies heavily on the encoding of configural information, expertise with non-face objects (e.g., bird watchers identifying birds) may also rely on processing configural information.

1) Sensitivity to first-order relations

Face detection is facilitated by the fact that all faces share the same first-order relations. As a result, face images can be superimposed, or averaged, and the resulting stimulus remains recognizably face-like (Diamond & Carey, 1986). Adults have a remarkable ability to detect faces, even in the absence of normal facial features. They readily detect faces in paintings in which faces are composed of objects such as an arrangement of fruit, vegetables, or rocks (Moscovitch, Winocur, & Behrman, 1997), or when presented with a two-tone Mooney face[1] (Kanwisher, Tong, & Nakayama, 1998), at

[1] Mooney faces are two-toned images that lack veridical facial features because the highlights have been rendered white and the shadows rendered black (see Chapter 4, Figure 1).

least when the stimuli are upright. Faces may play a special role in capturing attention. Patients with visual extinction are more likely to detect a face presented in the neglected hemifield than they are to detect a scrambled face, a name, or a meaningless shape (Vuilleumier, 2000). From very early in life, infants orient preferentially toward stimuli that have face-like first-order relations (e.g., Johnson, Dziurawiec, Ellis, & Morton, 1991; Mondloch et al., 1999) (but there are alternative explanations [Simion, Macchi Cassia, Turati, & Valenza, 2001; Turati, Simion, Milani, & Umilta, 2002]).

2) Holistic Processing

Once a stimulus is detected as a face, its parts become integrated into a whole or Gestalt-like representation, making information about individual features less accessible. A compelling demonstration of holistic processing is the *composite face effect* (Carey & Diamond, 1994; Hole, 1994; Hole, George, & Dunsmore, 1999; Young, Hellawell, & Hay, 1987). When a composite face is created by aligning the top half of one familiar face with the bottom half of a different person's face, it is very difficult to recognize either half (Young et al., 1987). Under these conditions, holistic processing binds the two halves of the face and thus creates the impression of a novel face. Performance improves after manipulations that disrupt holistic processing such as misaligning the two halves, or inverting the face (Hole 1994; Young et al., 1987). The composite face effect also has been shown for same/different judgments of unfamiliar faces (Hole, 1994). When the top half of one face is merged with two different bottom halves, holistic processing creates the impression that the top halves are different. This phenomenon demonstrates that when upright faces are processed, the internal features are so strongly integrated that it becomes difficult to parse the face into isolated features, at least at short exposures that prevent feature-by-feature comparisons (Hole, 1994). The composite face effect occurs even with upright faces that are presented as negatives (Hole et al., 1999), despite the fact that differences among individuals in the spacing of features are hard to detect in negatives (see *Sensitivity to Second-Order Relations* section below), a result suggesting separate effects of negation on holistic processing and on sensitivity to second-order relations. Holistic processing also makes it difficult to recognize that the internal features of two faces are identical when presented in different external contours (Sinha & Poggio, 1996). Similarly, after learning to recognize an individual's face, adults are better at recognizing the features of that face in the context of the whole face than in isolation, or when the face is inverted (*the whole/part advantage*) (Tanaka & Farah, 1993).

3) Sensitivity to Second-Order Relations

Because all faces share the same first-order relations, recognition of individual faces requires the encoding of information about subtle variations in the shape and/or spacing of the features. Second-order relations refer to the spatial distances among internal features (e.g., the distance between the eyes). Adults can detect variations in these distances as small as one minute of visual angle, a value close to the limits of visual acuity (Haig, 1984).

To tap processing of second-order relations, a set of faces can be created that differ from one another only in the spacing of individual features (e.g., varying the distance between the eyes and the mouth). This manipulation has minimal effect, if any, on information about local features, provided that the variations are not so extreme as to create a new facial feature (e.g., a broad nose between widely spaced eyes). To tap featural processing, a set of faces can be created that differ from one another in local information by changing the shape (Freire, Lee, & Symons, 2000; Le Grand, Mondloch, Maurer, & Brent, 2001), color (Leder & Bruce, 2000), luminance (Barton, Keenan, & Bass, 2001; Leder & Bruce, 2000) or distinctiveness (Leder & Bruce, 1998) (e.g., bushy eyebrows) of the features. Such manipulations have minimal effect on second-order relations provided that the size and location of individual features are kept similar across faces. Inversion severely impairs adults' ability to process second-order relations: they are significantly slower and less accurate in distinguishing faces that differ in the spacing of features when the faces are presented in an inverted orientation compared to their canonical upright orientation (Freire et al., 2000; Leder & Bruce, 2000; Le Grand et al., 2001). In contrast, inversion has little effect, if any, on adults' ability to distinguish between faces that differ in featural information (Barton et al., 2001; Freire et al., 2000; Leder & Bruce, 2000; Leder, Candrian, Huber, & Bruce, 2001; Le Grand et al., 2001). Similarly, adults rate faces with distortions in second-order relations (exaggerated spacing between the eyes) as less distinctive following inversion, whereas their ratings of faces with featural distortions (e.g., darkened eyebrows) do not change (Leder & Bruce, 1998). A similar pattern has been observed for ratings of bizarreness and grotesqueness (Murray, Yong, & Rhodes, 2000; Thompson, 1980). Taken together, these findings provide evidence that separate mechanisms are involved in second-order relational versus featural processing of individual faces. The difficulty in processing second-order relations in inverted faces likely occurs at the level of perceptual encoding rather than in memory retention because it is of similar magnitude when faces are presented simulateously as when they have to be remembered for up to 10 seconds (Freire et al., 2000).

Another technique for isolating second-order relational processing is to disrupt featural processing by blurring the stimuli to remove fine-detailed information about facial features (Costen, Parker, & Craw, 1994; Sergent, 1986). Adults are able to recognize the identity of blurred faces with reasonable accuracy (Hayes, 1988; Sergent, 1986), but are severely impaired in recognizing the identity of faces that are simultaneously blurred and inverted—presumably because blurring removes featural information and inversion disrupts sensitivity to second-order relations (Collishaw & Hole, 2000, 2002). Adding heavy random noise to face stimuli also eliminates useful featural information. Following training with upright versions of such stimuli, adults demonstrate categorical perception in making judgments about similarity and likeness. They do not show categorical perception if trained with isolated features or inverted faces, presumably because second-order relational information was not available (McKone, Martini, & Nakayama, 2001). Taken together, these results explain why inverted faces can be recognized at levels exceeding chance when featural information has not been removed by manipulations such as blurring or superimposing noise.

Negation does not disrupt holistic processing (see *Holistic Processing* section above), but it impairs the ability to distinguish between faces that differ in the spacing among features to the same extent as inversion disrupts discrimination of positive faces (Kemp, McManus, & Pigott, 1990). The disruption of sensitivity to second-order relations by negation is evident in the finding that it impairs recognition of faces from which the high spatial frequencies that specify features have been removed (i.e., low-pass faces), but not recognition of high-pass faces in which that featural information remains (Hayes, Morrone, & Burr, 1986).

Neural Correlates of Face Processing

Neuroimaging studies using various techniques such as event-related potentials (ERPs), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), and positron emission tomography (PET) have identified neural correlates of face processing. Through these studies, regions of the ventral occipitotemporal cortex, particularly an area of the fusiform gyrus referred to as the *FFA* (fusiform face area), have been implicated in the processing of faces (e.g., Haxby et al., 2001; Haxby, Hoffman, & Gobbini, 2000).

Studies using fMRI and PET have identified the FFA as a region that responds more to faces than to a variety of non-face objects (Aguirre, Singh, & D'Esposito, 1999; Dubois et al., 1999; Haxby et al., 2001; McCarthy, Puce, Gore, & Allison, 1997). The response to faces is generally found to be bilateral with a stronger response in the right hemisphere (Kanwisher, McDermott, & Chun, 1997; McCarthy et al., 1997). The FFA has been implicated in the perception of a stimulus as a face. Activity in the FFA is higher when the background encourages perception of the stimulus as a face than when it encourages perception of a vase (the Rubin face-vase illusion; Hasson, Hendler, Bashat, & Malach, 2001). Similarly, in a binocular rivalry task in which a face and a house are presented to different eyes, face percepts are accompanied by increased FFA responses

(Moutoussis & Zeki, 2002; Tong, Nakayama, Vaughan, & Kanwisher, 1998; see also Bentin et al., 2002). Inverting gray-scale faces causes little or no change in the magnitude of the FFA response (e.g., Aguirre et al., 1999; Kanwisher et al., 1998). In contrast, inverting Mooney faces disrupts the ability to detect a face, and produces a significant decrease in FFA activation (Kanwisher et al., 1998). The FFA also responds strongly to upright objects for which the observer has expertise, especially when the objects must be categorized at the subordinate level (see *Is Configural Processing Unique to Faces* section below).

The *N170*, the ERP negative potential that occurs over occipito-temporal areas at approximately 170 ms after stimulus onset, is of larger amplitude and shorter latency for faces than for many other stimuli including hands, houses, trees, cars and letters (Bentin et al., 1996; Botzel & Grusser, 1989; Botzel, Grusser, Haussler, & Naumann, 1989; Rossion, Dricot, et al., 2000). While the functional significance of the N170 has yet to be fully elucidated, like the FFA, it is also thought to reflect perceiving a stimulus as a face. The N170 component is affected by experimental manipulations that alter the basic structure of the face such as inversion and scrambling the features (Bentin et al., 1996; George et al., 1999; Rossion, Delvenne, et al., 1999; Rossion, Gauthier, et al., 2000; Sagiv & Bentin, 2001). The N170 is not modulated by how natural looking the face is (photograph, painting or schematic) (Sagiv & Bentin, 2001), the race of the face (Caldara et al., 2003), whether the face is familiar (Bentin & Deouell, 2000; Eimer, 2000; Rossion, Campanella, et al., 1999), or by stimulus repetition (Schweinberger, Pickering, Burton, & Kaufmann 2002; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002).

Interestingly, the prosopagnosic patient 'PHD' is unable to detect faces and also fails to show a face-sensitive N170 response (Eimer & McCarthy, 1999). Together these findings suggest that the N170 reflects the neural processing of face detection. Like the FFA, faces do not uniquely engage the N170: it is also modulated by degree of object expertise, and the level at which a stimulus is categorized (subordinate level versus basic level) (see *Is Configural Processing Unique to Faces* section below).

In studies using MEG, a corresponding response component called the M170 has been identified. Like the N170, its latency is much shorter and its amplitude is much larger for faces than for a variety of non-face stimuli such as animals, houses and hands (Liu, Harris, & Kanwisher, 2002; Liu, Higuchi, Marantz, & Kanwisher, 2000). The M170 is also thought to reflect face detection, as the strength of its activation is correlated with the correct categorization of a stimulus as a face (Liu et al., 2002). However, unlike the N170 its response is also correlated with successful face identification (Liu et al., 2002). A face-selective response has also been documented occurring 100 ms. after stimulus onset (the M100). Its response is also correlated with face detection, but unlike the M170, its response is not correlated with face identification (Liu et al., 2002).

Is Configural Processing Unique to Faces?

Although some researchers argue that configural processing is unique to faces, others suggest that it is used with other categories of objects, particularly if, like faces, the objects share the same first-order relations, and the subject has developed expertise in distinguishing members of the category at the subordinate level. This argument has been based primarily on the finding of an inversion effect for non-face objects for which the observer has expertise. Unfortunately, evidence of configural processing that is based on the finding of an inversion effect is inadequate. For example, dog judges and breeders, but not novices, are less accurate in recognizing which of two dogs they saw previously when the photographs are inverted—at least when the test sets include breeds for which the dog handlers are expert (Diamond & Carey, 1986). This result could reflect greater orientation-specific recognition of features or greater holistic processing or, as the authors hypothesize, greater skill in using second-order relations to individuate dog bodies. Surprisingly, dog experts in this study were no better than novices in recognizing upright dogs, perhaps because multiple cues were available.

Cortical areas that are involved in face processing have also been implicated in expert processing of non-face stimuli. Neuroimaging studies have shown the face-sensitive FFA also responds to objects for which the observer has expertise. There is enhanced activation of the FFA when bird and car experts categorize objects in their domain of expertise relative to when they categorize objects outside their domain of expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000). These same cortical areas also change from being relatively indifferent to greebles (see below for a description of greebles), to demonstrating greater activation for upright than for inverted greebles after extensive training with these stimuli. Furthermore, this differential activation is as large as that for upright versus inverted faces (Gauthier et al., 1999).

Similarly, electrophysiological studies using event-related potentials (ERPs) have shown that the magnitude of the face-sensitive N170 also varies for categories of non-face objects for which the observer has expertise. For example, the N170 is greater when dog and bird experts are presented with an object from their category of expertise than for control stimuli (Tanaka & Curran, 2001). However, irrespective of expertise, the N170 is larger when an object is categorized at the subordinate rather than the basic level (e.g., beagle vs. dog) (Tanaka, Luu, Weisbrod, & Kiefer, 1999). Inversion of non-face objects from a category of expertise (i.e., greebles) leads to a delay of the N170 similar to what is found for inverted faces (Rossion et al., 2002). Together, these results establish that the underlying neural markers of expert face and non-face processing are similar, and offer the possibility that expertise in processing non-face objects also engages at least one type of configural processing.

While several studies have demonstrated that faces are processed holistically, expertise with non-face objects may also engage holistic processing. For example, car experts are unable to simultaneously process faces and cars holistically. In a dual task that requires processing cars and faces holistically, car experts show an attenuation of the composite face effect (a standard measure of holistic processing) (Gauthier, Curran, Curby, & Collins, 2003). In contrast, car novices do not show such interference between car processing and holistic face processing. These findings suggest that while common objects normally do not engage holistic processing, objects for which the observer is an expert engage holistic processing and likely recruit the same neural networks as do faces.

Further evidence that adults use configural processing for non-face categories comes from Gauthier and Tarr's training studies with photographs of "greebles". Greebles share the first-order relations of having a body with two appendages near the top, a central appendage, and an appendage near the bottom, but the exact shape of the appendages varies so as to define genders, families, and individuals. After many hours of training to distinguish among several individual greebles and to recognize the gender (and families) of a larger set, subjects show some of the diagnostic effects for holistic processing (Gauthier & Tarr, 2002; Gauthier, Williams, Tarr, & Tanaka, 1998). There is a slowing of response or decrease in accuracy when an individual's part or top half has to be recognized in a configuration that is novel because other parts have been moved or because the top half has been fused with the bottom half of another greeble. Following training, accuracy is also impaired by negation, as would be expected if greebles are processed based on second-order relational information. However, these effects are not strong. For example, the context effect for the identification of parts was seen in the first study on measures of reaction time but not accuracy, and in the second study it was not significant for reaction time and affected accuracy significantly for certain features but not for others. Unlike faces, the advantage of judging the part in the original greeble, rather than in isolation, extended to inverted greebles and to novice subjects and the disadvantage for composite greebles was not alleviated by misaligning the top and bottom halves. Thus, although greeble expertise generates some of the effects observed in studies of face perception, the results diverge at multiple points. The divergence could reflect important differences between adults' processing of faces and other categories, or merely the effect of the many more hours of "training" adults have had with faces.

Acquisition of expert face processing

Very little is known about how expertise in face processing is acquired, and what drives the development of the neural substrate responsible for this expertise. Three influential developmental models (Johnson Model, de Schonen Model, and Nelson Model) have been offered to account for the acquisition of expert face processing. Despite their differences, the models share one commonality – they emphasize the importance of experience with faces during infancy, and suggest that this early experience is essential for the subsequent development of expert face processing.

1) Johnson Model

Johnson and colleagues (Johnson & de Haan, 2001; Johnson & Morton, 1991; Morton & Johnson, 1991) have proposed that two separate systems underlie the development of expert face processing. The first system, *Conspec*, is an innate mechanism that is mediated by a primitive subcortical circuit. The system operates from birth until four to six weeks to bias the infant to orient faces that are either moving or in their periphery. This bias allows ample exposure to faces during the first few months, and guarantees input to those cortical circuits that will become responsible for face processing. At about 6 weeks, the subcortical Conspec system is superseded by *Conlern*, a system mediated by cortical networks in the ventral visual pathway. Through lots of experience with faces, Conlern gradually begins to encode more and more information about facial identity, and sets up the neural circuitry that will become responsible for expert face processing.

2) de Schonen Model

de Schonen and Mathivet (1989) have proposed that newborns' visual constraints limit information available to the developing cortex, and lead to networks in the right hemisphere becoming specialized for expert face processing. During early infancy, regions of the right temporal cortex that receive information about faces become functional earlier than corresponding regions of the left hemisphere. Because young infants have poor visual acuity and contrast sensitivity (e.g., Banks & Salapatek, 1981; Mayer et al., 1995; for a review see Maurer & Lewis, 2001), the functional right hemisphere is exposed to low spatial frequency information that, for faces, specifies the location of features, but provides little information about feature details. As a result, these regions of the right hemisphere become specialized for processing spatial-relational information in faces. Once the corresponding regions of the left hemisphere become functional later in infancy, visual acuity has improved substantially, and input from higher spatial frequencies that specify feature details are available. As a result, regions of the left hemisphere that receive information about faces become specialized for encoding featural information. Indeed, several studies on the development of face processing in infancy have reported right hemisphere specialization for second-order relational information and left hemisphere specialization for featural information by 4 to 9 months (see *Face Processing in Infancy* section below).

3) Nelson Model

Nelson and colleagues (Nelson, 2001; Pascalis, de Hann, & Nelson, 2002) have proposed that expertise in face recognition is the result of a perceptual narrowing process that depends upon experience with faces during infancy. According to the model, regions of the temporal cortex that receive information about faces during early infancy are initially broadly tuned to stimuli from a number of categories including inverted faces and non-human faces. With increased exposure to upright human faces over the subsequent months and years, these cortical regions become more and more narrowly tuned, and eventually become specialized for recognition of such stimuli. This view has been supported by the finding of a decrease in discrimination ability for non-human faces with age: 6 month olds can discriminate between individual monkey faces and between individual human faces, whereas 9 month olds and adults are much better able to discriminate between individual human faces than they are to discriminate between individual monkey faces (Nelson, 1993; Pascalis et al., 2002).

Open Questions

Although all three models suggest that experience with faces during early infancy is important for the development of expert face processing, they fail to state whether there is a critical or sensitive period during which exposure to faces is necessary. For example, is exposure to faces during the first six months necessary for the normal development of face processing, or can experience with faces be delayed until later in infancy? The models also fail to specify exactly what kinds of face processing skills require early experience with faces. Do *all* components of configural face processing require exposure to faces during infancy, or only second-order relational processing? Finally, the models do not specify the level of plasticity afforded to the face recognition system. For example, in the event of early damage or deprivation of input to cortical areas normally involved in face processing, can other regions be recruited for the development of this expertise?

Face processing in infancy

The view that experience with faces during early infancy is important for the development of expert face processing is supported by the fact that during the first few months of life, infants receive a wealth of experience with faces, and several face-processing skills emerge. Newborn infants are drawn to face-like patterns over non-face patterns (e.g., Goren, Sarty, & Wu, 1975; Johnson, et al., 1991; Maurer & Young, 1983; Mondloch et al., 1999) - a result that suggests newborns can detect faces based on their first-order relations. This raises the possibility that a primitive neural network involved in face processing is present prior to visual experience. One alternative explanation is that infants are drawn to patterns with a greater number of high contrast elements in the upper visual field (Simion et al., 2001; Turati et al., 2002). A second alternative explanation is suggested by a recent neural network model of the newborn visual system that showed that the preference for face-like stimuli during early infancy may be a consequence of the infants' immature visual system (i.e., visual acuity and contrast sensitivity limited to low spatial frequency information) (Acerra, Burnod, & de Schonen, 2002). No matter the reason for the newborn bias to faces, it nevertheless allows for ample exposure to faces during early infancy.

Several pieces of research suggest that experience with faces alters the infants' face preferences. Over the subsequent months after birth, infants become more sensitive to the facedness of a stimulus, and to distortions in the first-order relations of faces. For example, six-week olds no longer show a preference for the config stimulus (a face-like stimulus consisting of an oval contour with three blobs in the correct location for facial features), but do show a preference for a stimulus with the phase spectrum of a face over the amplitude spectrum of a face (Kleiner & Banks, 1987; Mondloch et al., 1999). It is not until 12 weeks of age that infants prefer a positive-contrast face over a negative-contrast face (Dannemiller & Stephens, 1988; Mondloch et al., 1999). Experience with specific faces also affects face detection during infancy: six-month-olds show a preference for an intact Mooney face over a scrambled version only if they are first familiarized with the original photographic version of the Mooney face (Latour, Rousset, Deruelle, & de Schonen, 1999).

The ability to recognize individual faces emerges early in infancy. By 4 days after birth, infants can learn to recognize an unfamiliar face and can do so even after a 2-minute delay (Pascalis & de Schonen, 1994). They also show a preference to look at their mother's face over a stranger's face (Bushnell, 2001; Bushnell, Sai, & Mullin, 1989; Field, Cohen, Garcia, & Greenberg, 1984; Pascalis et al., 1995; Walton, Bower & Bower, 1992). The strength of this preference is associated with the amount of exposure infants have had with their mothers' face over the first 3 days after birth (Bushnell, 2001). The ability of newborns to discriminate and recognize faces is quite a feat considering that during the first few days after birth, infants spend only about 15% of their time awake (Freudigman & Thoman, 1993; Sadeh et al., 1995), and not all of this time is spent looking at faces. Despite being able to recognize individual faces, young infants do not encode all the information in the face. One-month-olds tend to scan only the external contour of the face, and devote long periods of time to a particular area (e.g., the chin) (Maurer & Salapatek, 1975). They do not recognize their mother's face in profile (Sai &

Bushnell, 1988) or when the internal features are visible, but the outer contour is masked by a headscarf (Pascalis et al., 1995). These findings suggest that young infants use the external contour of the face, such as the shape of the head and hairline, to recognize individual faces.

Over the next few months, infants begin to encode more information in the face. By two months, infants are able to recognize individual faces on the basis of the internal features. They scan the internal features of the face more extensively (Maurer & Salapatek, 1975), and can recognize their mother's face when the external contour is masked (Bartrip, Morton, & de Schonen, 2001; de Schonen, Gil de Diaz, & Mathivet, 1986; Morton, 1993). By three months of age, after becoming familiarized with an individual face wearing a scarf and posing with various head orientations, infants can recognize that face when presented in a new orientation, even 24 hours later (Pascalis, de Hann, Nelson, & de Schonen, 1998). This ability may denote the emergence of face recognition based on sensitivity to second-order relations: recognition of a face from varying points of view likely requires sensitivity to the spacing of features because the shape of individual features changes across head orientations (e.g, the shape of the nose changes), whereas the spacing among features remains relatively invariant. Three-month-olds show evidence of forming a prototype of a face (a mentally computed average) and, like adults, treat it as more familiar than the individual faces from which it was formed (de Haan, Johnson, Maurer, & Perrett, 2001). Thus, by 3 months of age, previous experience with faces affects how new faces are encoded. Faces may be encoded relative to a prototypical face, such as how the facial features and/or second-order relations of the new face deviate from a general face prototype.

There is some evidence that face processing based on holistic processing and second-order relations begins to emerge early in life. By six months, infants show evidence of the face-inversion effect: they are better able to discriminate among faces when they are presented upright rather than upside-down (Fagan, 1972; Fagan & Shepherd, 1979). The tendency to integrate the features of a face into a whole, rather than perceive the face as a collection of independent elements (a form of holistic face processing) also begins to emerge during infancy. After being habituated to two faces, 7-month-old infants treat a composite face consisting of the external portion of one familiar face and the internal portion of the other as if it were a novel face when upright, but not when inverted (Cohen & Cashon, 2001). These findings suggest that by 7 months, faces are processed holistically when upright, while inverted faces are processed based on the independent features. By seven months, infants may also be sensitive to the second-order relations of a face. Infants at this age look longer at faces with normal spacing of features (i.e., the eye-to-mouth distance is within normal limits) than faces that have exaggerated feature distances (Thompson, Madrid, Westbrook, & Johnston, 2001). While the authors argue that this suggests that infants can process second-order relational information, an alternative explanation is that infants can discriminate faces based on featural differences. This is because extreme variations in the spacing of the features can create a new facial feature (e.g., a large eye-to-mouth distance can create an unusually long looking nose).

Research on the hemispheric specialization of face processing in infants has also provided evidence for sensitivity to second-order relational information early in life. Between 4 and 9 months of age, infants exhibit the same right hemisphere advantage for face recognition as seen in adults: they are better able to recognize and distinguish among faces that are presented to the left visual field (i.e., right hemisphere) than to the right visual field (i.e., left hemisphere) (de Schonen et al., 1986; de Schonen & Mathivet, 1990). In such experiments, infants are unable to use their left hemisphere when stimuli are presented to the left visual field (right hemisphere) because at this age there is no inter-hemispheric transfer of visual information (Liegeois, Bentejac, & de Schonen, 2000; Liegeois & de Schonen, 1997). This right hemisphere advantage for face recognition may be the result of enhanced sensitivity to second-order relational information. By nine months, infants are better able to distinguish between faces that vary in the size of the eyes (a manipulation that alters mainly the spatial relations among the features) when the stimuli are presented to the right hemisphere rather than the left hemisphere (Deruelle & de Schonen, 1998). In contrast, nine-month-olds are better able to distinguish between faces that vary in the shape of the eyes (a manipulation that mainly alters featural information) when the stimuli are presented to the left hemisphere rather than the right hemisphere. This hemispheric asymmetry in the processing of featural versus spacing information may not be restricted to face processing; infants are better able to distinguish among geometrical patterns that differ in the spatial location of a component when the stimuli are presented to the right hemisphere rather than the left hemisphere. In contrast, infants are more accurate at distinguishing patterns that differ in the shape of individual elements when the stimuli are presented to the left hemisphere rather than the right hemisphere (Deruelle & de Schonen, 1995).

The neural correlates underlying face processing also undergo tremendous change during infancy. By 2 months of age, human faces activate a network of cortical areas predominantly in the right inferior-temporal cortex. This network includes regions within the fusiform gyrus that may be the homologue of the adult FFA (Tzourio-Mazoyer et al., 2002). By 3 months, faces activate a putative N170 that is larger for human than for monkey faces (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, in press). This response is delayed relative to the N170 in adults and, unlike the case in adults, is not affected by inversion (Halit et al., in press; de Haan et al., 2002). By 12 months, the response properties of the infant N170 become more adult-like: it is elicited more for upright versus inverted human faces (de Haan et al., 2002). These results suggest a gradual process of cortical specialization for face processing in infancy, likely influenced by the increased amount of exposure to faces that the infant has had during the first year of life.

Face processing in Childhood

Although various face-processing skills emerge during infancy, expertise in face processing is slow to develop and only becomes adult-like in adolescence. Compared to adults, school-aged children perform poorly on face encoding and recognition tasks (Chung & Thompson, 1995; Flin, 1985). Recognition of faces in a study set increases dramatically between 7 and 11 years of age, but even 14-year-olds make more errors than adults (Carey, Diamond, & Woods, 1980). Even in matching tasks, which eliminate memory demands, performance improves dramatically between 4 and 11 years of age (Bruce et al., 2000; Carey & Diamond, 1977, 1994).

Various studies have attempted to determine the nature of children's immaturity in face recognition. A failure to process faces holistically (see *Holistic Processing* section above) is an unlikely source of this immaturity. The magnitude of the composite face effect is the same in 6-year-olds (the youngest age tested) as it is in adults for both familiar (Carey & Diamond, 1994) and unfamiliar faces (Mondloch, Pathman, Le Grand, & Maurer, 2003). Like adults, 6-year-old children have severe difficulty recognizing the top half of a face when it is aligned with the bottom half of a different person's face, and their performance improves after manipulations that disrupt holistic processing such as misaligning the two halves. Six-year-olds also show the whole/part advantage for unfamiliar faces (Seitz, 2002; Tanaka & Farah, 1993), and the size of the effect is as large as in 11-year olds (the oldest age compared) (Joseph & Tanaka, 2003). As in adults, 6-year-olds recognize a facial feature better in the context of the whole face in which they learned it than in isolation, and the effect disappears when holistic processing is interrupted by inversion (Joseph & Tanaka, 2003; Tanaka et al., 1998). Because holistic processing appears to be mature by 6 years of age, it cannot account for the developmental changes in face processing that occur into adolescence.

A likely reason for children's immaturity in identifying faces is that they do not use the same encoding strategies as adults for recognition of individual faces. For example, adults rely more on internal facial features than on external features (e.g., hair) when recognizing familiar faces (Ellis, Shepherd, & Davies, 1979). In contrast, young children are better at recognizing faces from the external features; it is only when children are between 9 and 11 years of age that they show the adult-like pattern (Campbell & Tuck, 1995; Campbell, Walker & Baron-Cohen, 1995; Want, Pascalis, Coleman, & Blades, 2003). Children also rely more on superficial characteristics of the face: 6- and 8-year-olds are influenced more by paraphernalia (e.g., glasses, hats) than are 10-year-olds and adults when matching unfamiliar faces (Diamond & Carey, 1977; Ellis, 1992; Freire & Lee, 2001), although the influence is reduced when the faces presented look quite dissimilar (Baenninger, 1994).

The effect of inversion on children's processing of faces also suggests that they do not rely on the same types of information as adults. Unlike adults, who are severely impaired at identifying upside-down faces (see *Expertise in Face Recognition* section above), judgments of facial identity by young children are much less impaired by inversion (Brace et al., 2001; Carey et al., 1980; Carey & Diamond, 1977, 1994; Goldstein, 1975). With increasing age, the magnitude of the face-inversion effect becomes more adult-like. This is because children's accuracy for face recognition steadily improves with age for upright faces, but not for inverted faces (Carey et al., 1980; Goldstein, 1975). Because inversion mainly disrupts adults' recognition of faces based on second-order relational information (e.g., Freire & Lee, 2001; Mondloch, Le Grand, & Maurer, 2002), the attenuated face-inversion effect in young children may reflect less reliance on this type of information.

The most direct evidence that children are especially immature in processing second-order relational information comes from studies in which sets of faces have been created that differ either in the shape of individual features or in the spacing among those features (e.g., the distance between the eyes). By 4 years of age (the youngest age tested), children can recognize faces based on the spacing of the features, but their performance is only slightly better than chance (Freire & Lee, 2001). They are much better at recognizing faces that differ only in the shape of individual features. By 6 years, children are nearly as accurate as adults at differentiating faces that differ only in the external contour or the shape of the features (Mondloch et al., 2002). Even at ages 10, 12 and 14 years, the ability to discriminate faces based on the spacing of the internal features is not adult-like (Mondloch et al., 2002; Mondloch, Le Grand, & Maurer, in press).

Children's performance on other face-processing tasks may also vary with the extent to which individual features versus the spacing among features (i.e., second-order relations) provide critical information. Five- to ten-year-olds perform well when asked to identify a particular facial expression, sound being mouthed, or direction of eye gaze (Bruce et al., 2000; Mondloch, Geldart, Maurer, & Le Grand, 2003). Their good performance on these tasks may be due to the ability to identify the correct target based on an isolated feature (e.g., mouth shape) rather than having to process the spatial relations among multiple features. Consistent with this hypothesis, adults' performance on these tasks is not affected by inversion (Mondloch, Geldart, et al., 2003). In contrast, young children have difficulty matching faces that differ in pose, facial expression or lighting (Benton & Van Allen, 1973 as cited in Carey et al., 1980; Ellis, 1992; Mondloch, Geldart, et al., 2003). Such changes render second-order relations more important because faces no longer can be matched accurately based on the appearance of individual features (i.e., the individual features change in shape when the orientation of the face changes). Even 10-year-olds are not adult-like at matching identity despite changes in head orientation. This ability likely requires sensitivity to second-order relations, as adults' accuracy on this task decreases when the stimuli are inverted (Mondloch, Geldart. et al., 2003). Taken together, these studies suggest that the slow development of expertise in face processing is related to the slow development of sensitivity to second-order relational information.

Electrophysiological studies have shown that the functional specificity of the N170 continues to become more adult-like throughout childhood. Between 4 and 14 years of age, there is a gradual increase in amplitude and a decrease in latency of the N170 in response to upright human faces (Taylor, Edmonds, McCarthy, & Allison, 2001; Taylor, McCarthy, Saliba, & Degiovanni, 1999). However, even at 14 years, the N170 is not completely adult-like (Taylor et al., 1999). Together with developmental behavioral studies, neuroimaging studies suggest that there is a gradual process of cortical specialization for face processing that emerges in infancy, and with increased experience with faces, continues to develop throughout childhood and into adolescence.

Effects of early visual deprivation

In an initial study on the effects of early visual deprivation on various real-life face processing skills, patients treated for bilateral congenital cataract were tested on their ability to 1) identify a face despite a change in head orientation; 2) identify a face despite a change in facial expression; 3) match facial expressions despite changes in identity; 4) match sound being mouthed despite changes in identity; and 5) match direction of gaze despite changes in head orientation and identity (Geldart et al., 2002). The results showed that early visual experience is necessary for the later development of some, but not all, components of face processing. Patients perform normally when matching faces on emotional expression, vowel being mouthed, and direction of eye gaze. Their normal performance is likely due to the ability to identify the correct target based on an isolated feature (e.g., mouth shape) rather than having to integrate the spatial relations among features. As would be expected if these tasks can be solved based on featural processing, 8-years-olds with normal visual histories perform well on them despite immaturity in second-order relational processing, and adults' performance on these tasks is not affected by inversion (Mondloch, Geldart, et al., 2003). The deprived patients have severe difficulty in matching facial identity when the face to-be-recognized is presented in a novel point of view. This task likely requires sensitivity to second-order relations, because faces that vary in head orientation cannot be matched accurately based on the appearance of individual features. This is consistent with the finding that 10-year-olds are not adult-like on this task, and adults' accuracy decreases when the faces are inverted (Mondloch, Geldart, et al., 2003).

Previous studies on patients treated for bilateral congenital cataract suggest that there is a relationship between the influence of deprivation on the development of visual capabilities mediated by the geniculo-striate pathway and the level of maturation of that visual function at birth (for a review see Maurer, Lewis, & Brent, 1989). Functions that are least affected by early visual deprivation are those that are relatively mature at birth. For example, young infants have the ability to discriminate an object's shape (Slater, Rose, & Morison, 1984) and color (Adams, Maurer, & Davis, 1986; Maurer & Adams, 1987), and these visual functions are not affected by early visual deprivation, even when the initial deprivation lasts over a year (Maurer et al., 1989). Similarly, temporal vision (the critical flicker fusion frequency) becomes adult-like during early infancy (Regal, 1981), and is not affected by early visual deprivation (Ellemberg et al., 1999). In contrast, the functions that are most severely affected by deprivation are those that are immature at birth and develop over the subsequent months and years. For example, visual acuity, spatial contrast sensitivity, and sensitivity to low temporal frequencies, are very immature at birth and take several years to develop fully (reviewed in Maurer & Lewis, 2001). Early deprivation severely impairs the normal development of these visual abilities (e.g., Ellemberg et al., 1999; Maurer, Lewis, Brent, & Levin, 1999).

Early visual experience may also be necessary for the development of the various components of expert face processing that rely on extrastriate ventral processing. In the following four manuscript chapters, I tested this hypothesis by examining the effects of early visual deprivation on second-order relational versus featural processing (chapters 2 and 5); holistic face processing (chapter 3), and face detection (chapter 4).

Organization of the Thesis

This thesis presents a unified set of studies that investigate the role of early visual experience in the development of configural versus featural face processing. It compares the face processing skills of children and adults with normal visual experience to those of patients who were deprived of visual input to one or both eyes during early infancy because of congenital cataracts. The cataract was present at birth and prevented patterned visual input from reaching the retina until the eye was treated by surgical removal of the natural lens and fitting of an optical correction (a contact lens) that provided nearly normal visual input (see Maurer et al., 1989). Because the cataract deprived patients of all patterned input, and not just input from faces, the studies reported here are an indirect assessment of whether the development of expert face processing requires early experience with faces. Patients treated for bilateral congenital cataract were deprived of early visual experience from birth until age 2-6 months, and thus allowed for the study of the development of expert face processing in the absence of vision during early infancy. Patients born with a unilateral cataract (cataract in one eye) were deprived of visual input mainly to the contralateral hemisphere during infancy (because of slow growth of the nasal visual field and lack of functional integration of visual input across the corpus callosum). The unilateral deprivation lasted from birth until age 2-28 months, and thus allowed for an evaluation of the degree of plasticity during early infancy in the lateralization of networks underlying expert face processing. In all the studies reported here, the patients were tested later in life and after many (at least 8) years of visual experience following treatment, to allow for recovery from the initial deprivation.

This thesis includes four manuscript chapters. Chapter 2 examines the role of early visual input in the development of the ability to identify faces based on featural and second-order relational processing. Two sets of face stimuli were created to tap sensitivity to featural versus second-order relational information. The face stimuli differed either in the shape of two features (eyes and mouth; featural set) or the spacing of the features (spacing set). To test the validity of the two stimulus sets, visually normal adults discriminated sequentially presented pairs of faces from each set in both upright and inverted orientations. To examine the role of early visual input in the development of featural versus second-order relational processing, visually normal individuals were compared to individuals deprived of early visual experience because of bilateral congenital cataract on their ability to discriminate faces from the two face sets.

The ease with which adults are able to identify faces depends in part on holistic processing. Chapter 3 examines the role of early visual experience in the development of holistic face processing. The study examines the same cohort of patients deprived of early visual input on the composite face task, a measure of holistic processing (see *Holistic Processing* section above). In Experiment 1, we tested visually normal adults on the composite face task to evaluate its appropriateness for testing deprived patients. We wanted to create a highly robust composite face effect that was not influenced by ceiling and/or floor effects. In Experiment 2, we compared the size of the composite face effect in deprived patients to control subjects in order to determine the role of early visual input in the development of holistic face processing.

Chapter 4 presents research that investigates the role of early visual experience in driving the development of normal sensitivity to the first-order relations that underlie face detection. The study compares patients with a history of visual deprivation during infancy due to bilateral congenital cataract to visually normal control subjects on their ability to classify a series of ambiguous stimuli—Mooney faces and scrambled Mooney faces—as either a face or nonface. Mooney faces were chosen because they are more difficult to classify than either gray-scale images or schematic faces, and cannot be classified as faces based on individual features.

The research reported in Chapter 5 was designed to evaluate the contribution of visual input to the right versus left hemisphere during early infancy in setting up the neural substrate that will later become specialized for expert face processing. The study used the same face discrimination task as in Chapter 2 to compare visually normal individuals to patients for whom visual input had been restricted mainly to one hemisphere during infancy. Because expertise in second-order relational processing is mediated largely by neural networks in the right hemisphere, I predicted that early deprivation of visual input to the right hemisphere would severely impair sensitivity to second-order relational information, while deprivation restricted mainly to the left hemisphere would not.

The findings showed that the deprived patients were severely impaired at differentiating faces from the spacing set, but not the featural set (Chapter 2). These results show that the development of second-order relational processing, but not featural processing, requires early visual input. Deprived patients also did not demonstrate a composite face effect (Chapter 3). Because visually normal individuals process faces holistically, they had severe difficulty in differentiating the identical top halves of two faces that were aligned with different bottom halves versus when the halves were misaligned. In contrast, the deprived patients performed equally well in both the aligned and misaligned conditions, and performed better than normal in the aligned condition. Thus, early visual experience is necessary for the normal development of holistic face processing. Furthermore, the patients' failure to integrate the facial features and process the face as a whole, may have caused them to be insensitive to the spacing of features (as measured in Chapter 2). Despite impairment in holistic face processing and second-order relational processing, the deprived patients were nevertheless able to detect Mooney faces based on the first-order relations (Chapter 4). Thus, their impairments cannot be attributed to a failure to process the first-order relations of a face. Furthermore, these results demonstrate that not all components of configural face processing require early visual input. The right hemisphere might be particularly important for face-processing: patients deprived of early visual input to mainly the right hemisphere, but not to the left hemisphere, were severely impaired at discriminating among faces that differ only in the spacing of the features (Chapter 5). These findings indicate that early visual input to the right hemisphere, but not the left hemisphere, is necessary for the normal development of second-order relational processing of faces.

Together, the results of these studies show that early visual experience is necessary for the later development of expert face processing. Holistic face processing, and face identity based on second-order relational information (abilities that are considered essential for expert face processing) are severely impaired following early visual deprivation. The development of the normal ability to detect faces based on first-order relations is not prevented by visual deprivation early in infancy. Furthermore, input specifically to the right hemisphere during early infancy is critical to set up and/or maintain the neural network that will become specialized for expert face processing.

Because this thesis consists of four related yet independent manuscripts, there is some degree of overlap between the chapters. Parts of the background literature presented in the introductory chapter also appear as background material in the manuscript chapters. This is especially true for the literature review on configural face processing and its developmental progression. Furthermore, the studies reported in Chapters 2 and 5 use the same experimental design and methodology. Thus, the methods sections of these chapters are highly similar.

Chapter 2

Early Visual Experience and Face Processing

Richard Le Grand, Catherine J. Mondloch, Daphne Maurer, & Henry P. Brent (2001).

Brief Communication

Nature 2001. Volume 410, page 890.

Adult-like expertise in processing face information takes many years to develop[1] and is mediated in part by specialized cortical mechanisms[2] sensitive to the spacing of facial features (configural processing)[3]. Here we show that deprivation of patterned visual input from birth until 2-6 months of age results in permanent deficits in configural face processing. Even after more than nine years' recovery, patients treated for bilateral congenital cataracts were severely impaired at differentiating faces that differed only in the spacing of their features, but were normal in distinguishing those varying only in the shape of individual features. These findings indicate that early visual input is necessary for normal development of the neural architecture that will become specialized for configural processing of faces over subsequent years.

To recognize individual faces, it is necessary to encode information about subtle differences in the shape of specific features such as the eyes (featural information) and/or in the spacing among the features (second-order relational information). Following the method described by Freire et al.[4], we created two sets of face stimuli that differentiated second-order relational from featural processing (Fig. 1a, b). We asked 26 normal right-handed adults to view the faces from each set binocularly and to make same/different judgments about them when presented upright or inverted. Adults were equally accurate in differentiating faces from the two sets in their canonical upright position (Table 1). Consistent with previous findings that inversion impairs configural processing[4,5], inverting the faces decreased adults' accuracy for the spacing set much more than it did for the featural set.

We next used these stimuli to examine the face processing abilities of 14 patients (6 male; 13 right handed; 11 Caucasian) who were born with a dense, central cataract in each eye that prevented patterned stimulation from reaching the retina (see Ellemberg et al.[6] for selection criteria). The eyes were treated by surgical removal of the natural lens and fitting of an optical correction that provided focused visual input (mean duration of deprivation = 118 days from birth, range = 62-187 days). The patients had had at least nine years of visual experience after treatment prior to testing and, when necessary, wore an additional optical correction to focus the eyes at the testing distance.

Compared to age-matched normal subjects, the deprived patients performed normally in distinguishing faces from the featural set, but were significantly impaired in distinguishing faces from the spacing set when presented upright (Table 1). Performance was not related to the duration of the deprivation for either set ($P > 0.10$; Fig. 1c). There was no correlation between acuity (which ranged from 20/25 to 20/80 in the better eye; median = 20/40) and patients' accuracy on either set ($P > 0.10$).

Our results indicate that visual experience during the first few months of life is necessary for the normal development of expert face processing. Because normal infants have poor visual acuity[7], their cortex is exposed only to low spatial frequency information that, for faces, specifies the global contour and location of features, but provides little information about feature details[8]. This low spatial frequency information appears to set up the neural architecture that will become specialized for expert configural processing of faces over the next 10-12 years[9, 10]. When visual input is delayed by as little as 2 months, permanent deficits result.

In a separate study, patients performed normally on a task requiring the discrimination of geometric patterns based on the location of an internal feature[11]. This suggests that patients' deficits in configural processing may be restricted to the processing of faces, as would be expected from the abundance of evidence that normal adults use separate systems for processing face and non-face objects[12,13].

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Figure Captions

Figure 1 Measurement of configural versus featural processing. Examples of stimuli from **a,** the spacing set (created by moving the eyes and mouth), and **b,** the featural set (created by replacing the eyes and mouth). On each trial, one of five possible faces appeared for 200 msec, and following an inter-stimulus interval of 300 msec, a second face appeared until the subject responded same or different. **c,** Patients' performance on the upright spacing set plotted as a function of the duration of deprivation from birth. Each circle represents the difference between the accuracy (percent correct) of one patient and his/her aged-match control.

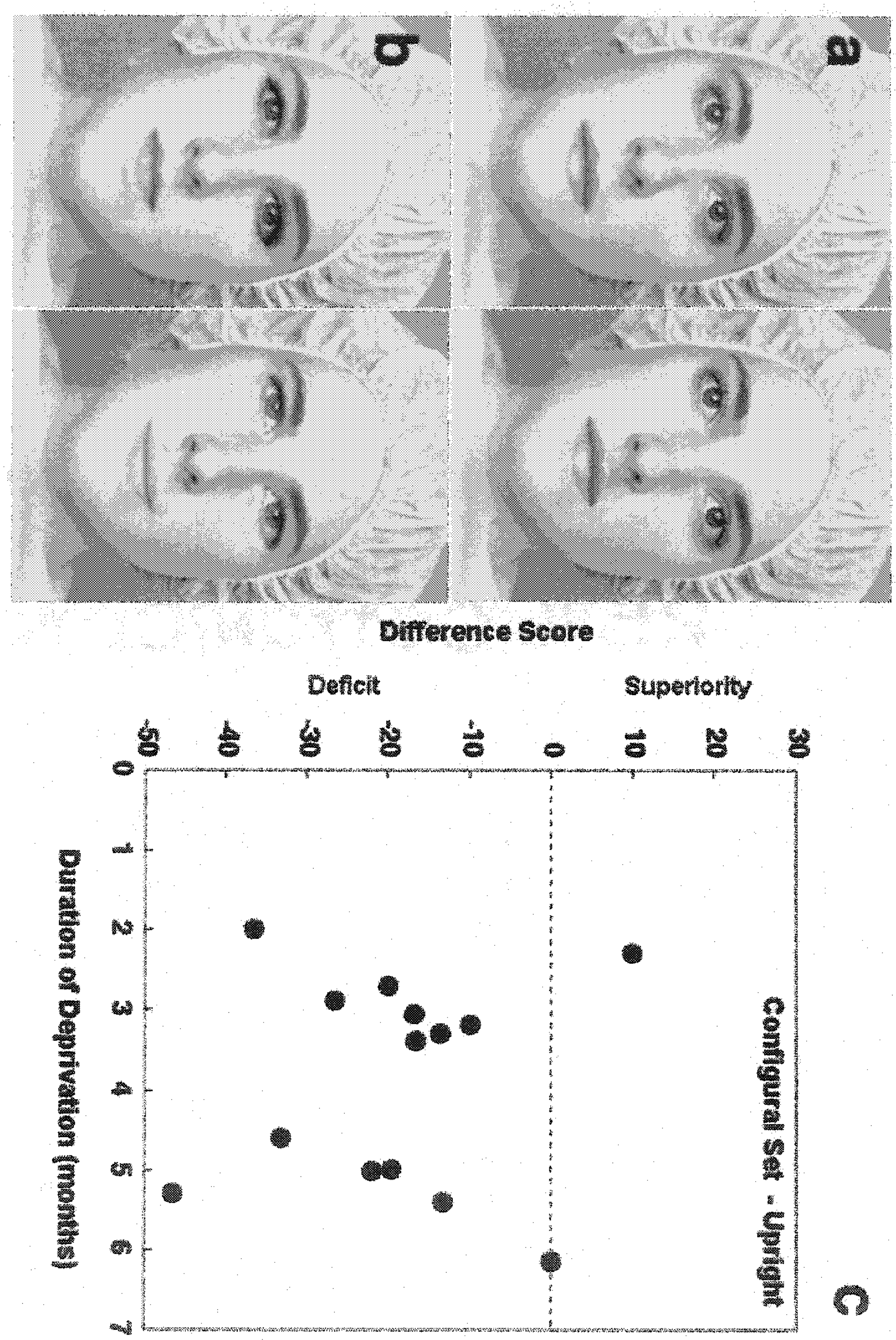
a
b
c
Configural Set - Upright
Difference Score
Superiority
Deficit
30
20
10
0
-10
-20
-30
-40
-50
0
1
2
3
4
5
6
7
Duration of Deprivation (months)

Figure 1

Group	N	Mean Age (range)	Mean Accuracy (s.e.)			
			Spacing		Featural	
			UP	INV	UP	INV
Adults	26	19 (18 – 22)	80 (1.9)	63 (2.2)	89 (1.4)	81 (1.8)
Controls	14	14 (9 - 21)	81 (2.7)	59 (1.8)	89 (1.9)	80 (2.9)
Patients	14	14 (9 – 21)	62 (3.2)	55 (3.0)	85 (2.4)	78 (3.1)

Table 1

Mean accuracy (percent correct) for detecting spacing and featural differences in upright (UP) and inverted (INV) faces. There were 30 trials for each of the 4 conditions, which were presented in separate blocks. For adults, inversion decreased accuracy for the spacing set significantly more than for the featural set (significant interaction between orientation and stimulus set {$F_{1,25} = 13.13$, $P < 0.01$}, followed by analyses of simple effects {$F_{1,27} = 62.57$, $P < 0.01$}). Patients were less accurate than controls (matched on age, gender, race, and handedness) only for the upright spacing set (significant interaction between group, orientation and stimulus set {$F_{1,26} = 4.15$, $P < 0.05$}, followed by analyses of simple effects {$F_{1,26} = 21.92$, $P < 0.01$}).

Chapter 3

When the Whole is No Greater Than the Sum of its Parts:

Impairment in Holistic Face Processing Following Early Visual Deprivation

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Visual experience during early infancy is necessary for the normal development of some, but not all, face processing skills. Here we examined the influence of early visual input on the development of holistic face processing (the tendency to process the face as a whole rather than as independent features). We compared individuals with normal visual histories to patients deprived of early visual experience on a measure of holistic processing - the composite face task (Hole, 1994). The patients were deprived from birth until 3 to 6 months, and were tested following treatment and after several years of visual experience (at least 8 years). Visually normal adults (Experiment 1) and control subjects (Experiment 2) had difficulty perceiving that the top halves of two faces where the same when they were aligned with different bottom halves, compared to when holistic processing was disrupted by misaligning the top and bottom halves (the composite face effect). Deprived patients (Experiment 2) showed no evidence of holistic processing: instead of demonstrating the normal composite face effect, the patients were superior to controls on the aligned condition, and did not benefit from misalignment. These findings suggest that early visual experience is necessary to set up or maintain the neural substrate that underlies holistic face processing.

Face recognition tends to engage holistic processing. When a stimulus is detected as a face, its parts become integrated into a whole or Gestalt-like representation, making information about individual features less accessible (for a review see Maurer, Le Grand & Mondloch 2002). A compelling demonstration of holistic processing is the *composite* *face effect* (Carey & Diamond, 1994; Hole, 1994; Young, Hellawell & Hay, 1987; Hole, George & Dunsmore, 1999). Adults find it very difficult to recognize the top half of a celebrity's face when it has been aligned with the bottom half of a different person's face (Young et al., 1987). Presumably holistic processing binds the two halves of the face thus creating the impression that it is a novel face. Adults perform better after manipulations that disrupt holistic processing such as misaligning the two halves or inverting the face (Young et al., 1987). The composite face effect also has been shown for same/different judgments of unfamiliar faces (Hole, 1994). When adults see two faces that have the identical top half of an unfamiliar face, but they are merged with two different bottom halves, holistic processing creates the impression that the top halves are different (see Figure 1). Holistic processing also makes it difficult to recognize that the internal features of two faces are identical (e.g., both from George Bush) when presented in different external contours (e.g., from George Bush and Dick Cheney) (Sinha & Poggio, 2002; Sinha & Poggio, 1996). Similarly, adults recognize the features from an individual's face more easily in the context of their whole face (e.g., Larry's nose in Larry's face) than in isolation (*the whole/part advantage*) (Tanaka & Farah, 1993). These findings demonstrate that facial features are not encoded individually, but rather are integrated into a holistic representation. Little or no attention to the face may be required for it to be processed holistically, as the composite face effect is also found under conditions of divided attention (Boutet, Gentes-Hawn & Chaudhuri, 2003; but see Reinitz et al., 1997).

The tendency to integrate the features of a face into a whole, rather than perceive the face as a collection of independent elements, begins to emerge during infancy. After being habituated to two faces, 7-month-old infants treat a composite consisting of the external portion of one familiar face and the internal portion of the other as if it were a novel face, but only when the faces are presented upright (Cohen & Cashon, 2001). By middle childhood, adult-like holistic face processing is evident. Six-year-old children (the youngest age tested) show an adult-like composite face effect for both familiar faces (Carey & Diamond, 1994), and unfamiliar faces (Mondloch, Pathman, Le Grand, & Maurer, 2003). Similarly, 6-year-olds show the whole/part advantage for unfamiliar faces (Tanaka, Kay, Grinnel, Stansfield, & Szechter, 1998), and the size of the effect is as large as in 11-year olds (the oldest age compared) (Joseph & Tanaka, 2003).

Several theorists have argued that exposure to faces during early infancy is critical for the development of the cortical networks that will become responsible for expert face processing (e.g., de Schonen & Mathivet, 1989; Morton & Johnson, 1991; Nelson, 2001). In support of such theories, we have previously shown abnormalities in some aspects of face processing in patients deprived of early visual experience (Mondloch, Le Grand & Maurer, in press). The patients were deprived of patterned vision during early infancy due to dense cataracts present in both eyes from birth. Despite years of compensatory visual input following treatment for the initial deprivation, the patients show deficits later in life on tasks that require sensitivity to the spatial relations among facial features (second-order relational processing). They have deficits in distinguishing faces that differ only in the spacing among features such as the distance between the eyes (Le Grand, Mondloch, Maurer & Brent, 2001), and matching faces' identity when the matching face is presented from a novel point of view (Geldart, Mondloch, Maurer, de Schonen &

Brent, 2002) – tasks that require sensitivity to second-order relations (Mondloch, Geldart, Maurer, & Le Grand, in press). In contrast, early visual deprivation has no apparent effect on the later development of processing faces based on individual features (featural processing). These same patients can easily distinguish faces that differ only in the shape of individual features (Le Grand et al., 2001), and can match faces based on emotional expression, vowel being mouthed, and direction of eye gaze (Geldart et al., 2002) – tasks that can be performed by processing local features.

In the present study we evaluated the role of early visual experience in the development of holistic face processing by comparing the size of the composite face effect in individuals treated for bilateral congenital cataract and individuals with a normal visual history. This particular task was chosen because patients are normal at discriminating faces based on individual features (Le Grand et al., 2001), and should therefore be able to discriminate the top halves of composite faces by using featural information (e.g., the shape of the eyes).

Experiment 1: The composite face effect – a measure of holistic processing.

The purpose of Experiment 1 was to test our version of the composite face task in normal adults to evaluate its appropriateness for testing patients. We wanted to create a highly robust composite face effect that was not influenced by ceiling and/or floor effects. We predicted that trials in the aligned condition with the same top halves (same/aligned) should be particularly difficult. This is because holistic processing 'binds' the top and bottom halves thus creating the impression that two identical top halves are in fact different. On the other hand, trials in the misaligned condition with the same top halves (same/misaligned) should be less difficult, as misaligning the faces prevents holistic processing. For different trials we predicted that adults would perform as well or better on aligned trials relative to misaligned trials. Adults may perform better on aligned-different trials because in addition to the faces differing in featural information (e.g., the shape of the eyes), they also differ in second-order relational information (e.g., the distance between the eyes and mouth).

Method

Participants

Twenty-four (12 female; mean age = 20 years, range 18 – 22 years) undergraduate students at McMaster University participated in the experiment for course credit. None of the participants had a history of eye problems and all met our criteria on a visual screening exam described elsewhere (Mondloch, Le Grand & Maurer, 2002). All participants were Caucasian and right-handed. Three additional participants were tested but excluded because they failed visual screening.

Apparatus

The experiment was conducted on a Macintosh LC-475 computer using the experimental software Cedrus Superlab. The stimuli were presented on a monochrome Radius 21-GS monitor. Participants signaled their responses via a joystick, and the experimenter initiated trials by pressing a key on the keyboard.

Stimuli

Fifty-two face composites were created from gray scale digitized images of adult Caucasian faces. Models wore no jewelry, glasses or makeup, and a surgical cap covered their hair and ears. Using the graphics software program Adobe Photoshop, face composites were created by splitting face images in half horizontally across the middle of the nose, and then recombining the faces using the top and the bottom halves of different individuals. The same face composites were used in the two conditions tested: aligned faces and misaligned faces. In the aligned condition, the top and bottom face segments were properly aligned. In the misaligned condition, the top half of each face was misaligned by shifting it horizontally to the left so that the right-most edge of the top half was aligned with the middle of the nose in the bottom half of the image (see Figure 1). For every trial, the location of the top half of each face remained constant. Stimuli in the aligned condition were 9.8 cm. wide and 14 cm. high (5.6 x 8 visual degrees from the testing distance of 100 cm.). Stimuli in the misaligned condition were 12.8 cm. wide and 14 cm. high (7.3 x 8 visual degrees from the testing distance of 100 cm). Although the misaligned stimuli occupied a wider horizontal visual angle, the face halves were of identical size in both conditions.

Design & Procedure

The participant sat in a dimly lit room 100 cm from a computer monitor. On each trial, a composite face appeared for 200 ms., and following a 300 ms. inter-stimulus interval, a second composite face appeared for 200 ms. The participant was asked to judge as quickly and accurately as possible whether the top half of the two faces were the same or different. Participants moved a joystick forward if they believed the top half of the two faces were the same, and back if they believed that the top halves were different. The two conditions (*misaligned* faces and *aligned* faces) were blocked, with half the participants receiving the misaligned condition first, and half receiving the aligned condition first. Within each block, half of the trials consisted of pairs of faces that shared the identical top halves (*same trials*), and half of the trials consisted of pairs of faces with different top halves (*different trials*). On every trial the bottom halves were different. Same and different trials were intermixed randomly within each block. Prior to each block, the participant received four practice trials presented without feedback. Percent correct and median reaction times for correct responses were recorded.

Results and Discussion

Analyses

For both accuracy and reaction time, an ANOVA was conducted with one between-subjects factor (Order: aligned first / misaligned first) and two within-subjects factors (Condition: aligned / misaligned, and Response Type: same / different). To explore significant 2-way interactions, we conducted separate ANOVAs for the two response types.

Accuracy

Aligning the face halves had a noticeable effect on accuracy for same trials, but not for different trials (see Figure 2a). Adults were much less accurate on same/aligned trials (mean = 63 %) than on same/misaligned trials (mean = 86 %). The ANOVA revealed significant main effects for Condition (aligned versus misaligned; $F_{1, 22} = 23.76$,

$p < 0.001$), and Response Type (same versus different; $F_{1, 22} = 17.84$, $p < 0.001$), but no main effect of Order ($p > 0.1$). There was also a significant 2-way interaction between Condition and Response Type ($F_{1, 22} = 24.53$, $p < 0.001$). All other interactions were not significant (all ps > 0.1). The analysis of simple effects revealed a significant effect of Condition for *same* trials ($F_{1, 23} = 26.98$, $p < 0.001$), but not for *different* trials ($p > 0.1$).

Reaction Time

As shown in Figure 2b, alignment affected reaction time on same trials, but not on different trials. Adults took longer to respond on same/aligned trials (mean = 815 ms.) than on same/misaligned trials (mean = 621 ms.). The ANOVA revealed a significant effect for Condition ($F_{1,22} = 19.83$, $p < 0.001$) and a significant interaction between Condition and Response Type ($F_{1,22} = 18.35$, $p < 0.001$). All other effects were not significant (all Ps > 0.1). The analyses of simple effects showed a significant effect of Condition for *same* trials ($F_{1,23} = 28.21$, $p < 0.001$), but not for *different* trials ($P > 0.1$).

Discussion

The results from visually normal adults demonstrate a strong *composite face effect*. In the aligned condition, processing the images holistically created the impression that the top halves were always different. This led to a high error rate and long reaction times on same/aligned trials. When holistic processing was disrupted by misaligning the face halves, accuracy on same trials increased by 23% and reaction time decreased by 194 ms. Adults' accuracy was not affected by ceiling or floor levels on any condition (see Figure 2a). This finding of a robust composite face effect demonstrates that the task is a sensitive measure of holistic face processing.

Experiment 2: The role of early visual experience in holistic face processing.

In Experiment 2, we evaluated the influence of early visual experience on the development of holistic face processing. Patients, who were deprived of patterned vision during early infancy, were tested on the composite face effect after treatment and following many years of visual experience. To assess the effects of the initial deprivation on holistic face processing, we compared the size of the composite face effect of the deprived patients to visually normal controls.

Method

Participants

Deprived Patients: Twelve right-handed Caucasian patients treated for bilateral congenital cataract participated in the experiment (8 male; mean age at test = 15 years, range 9 – 23 years). All patients were diagnosed with dense central cataracts in both eyes that blocked all patterned input on their first eye exam and before 6 months of age (see Ellemberg, Lewis, Maurer, Liu, & Brent, 1999 for detailed criteria). Because it would be unusual to have dense cataracts develop rapidly between birth and 6 months, duration of deprivation was defined as the period extending from birth until the age of first optical correction following surgery to remove the cataract (i.e., the first time the infant received focused visual input onto the retina), which ranged from 3.2 months to 6.2 months (mean = 4.6 months). Input from this point was only nearly normal because the contact lenses focused input perfectly for only one distance and the eyes could not accommodate for other distances. Patients were tested later in life (at least 8 years after surgery) to allow for potential recovery from the initial visual deprivation. Visual acuity at test in the better eye ranged from 20/32 to 20/63 (median = 20/50). When necessary at testing, the patient wore an additional optical correction so that the eyes were focused at the testing distance.

Visually normal controls: The results of the deprived group were compared to a visually normal control group matched on handedness, gender, race and age and tested under the same conditions. None of the participants had a history of eye problems and all met our criteria on a visual screening exam described elsewhere (Mondloch, Le Grand & Maurer, 2002). One additional participant was tested, but was excluded because he failed visual screening.

Procedure

All participants were tested binocularly on the same procedure described in Experiment 1. Because performance was not affected by order of condition in Experiment 1, all participants in Experiment 2 were presented with the same order of conditions (Misaligned first and Aligned second). This order was chosen because it rules out the possibility that the composite face effect is the result of trials from the most difficult condition (same/aligned) being presented first. Furthermore, the results of Experiment 1 showed that even though participants successfully ignored the bottom halves of the faces in the initial misaligned condition, they nevertheless performed poorly in the subsequent same/aligned trials.

Analyses

For both accuracy and reaction time, an ANOVA was conducted with one between-subjects factor (Group: deprived / control) and two within-subjects factors (Condition: aligned / misaligned, and Response Type: same / different). To explore the significant 3-way interaction, we conducted separate ANOVAs for the two groups: significant interactions between Condition and Response Type for any group were investigated with analyses of simple effects that analyzed the effect of Condition for each Response Type.

Results and Discussion

Accuracy

Unlike the control group, deprived patients did not benefit from misalignment on *same* trials; they were equally accurate on same/aligned trials (mean = 76%) as same/misaligned trials (mean = 76%), and actually performed better than the control group (mean = 56%) on *same* trials when the faces were aligned (see Figure 3a).

The ANOVA on accuracy revealed main effects for Condition ($F_{1,22} = 23.24$, $p < 0.001$) and Response Type ($F_{1,22} = 17.02$, $p < 0.001$). The ANOVA also revealed significant interactions between Group and Condition ($F_{1,22} = 38.70$, $p < 0.01$), and Condition and Response Type ($F_{1,22} = 35.65$, $p < 0.001$), as well as a 3-way interaction between Group, Condition and Response Type ($F_{1,22} = 18.34$, $p < 0.001$).

Control Group.

The control group was affected by alignment (see Figure 3a). They performed significantly worse on same/aligned trials (mean = 56 %) compared to same/misaligned trials (mean = 86 %). The ANOVA on accuracy for the control group revealed main effects for Condition ($F_{1,11} = 35.48$, $p < 0.01$) and Response Type ($F_{1,11} = 8.83$, $p < 0.01$), as well as a significant interaction for Condition and Response Type ($F_{1,11} = 41.34$, $p < 0.01$). The analyses of simple effects revealed a significant effect of Condition for *same* trials ($F_{1,11} = 53.13$, $p < 0.001$), but not for *different* trials ($p > 0.1$).

Deprived Group.

The ANOVA on accuracy for the deprived group revealed a significant main effect for Response Type ($F_{1,11} = 9.68$, $p < 0.01$). Deprived patients were more accurate on different trials than same trials. However, this pattern did not vary with alignment (see Figure 3a).

Size of the Composite Face Effect.

To directly compare the size of the composite face effect between the deprived and control groups, for each participant we calculated a difference score (same/misaligned trials minus same/aligned trials). A planned comparison showed that the size of the composite face effect was significantly larger in the control group (mean = 30%) compared to the deprived group (mean = 0%) ($t_{1,22} = 6.80$, $p < 0.001$). The lack of the composite face effect in the deprived group was found in all patients - even the patient with the shortest duration of deprivation. The size of the composite face effect in the deprived group was not correlated with age at test or acuity in the better eye (ps > 0.1).

Reaction Time

As shown in Figure 3b, reaction times of both groups were longer on *same* trials when the stimuli were aligned than when stimuli were misaligned, but the effect was much smaller for the deprived group than the control group. The ANOVA for RT showed a significant main effect for Response Type ($F_{1,22} = 6.42$, $p < 0.05$) and a significant interaction between Condition and Response Type ($F_{1,22} = 14.99$, $p < 0.001$). However, there was no effect of Group (all ps > 0.1). The analyses of simple effects showed that reaction times were significantly slower when faces were aligned than when faces were misaligned on *same* trials ($F_{1,22} = 8.74$, $p < 0.01$), but not *different* trials ($p > 0.1$).

Size of the Composite Face Effect.

A planned comparison showed that the size of the composite face effect (as measured by the difference in RT between same/misaligned and same/aligned trials) was significantly larger in the control group (mean = -341 ms.) than the deprived group (mean = -75 ms.) ($t_{1,22} = 6.8$, $p < 0.001$). The lack of RT composite face effect was found even in the patient with the shortest duration of deprivation, and the size of the effect did not correlate with the patients' age or acuity (*p*s > 0.1).

Discussion

The results of Experiment 2 indicate that early visual deprivation impairs the development of holistic face processing. As expected, the control group showed a strong composite face effect. On same trials, disrupting holistic processing by misaligning the face halves led to a 30% increase in accuracy and a 341 ms. decrease in RT. In contrast, the deprived group showed little evidence of a composite face effect (no change in accuracy and only a 75 ms. decrease in RT). Indeed, the deprived group performed significantly better than the control group on same/aligned trials (see Figure 3; $p < 0.01$). This result is particularly striking: the deprived patients' impairment in holistic processing is demonstrated here by *enhanced* performance relative to the control group. Presumably, patients deprived of early visual input fail to integrate the facial features into a Gestalt. As a result, they can accurately make same/different judgments for the top halves of faces irrespective of whether the halves are aligned or misaligned[1].

Compared to normal controls, deprived patients had difficulty on same trials when the faces were misaligned. This difficulty may be related to the patients' deficit in processing second-order relations (the spacing among the internal facial features) (Le Grand et al., 2001). That deficit may cause patients to be less certain that the top halves of two faces are identical, and may explain their longer reaction times overall (cf. Figure 3b & 3c). In contrast, patients performed well when the top halves were different, presumably because they could use featural processing to differentiate the faces (cf. accuracy for different versus same trials in Figure 3c). Despite the patients' difficulty in matching the top halves of identical faces, they nevertheless performed much better than visually normal individuals when the top halves were identical and aligned.

[1] In a separate experiment, we tested the same deprived patients that participated in Experiment 2 on a composite face task that required making judgments for the bottom halves of faces. Similar to the findings in Experiment 2, the deprived patients did not benefit from misaligning the face halves, and performed significantly better than normal on same/aligned trials. Thus, whether the composite face task requires attending to the top or bottom half of the face, deprived patients do not show the composite face effect.

General Discussion

The results of the present study indicate that early visual experience is necessary for the normal development of holistic face processing. Patients deprived of patterned vision during early infancy due to bilateral congenital cataracts fail to demonstrate the normal composite face effect, an index of holistic processing. Although holistic processing normally aids in face recognition, it is disadvantageous in the experimental situation tested here: judging whether two faces share the same top halves when aligned with different bottom halves. Under such conditions, patients deprived of early visual experience show supernormal abilities: they are 20% more accurate and 175 ms. faster than controls in seeing that two top halves are identical despite being aligned with different bottom halves. This, along with their failure to demonstrate a composite face effect, indicates that they fail to process faces in a holistic manner. Thus, for face processing following early visual deprivation, the whole is no greater than the sum of its parts. The impairment in holistic face processing may be caused by early visual deprivation per se, or perhaps more specifically to a lack of experience with human faces during early infancy. Although testing individuals treated for bilateral congenital cataracts cannot separate these two alternatives, several theorists have argued that exposure to faces during early infancy is essential for the normal development of face processing skills (de Schonen & Mathivet, 1989; Morton & Johnson, 1991).

Previous research has shown that early visual deprivation lasting as little as the two months prevents the later development of the ability to recognize faces based on the spacing of facial features (second-order relations), but not of processing faces based on individual features (featural processing) (Le Grand et al., 2001; Geldart et al., 2002). It is possible that the impairment in holistic face processing, which prevents the proper integration of facial features, also leads to a failure to properly process the spatial relations among the features (second-order relational processing). That is, for normal processing of second-order relations, holistic processing is required. This possibility is consistent with evidence that holistic processing becomes adult-like by 6 years of age (Carey & Diamond, 1994; Mondloch, Pathman, Le Grand, & Maurer, 2003), whereas second-order relational processing is still not adult-like at 14 years of age (Mondloch et al., 2002).

Relative to most common objects, faces are processed in a more holistic manner (Tanaka & Farah, 1993). However, converging evidence suggests that expertise with non-face objects may also engage holistic processing. Adults who have extensive training at recognizing a class of homogeneous non-faces objects (Greebles) at the individual level show evidence of holistic processing on the composite face task (Gauthier & Tarr, 2002). In a dual composite task requiring simultaneous processing of faces and cars, car experts (but not novices) show behavioral interference of car processing on holistic face processing, as indicated by an attenuated composite face effect (Gauthier, Curran, Curby & Collins, 2003). While the results of the present study establish that early visual experience is necessary for the development of normal holistic processing for faces, further research is required to determine whether early vision is also necessary for holistic processing of non-face objects.

Previous research suggests that neural networks within the right hemisphere are involved in face processing. Neuroimaging studies of adult humans typically find greater activation for faces than objects in areas of the right hemisphere (including the putative fusiform face area-FFA) (George et al., 1999; Kanwisher, McDermott & Chun, 1997; McCarthy, Puce, Gore & Allison, 1997). This right hemisphere activation is much stronger for matching whole faces than matching face parts (Rossion et al., 2000). Cortical damage to the right hemisphere, but not the left hemisphere, can lead to severe impairment in face recognition (prosopagnosia) (de Renzi, Perani, Caresimo, Silveri & Fazio, 1994), a condition that includes deficits in holistic face processing (Saumier, Arguin & Lassonde, 2001). Split-brain monkeys have a right hemisphere advantage for recognizing upright monkey faces (Vermeire, Hamilton, & Erdmann, 1998). However, this advantage disappears when the stimuli are inverted (Vermeire & Hamilton, 1998). Together these findings suggest that the right hemisphere may play an important role in holistic face processing. Previously we have shown that patients deprived of early visual input to the right hemisphere, but not the left hemisphere, are severely impaired at processing second-order relational information in faces (Le Grand, Mondloch, Maurer & Brent, submitted). Perhaps early visual input to the right hemisphere is necessary for holistic face processing to develop normally. Further research is necessary to determine the role of early visual input to the respective hemispheres in setting up the neural architecture that will become responsible for holistic face processing.

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Figure captions

Figure 1. Composite face stimuli. Face pairs from the aligned condition (top row) and the misaligned condition (bottom row). The face pairs either have the identical top halves (left column), or the top halves are different (right column). For all face pairs, the bottom halves are different.

Figure 2. Mean accuracy scores (panel a) and mean reaction times (panel b) of visually normal adults on the composite face task. Because the study used a within-subject design (and thus the variance within conditions is irrelevant), the standard error bars represent intra-subject variability between conditions (see Loftus & Masson, 1994).

Figure 3. Mean accuracy scores of the deprived patients (panel a) and the control subjects (panel b) on the composite face task. The standard error bars represent the intra-subject variability between conditions for each group (see Loftus & Masson, 1994).

Figure 4. Mean reaction times of the deprived patients (panel a) and the control subjects (panel b) on the composite face task. The standard error bars represent the intra-subject variability between conditions for each group (see Loftus & Masson, 1994).

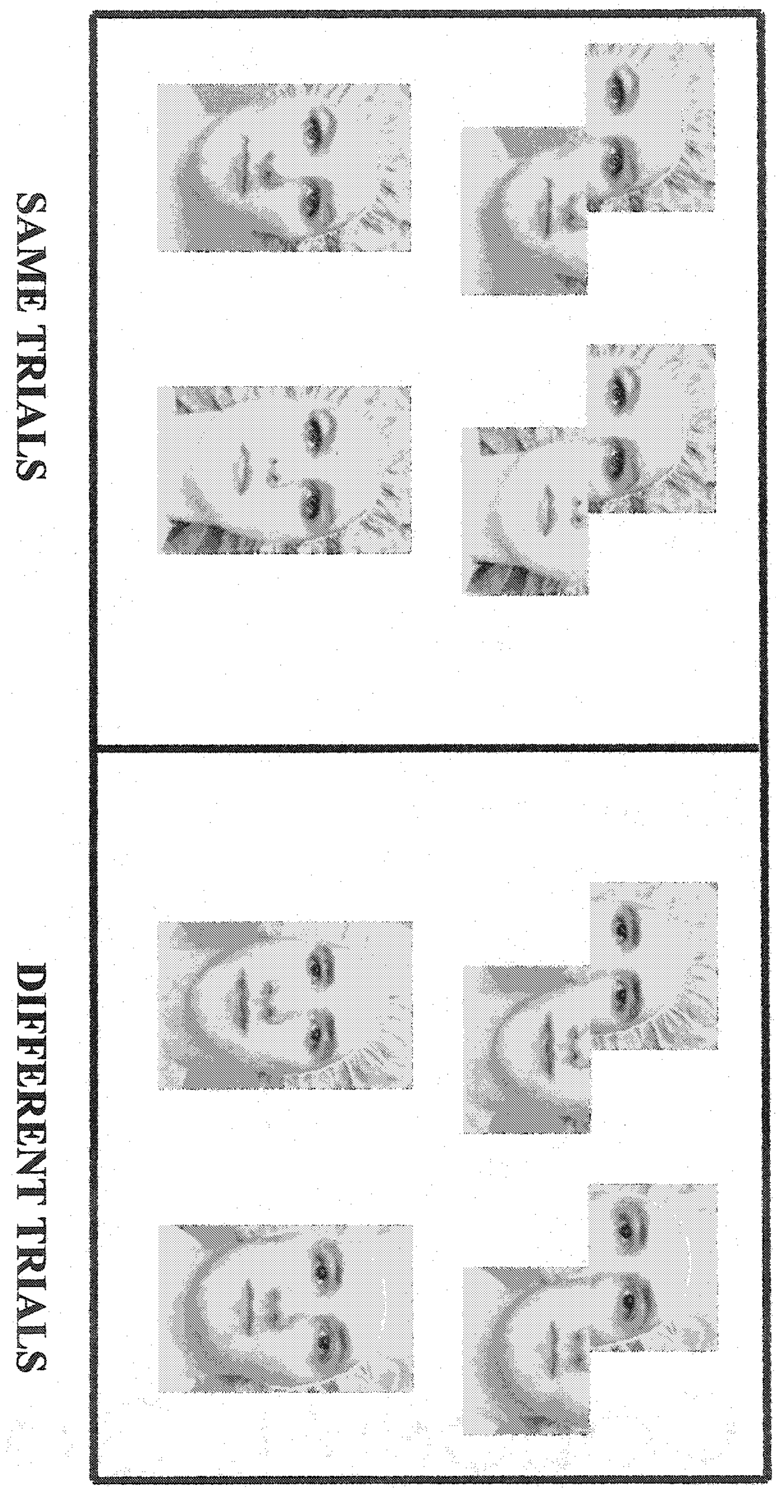

Figure 1. Composite Face Stimuli

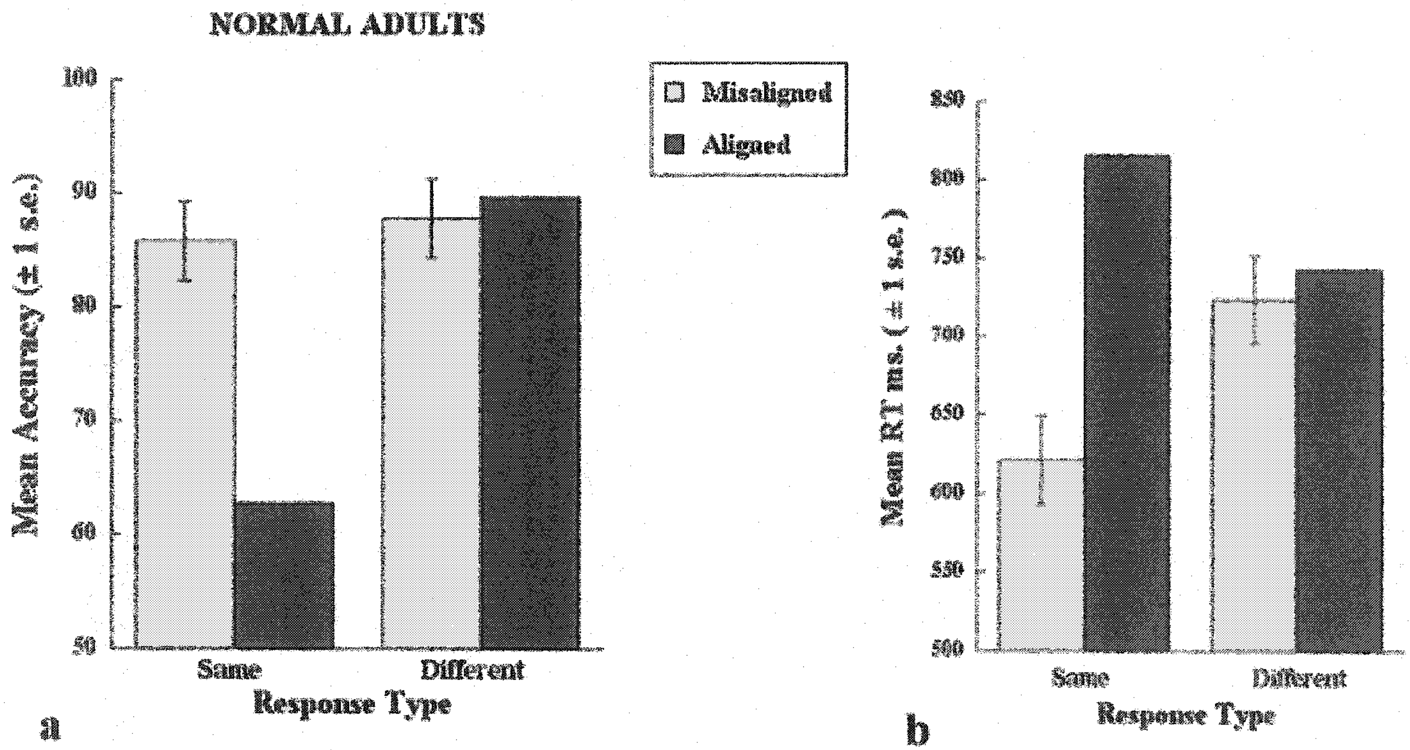

Figure 2. Mean accuracy scores (panel a) and mean reaction times (panel b) of visually normal adults on the composite face task.

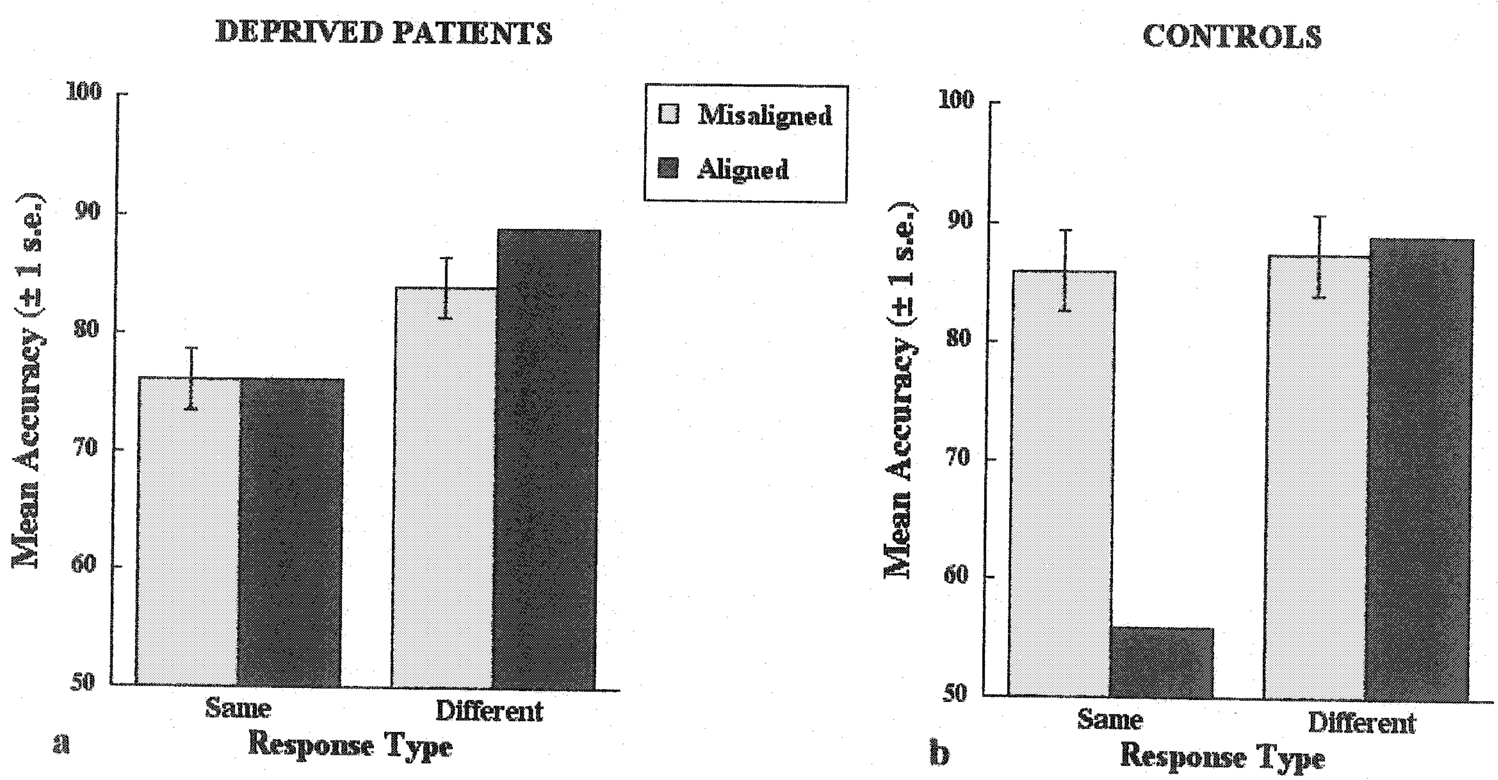

Figure 3. Mean accuracy scores of the deprived patients (panel a) and control subjects (panel b) on the composite face task.

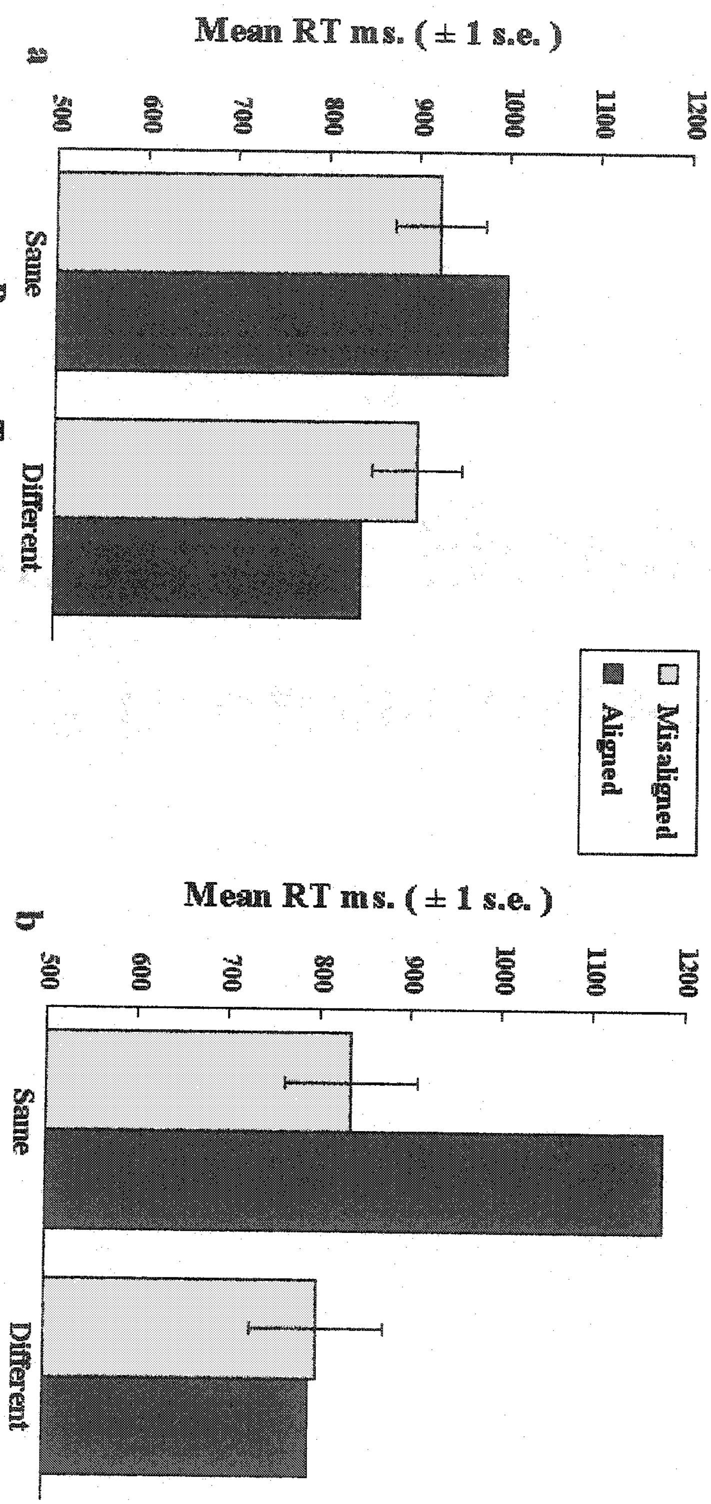

Figure 4. Mean reaction times of the deprived patients (panel a) and control subjects (panel b) on the composite face task.

Chapter 4

Early Visual Deprivation Does Not Prevent the Eventual Development of Normal Face Detection

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Adults are experts at configural face processing. They 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), process faces holistically (integrate the features into a Gestalt), and they are sensitive to differences among individual faces in their second-order relations (small differences between individuals in the spacing among the facial features). Several theorists of face processing argue that exposure to faces during early infancy is necessary for the normal development of expert face processing and the underlying cortical mechanisms. Previously we have shown that early visual deprivation disrupts the later development of holistic processing (Le Grand, Mondloch, Maurer, & Brent, 2002; submitted) and of sensitivity to second-order relations (Le Grand, Mondloch, Maurer, & Brent, 2001), but not the later development of featural processing. Here we investigated the role of early visual experience in driving the development of normal face detection. We tested the ability of patients (n=11), who had been deprived of early visual experience by bilateral congenital cataracts, to make face/nonface judgments about Mooney stimuli. When tested later in life, after treatment for cataract and many years of visual input (<u>M</u> age at test = 14.5 years), patients were as accurate and as fast as age-matched control subjects at detecting faces in degraded Mooney stimuli. The results suggest that early visual deprivation does not prevent the development of normal sensitivity to the first-order relations that underlie face detection, and that the patients' deficits in holistic processing and sensitivity to second-order relations are not caused by impairment in face detection.

Adults are 'experts' at face processing: they can recognize thousands of individual faces rapidly and accurately, and they can easily decipher specific cues in a single face, including emotional expression, head orientation, direction of gaze, and sound being mouthed (Bahrick, Bahrick, & Wittlinger, 1975; see Bruce & Young, 1998 for a review). In order to determine the role of early visual experience in the development of normal face processing, we are studying patients who were deprived of early visual experience due to bilateral congenital cataract that blocked all patterned input from reaching the retina. Early visual input was delayed until later in infancy when the cataractous lens was surgically removed and the eyes were fitted with compensatory contact lenses. We have tested these patients on a variety of face-processing tasks after they had had many years of visual experience following treatment (at least 8 years) and compared their performance to that of age-matched control subjects with a normal visual history. In an initial study (Geldart, Mondloch, Maurer, de Schonen & Brent, 2002), we showed that early visual experience is necessary for the later development of normal performance on some, but not all, components of face processing. Patients perform normally when asked to match faces based on emotional expression, vowel being mouthed, and direction of eye gaze, but have deficits in matching facial identity when the face to-be-recognized is presented in a novel point of view. Patients also tend to perform worse than normal when matching facial identity if the face-to-be recognized displays a novel emotional expression. In subsequent studies we have explored patients' deficits in face processing by assessing four processes which adults use in processing faces—face detection, holistic processing, and processing differences among individuals' faces based on differences in the shape of features (i.e., featural processing) or in the spacing of the features (i.e., sensitivity to second-order relations) (reviewed in Maurer, Le Grand, & Mondloch, 2002).

Face detection is facilitated by the fact that all faces share the same ordinal relations of features: the two eyes are positioned above the nose, which is above the mouth. These have been described as the "first-order relations" of faces and they differ from the first-order relations among the features of other objects (Diamond & Carey, 1986). When the first-order relations of a face are distorted (e.g., by positioning the mouth above the eyes), individual facial features can still be recognized but the stimulus no longer looks like a face. Adults have a remarkable ability to detect that a stimulus is a face based on first-order relations: 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 there are no normal facial features, as long as the components can be interpreted as having the correct first-order relations for a face. For example, they readily detect a face when presented with a painting by Arcimbaldo in which an arrangement of fruit or vegetables forms the correct first-order relations for a face (Moscovitch, Winocur, & Behrman, 1997) and when looking at the clouds in the sky. Similarly, they can detect a face in a two-tone Mooney stimulus (see Figure 1) in which the perception of individual features has been degraded by transforming all luminance values to black or white, at least when the stimuli are upright (Kanwisher, Tong, & Nakayama, 1998). Indeed, faces may play a special role in capturing attention: patients with visual extinction are more likely to detect a face presented in the neglected hemifield than they are to detect a scrambled face, a name, or a meaningless shape (Vuilleumier, 2000).

When a stimulus is detected as a face, adults tend to engage in *holistic processing*—they process the stimulus as a Gestalt, making it harder to process individual features. The most convincing demonstration of holistic processing is *the composite face effect.* Adults are slower and less accurate in recognizing the top half of a familiar face presented in a composite with the bottom half of another face when the composite is upright and fused than when the composite is inverted or the two halves are offset laterally--manipulations that disrupt holistic processing. This phenomenon demonstrates that when upright faces are processed, the internal features are so strongly integrated that it becomes difficult to parse the face into isolated features, at least at short exposures that prevent feature-by-feature comparisons (Young, Hellawell, & Hay, 1987). A similar effect occurs when adults are asked to make same/different judgments about the top halves of unfamiliar faces (Hole, 1994).

Because all faces share the same first-order relations, recognition of individual faces requires sensitivity to subtle differences in the shape of individual features (e.g., chin, eyes, mouth) and in the spacing among those features (e.g., distance between the eyes). Recognition based on these cues depends on *featural processing* and *second-order relational processing*, respectively. Featural and second-order relational processing develop at different rates (Freire & Lee, 2001; Mondloch, Le Grand, & Maurer, 2002) and are differentially affected by inversion (Freire, Lee, & Symons, 2000; Collishaw & Hole, 2000; Leder & Bruce, 2000; Le Grand & Maurer, 2003; Mondloch et al., 2002;

Rhodes, Brake, & Atkinson, 1993), a pattern of results suggesting a qualitative difference between the two processes. Because under some conditions featural processing of faces is not effective (e.g., changes in hairstyle, lighting or angle of view), adults' expertise in recognizing the identity of individual upright faces is likely to rely heavily on sensitivity to second-order relations.

Following early visual deprivation, patients perform normally when asked to discriminate among faces that differ only in the shape of individual internal facial features (eyes, mouth) (Le Grand et al., 2001) or only in the shape of the external contour (Mondloch, Le Grand, & Maurer, in press). These results demonstrate that early visual experience is not necessary for the later development of normal featural processing—hence patients' normal performance on matching faces based on emotional expression, vowel being mouthed, and direction of eye gaze (Geldart et al., 2002), tasks that may be performed based on local features (Mondloch, Geldart, Maurer & Le Grand, in press). In contrast, patients have deficits in discriminating among faces that differ only in the spacing among the internal features (Le Grand et al., 2001), an ability that seems crucial for adults' expertise in the recognition of individual faces (Maurer et al., 2002). Patients' deficit in processing second-order relations may explain their poor performance when matching facial identity across changes in point of view; this task likely taps sensitivity to second-order relations because the shape of the features in an individual's face changes across head orientations (e.g., the nose looks pointed in profile but not enface), whereas the spacing among the individual's features remains relatively invariant (e.g., the nose is still farther from the eyes than in an average face) (Geldart et al., 2002; Mondloch, Geldart, Maurer, & Le Grand, in press).

Patients treated for bilateral congenital cataract also have deficits in holistic processing (Le Grand, Mondloch, Maurer, & Brent, 2002; submitted). Unlike visually normal individuals, patients perform just as well (M = 76% correct) when the same top halves of composite faces are fused with different bottom halves as when the two halves are misaligned, and in fact, they perform significantly better (76% correct) than normals (56% correct) in the fused condition where holistic processing interferes with accuracy.

Although the relations among various face processing skills are not known (see Maurer et al., 2002), it is possible that patients' deficits in holistic processing and second-order relational processing are attributable to deficits in sensitivity to the first order relations that define a stimulus as a face. This hypothesis is supported by a recent MEG study (Liu, Harris, & Kanwisher, 2002) in which adults were presented with pairs of stimuli consisting of two faces, two houses, or one member of each category. They were asked to indicate whether the two stimuli were members of the same category or whether the two stimuli were identical exemplars (i.e., pictures of the same face). The earliest face-specific response (M100) was correlated only with correct categorization of the stimulus as a face whereas a later response (M170) was correlated with correct matching of two faces. Data from prosopagnosics also suggest that deficits in identifying faces may be associated with deficits in face detection: patient PHD lacks an N170—a face-specific ERP response, and has severe difficulty in both detecting and identifying faces (Eimer & McCarthy, 1999) and other prosopagnosics have difficulty detecting faces in Mooney stimuli (Davidoff & Landis, 1990). If face detection precedes both holistic and second-order relational processing, it is possible that patients' deficits both in holistic and second-order relational processing of faces stem from a deficit in face detection.

Indeed, our tests of infants immediately following treatment for bilateral congenital cataract suggest that early visual deprivation does affect the normal development of face detection. Using a standardized method modeled on the Teller acuity card procedure (Teller, McDonald, Preston, Sebris & Dobson, 1986), we have studied the development of face detection during early infancy by testing the face preferences of visually normal newborns less than 2 hours old, 6-week-olds and 12-week-olds (Mondloch et al., 1999). We presented infants with 5 cards: 3 experimental cards contrasting face/nonface stimuli, and two control stimulus cards (see Figure 2). The three experimental cards (see Figures 2a, 2b, and 2c,) were face-nonface stimulus pairs and the two control cards (see Figures 2d and 2e) were designed to assess the validity of the test and to ensure that at each age tested, there was at least one card that should elicit a visual preference (Figure 2d) and one card that should not (Figure 2e). An observer, unaware of the exact stimuli presented during each trial, used any cues—primarily direction of first look and duration of looking—to decide whether or not an individual infant preferred one of the two stimuli. Newborns preferred *config* (Figure 2a)—a simple head outline with three blobs in the correct location for facial features—over the same head outline with the array of blobs inverted. The newborn's preference for *config* disappeared by 6 weeks of age, and by 12 weeks of age the infants preferred the positive-contrast face over the negative-contrast face (Figure 2c) (see Table 1). These results suggest that an innate mechanism attracts newborns to look at simple stimuli that are more facelike (but see Simion, Macchi Cassia, Turati, & Valenza, 2001; Turati, Simion, Milani & Umiltà, 2002 for evidence that the critical attractor may be an oval with relatively more energy in the upper visual field). Nevertheless, the postnatal changes suggest that, with increasing age, the baby develops increasing sensitivity to the characteristics that define a human face.

To measure the influence of early visual experience on the development of face detection during infancy, we have tested 5 infants treated for bilateral congenital cataract (Mondloch, Lewis, Maurer & Levin, 1998). Each patient was tested after the eye had healed from the cataract surgery and after no more than 2 hours of visual input following the insertion of compensatory contact lenses that afforded their first exposure to patterned visual input. Thus, they had the same amount of visual experience before the test as the group of visually normal newborns. However, at the time of test each infant was at least 6 weeks old (7 weeks (n=2); 13-17 weeks (n=3)), the age at which the newborn's preference for config disappears. We also tested an age-matched control infant (± 2 days) for each patient. Like normal newborns, 3 of the 5 patients looked preferentially toward *config*. As expected from our own previous results (Mondloch et al., 1999), none of the age-matched controls showed a preference for this pair (see Table 2). Of the 3 patients who were over 12 weeks of age on the day of first patterned visual input, none preferred the positive-contrast face, unlike their age-matched controls and 12-week-olds with normal visual histories. These results suggest that in the absence of visual experience, the primitive mechanism that causes preferential orienting towards face-like stimuli at birth continues to operate. Furthermore, these data suggest that more sophisticated preferences for face-like stimuli do not emerge at the normal rate in the absence of visual input.

To determine whether early visual deprivation has long-term consequences for face detection, in the present study we tested older patients with a history of early visual deprivation from cataract on a face/nonface task using Mooney stimuli. We showed patients and visually normal control subjects brief presentations of a series of ambiguous stimuli—Mooney faces and scrambled Mooney faces—and asked them to classify each stimulus as a face or nonface. We selected Mooney faces because they are more difficult to classify than either gray-scale images or schematic faces and because they cannot be classified as faces based on individual features (see Figure 1). We reasoned that if patients' deficits in holistic processing and processing second-order relations were attributable to deficits in face detection, they should be less accurate and/or slower than control subjects when asked to classify Mooney stimuli.

Method

Subjects

The participants included 11 patients (6 females; 10 right-handed; 9 Caucasian) who were born with a dense, central cataract in each eye that prevented patterned stimulation from reaching the retina (see Ellemberg, Lewis, Liu, Maurer, & Brent, 1999, for selection criteria). The eyes were treated by surgical removal of the natural lens and fitting of an optical correction that provided focused visual input (mean duration of deprivation = 118 days from birth, range = 62 to 161 days). The patients had a mean age of 14.5 years at the time of testing (range = 9 to 20 years), and thus had had at least 9 years of visual experience after treatment prior to testing. Testing was binocular, and patients' acuity in the better eye ranged from 20/25 to 20/80 (M = 20/45); when necessary, patients wore an additional optical correction to focus the eyes at the testing distance.

In addition, a group of 11 age-matched control subjects with normal visual experience were tested. None of the control subjects had a history of eye problems, and all met our criteria on a visual screening exam. Specifically, all participants had Snellen acuity of at least 20/20 in each eye without optical correction, worse acuity with a +3 diopter lens (to rule out farsightedness of greater than 3 diopters), fusion at near on the Worth Four dot test, and stereoacuity of at least 40 arc s on the Titmus test. The control group matched the patient group on age, handedness, race and gender.

Stimuli & Apparatus.

The stimuli were thirteen black-and-white Mooney faces and a scrambled version of each of these faces; one pair of stimuli was presented on practice trials and the remaining 24 were presented on test trials (see Figure 1 for examples). All stimuli were 10.2 cm. wide and 15.2 cm. high (5.8 x 8.7 visual degrees from the testing distance of 100 cm.). The stimuli were created by scanning colour photographs of women's faces. The photographs were all full frontal views, but were taken under different lighting conditions (e.g., light coming from the top, from the right, etc.). The size of the images and the number of pixels per cm^2 was adjusted to the same value for all photographs. Using Adobe Photoshop, the contrast of each face was maximized and it was converted to a grey-scale image. Contrast was further adjusted such that all pixels were either black or white. Any isolated pixels (e.g., single black pixels in a white patch) were converted to match their surround. Adults reported that the printed version of these stimuli were all face-like.

A scrambled version of each face was created by cutting each face into 8 pieces and re-arranging these pieces while maintaining, as much as possible, the number of transitions from black to white. These manipulations produced several scrambled versions of each face. We retained the version that resulted in white or black areas with the greater surface and that adults and children judged as nonfaces after viewing the intact face stimuli. In some cases, isolated black or white pixels had to be transformed to match the surrounding pixels. Whenever a pixel (e.g., black) was transformed, another pixel (i.e., white) was also transformed so as to keep constant the number of black and white pixels.

The stimuli were presented on a monochrome Radius 21-GS monitor controlled by a Macintosh LC-475 computer and Cedrus Superlab software. A fixation cross was presented prior to each face stimulus. Each bar was 9 mm long (.52 visual degrees from the testing distance of 100 cm) and 3 mm thick. Participants signalled their responses via a joystick and the experimenter initiated each trial by pressing a key on the keyboard.

Procedure

Informed consent was obtained after the procedures were explained. The participant sat in a darkened room with his/her eyes 100 cm. from the monitor. Prior to the test trials, the experimenter explained the task while showing the participant one trial with a Mooney face and one trial with a scrambled Mooney face. The participant then saw each of these trials again at the normal presentation time of 100 msec and was asked to move the joystick forward if the stimulus was a face and backwards if the stimulus was not a face. Feedback was provided during the demonstration trials but not during the test trials.

Trials were initiated only when the experimenter judged that the participant fixated on a central fixation cross. Then the fixation cross was replaced by a face or scrambled face for 100 msec. Each subject was tested on 24 upright trials; trials were presented in a different random order to each participant.

Results & Discussion

For each subject, we calculated accuracy and median reaction time for correct trials. An unpaired t-test (one-tailed) on accuracy revealed no effect of group, t (20) = 1.03, $p > 0.10$. As shown in Figure 3a, patients were as accurate (M = .92) as the age-matched control subjects (M = .89). The t-test on median reaction times also revealed no effect of group, t (20) = .215, $p > .10$. As shown in Figure 3b, patients were as fast (M = 824.0 msec) as the age-matched control subjects (M = 799.2).

Patients' normal performance cannot be attributed to a ceiling effect: only 1 normal control obtained 100% accuracy. Furthermore, there was no effect of visual deprivation on reaction time, a variable that is not limited by a ceiling effect. Data from an ongoing study of the normal development of face detection also indicate that the task is difficult for children. To date we have tested 6-year-olds, 8-year-olds and adults (n=24 per group) on the same Mooney task. Both six-year-olds (M = .73, sd = 0.14) and 8-year-olds (M = .84, sd = .12) are less accurate than adults (M = .95, sd = .06). Even when we presented the same stimuli to 6-year-olds for an unlimited time, their accuracy ($\underline{M}$ = .68, $\underline{sd}$ = .18) was well below that of adults and patients in the speeded condition. Thus, patients' performance on this task cannot be attributed to the task being extremely easy. Rather, our results suggest that normal sensitivity to first-order relations can develop despite the absence of early visual input—even when no unambiguous facial features are present and when the task is difficult for children with normal visual histories.

The results from patients could reflect an innate programming of sensitivity to first order relations that is not affected adversely by visual deprivation. Alternatively, and more likely, it reflects a mechanism that can be trained equally well by visual input from birth or after a delay. Several pieces of evidence indicate that experience alters the face preferences of visually normal infants and hence favor the second alternative. Although even newborns orient preferentially towards stimuli with face-like first-order relations (e.g., Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991; Mondloch et al., 1999; Valenza, Simion, Macchi Cassia, & Umiltà, 1996), this early preference might be mediated sub-cortically (Johnson & Morton, 1991; Simion, Valenza, Umiltà & Dalla Barba, 1998) and it might be based on a low-level feature like relative energy in the top half of the stimulus (Simion et al., 2001; Turati et al., 2002). Over the first 2-3 months babies become more sensitive to distortions in the first-order relations of faces and demonstrate preferences that cannot be mediated sub-cortically or based on low-level features (e.g., Dannemiller & Stephens, 1988; Kleiner & Banks, 1987; Mondloch et al., 1999). Our own preliminary data from 5 infants treated for bilateral congenital cataract after 6 weeks of age indicate that the pattern of face preferences on the day they can first see is like that of newborns, rather than that of infants of the same age who had normal visual experience—a pattern suggesting that the postnatal increase in sensitivity to first-order relations is driven by visual input (Mondloch et al., 1998; See Table 2). Experience with specific faces also affects face detection during early infancy: six-month-old infants show a preference for an intact Mooney face over a scrambled version only if they are first familiarized with the original photographic version of the Mooney face (Latour, Rouusset, Deruelle, & de Schonen, 1999). These results suggest a gradual process of cortical specialization for face detection, likely influenced by the massive exposure babies have to faces—because of their omnipresence in the baby's environment and the baby's attentional biases. One interpretation of the results of the present experiment is that delayed visual input allows patients treated for bilateral cataract to "catch up" so that their sensitivity to first-order relations reaches normal level sometime before late childhood.

The absence of permanent deficit in sensitivity to the first-order relations in faces contrasts with the permanent deficits in sensitivity to second-order relations (i.e., the spacing among features in individual faces): patients are less accurate than normal control subjects when making same/different judgments about pairs of faces that differ only in the spacing among features (Le Grand et al., 2001), an ability that continues to improve in visually normal children past 10 years of age (Mondloch et al., 2002; Mondloch, Le Grand, & Maurer, in press). It also contrasts with the permanent deficits in holistic face processing (Le Grand et al., 2002; submitted): unlike visually normal control subjects, patients' ability to make same/different judgments about the top halves of fused composite faces is unaffected by whether the two face halves are aligned or misaligned. The results from the present study indicate patients' deficits in holistic processing and processing of second-order relations cannot be attributed to deficits in face detection. Studies of individuals with acquired prosopagnosia (an impairment of face recognition following brain injury) also report deficits in holistic face processing (Saumier, Arquin & Lassonde, 2001) and impaired sensitivity to second-order relations (Barton, Press, Keenan & O'Connor, 2002) despite sparing of sensitivity to the first-order relations that support face detection.

Although patients performed normally on a face detection task that cannot be solved based on featural processing and that school-aged children find difficult, we cannot conclude that the underlying neural mechanisms are impervious to visual deprivation. Studies using event-related potentials (ERPs), magnetic encephalogram (MEG) and functional magnetic imaging (fMRI) have identified neural correlates of detecting a face. The earliest face-specific MEG response (M100) is correlated with correct categorization of a stimulus as a face (Liu et al., 2002). The ERP negative potential called the N170 is larger for faces than for many other stimuli, including hands, houses, and cars (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 2000). fMRI activation in regions of the ventral occipitotemporal cortex, the inferior occipital gyrus, and the lateral fusiform gyrus, i.e., the fusiform face area (FFA), is larger for faces than for a variety of nonface objects, including cars, houses, hands, and furniture (Aguirre, Singh, & D'Esposito, 1999; Haxby, Gobbini, Furey, Ishai, Schouten, & Pietrini, 2001; McCarthy, Puce, Gore, & Allison., 1997). Ongoing studies using ERP and fMRI are necessary 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.

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Figure Captions

Figure 1. A Mooney face (left), and a scrambled Mooney face (right) are shown. Mooney faces are comprised of shadows and lack veridical facial features.

Figure 2. The three face-nonface stimulus pairs and two control stimuli. Panel 2a shows config and its inversion (Johnson et al., 1991). The left side of Panel 2b shows a stimulus with the phase spectrum of a face but the amplitude spectrum of a lattice. The right side of Panel 1b shows a stimulus with the amplitude spectrum of a face but the phase spectrum of a lattice (Kleiner, 1987). Panel 2c shows the positive-contrast face and the negative-contrast face (Dannemiller & Stephens, 1988). The control stimuli consisted of 2.5-cm-wide black-and-white stripes on both sides (Panel 2d) or on one side of center (Panel 2e). There were five additional stimulus cards with the stimuli reversed left-to-right. Reprinted, by permission, from Psychological Science, 1999, vol. 10, pp. 419-422 (Blackwell Publishing, Oxford).

Figure 3. Mean accuracy scores (Panel A) and mean reaction times (Panel B) when upright stimuli were presented to patients (black bars) versus visually normal control subjects (white bars).

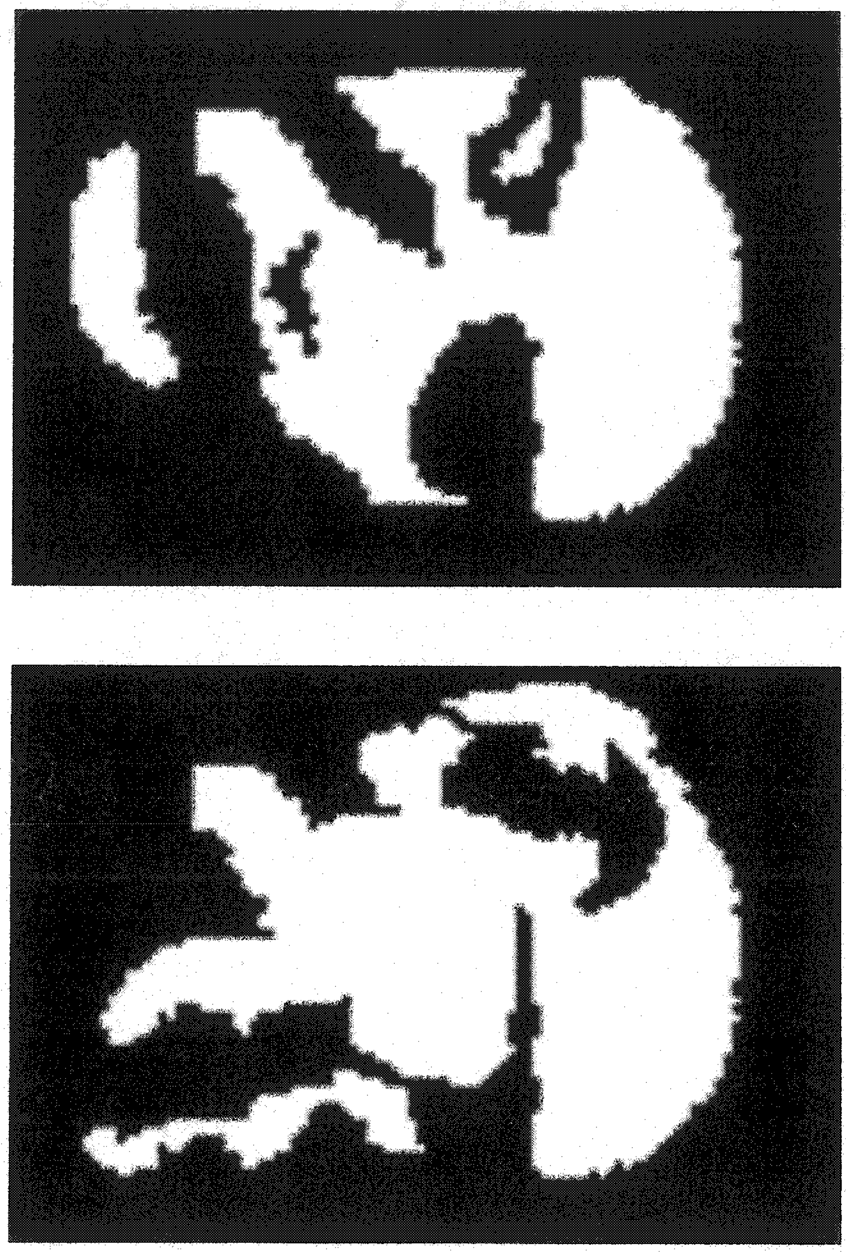


Figure 1. Mooney face (left), and a scrambled Mooney face (right).

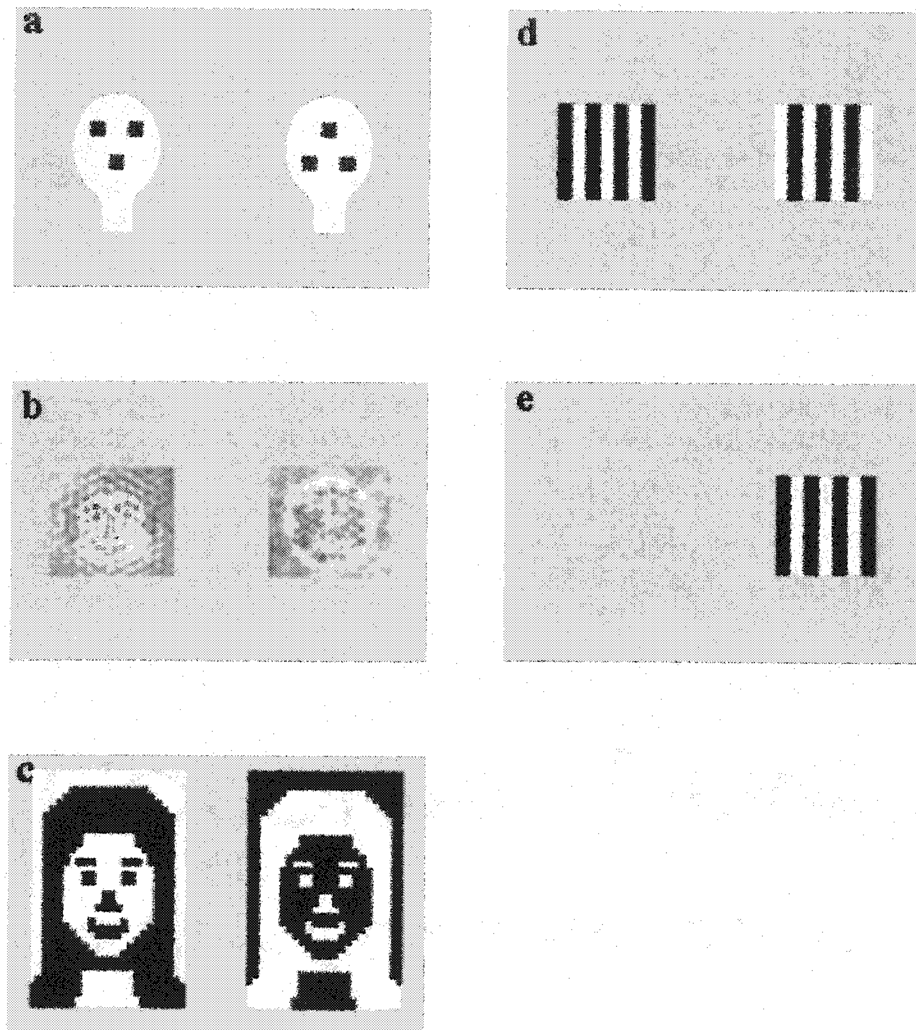


Figure 2. The three face-nonface stimulus pairs and two control stimuli.

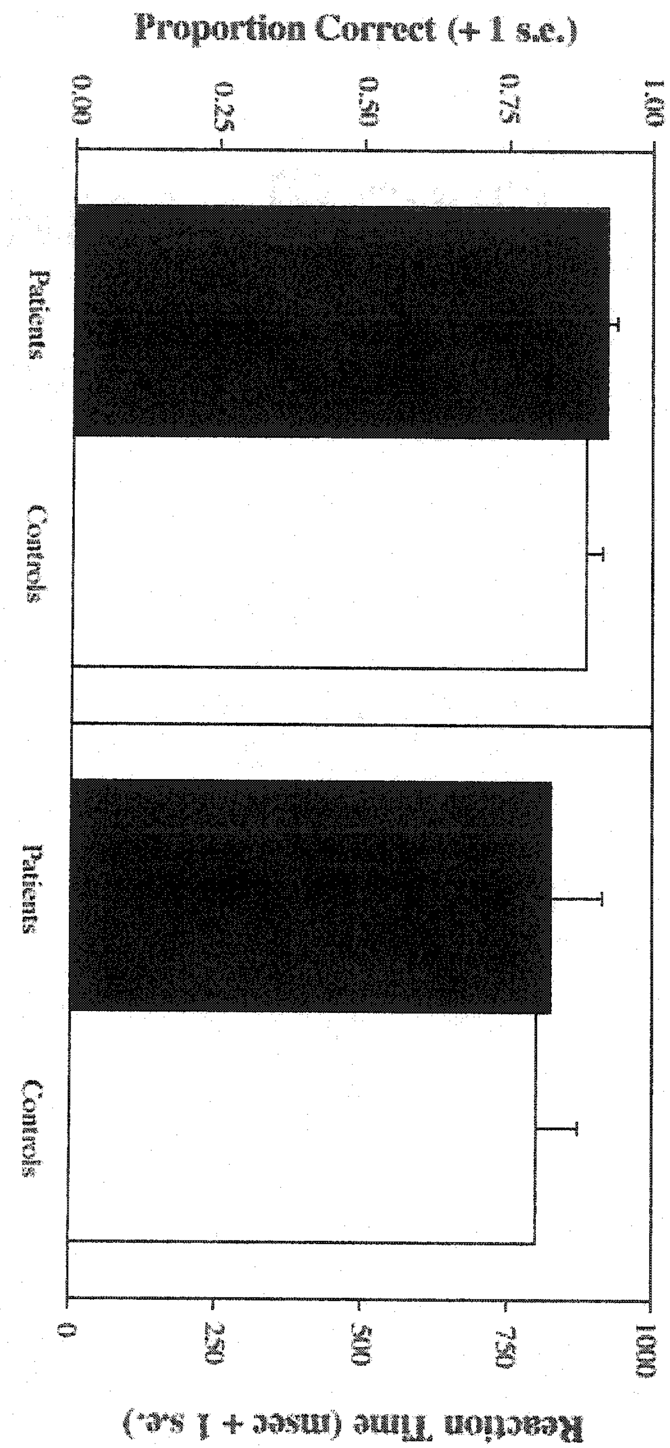


Figure 3. Mean accuracy scores (left) and mean reaction times (right)

Table 2. For each pair of stimuli, the number of patients who preferred the face, the nonface, or neither member, when tested within 2 hours of receiving their first patterned visual input, compared to age-match controls with normal visual histories.

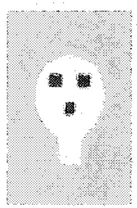
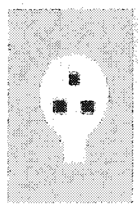
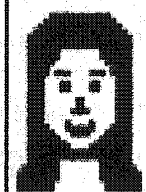
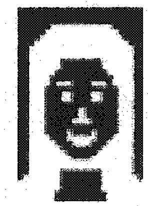
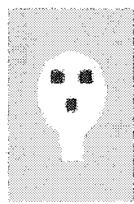
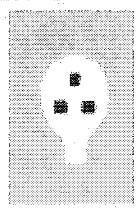
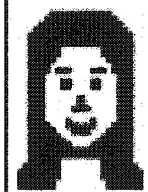
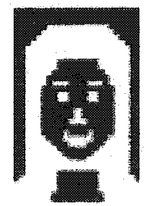
Group	 *config*	 inverted version	neither	 positive contrast	 negative contrast	neither
Patients (n=5)	3	1	1	0	0	3
Age Matches (n=5)	0	0	5	3	0	0

Table 1. For each pair of stimuli, the number of babies who preferred the face, the nonface, or neither member.

Age	 *config*	 inverted version	neither	 positive contrast	 negative contrast	neither
Newborns (n=12)	9*	1	2	0	0	12
6-week-olds (n=12)	0	0	12	3	0	9
12-week-olds (n=12)	0	1	11	12**	0	0

* $p < .05$; 2-tailed binomial test

** $p < .001$; 2-tailed binomial test

all other ps > .10

Chapter 5

Expert Face Processing Requires Early Visual Input to the Right Hemisphere During Infancy

Richard Le Grand, Catherine J. Mondloch, Daphne Maurer, & Henry P. Brent

Research Article

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Adult expertise in face processing is mediated largely by neural networks in the right hemisphere. Here we evaluate the contribution of early visual input in establishing this neural substrate. We compared visually normal individuals to patients for whom visual input had been restricted mainly to one hemisphere during infancy. We show that early deprivation of visual input to the right hemisphere severely impairs the development of expert face processing, while deprivation restricted mainly to the left hemisphere does not. The results demonstrate that the neural circuitry responsible for adults' face expertise is not pre-specified, but requires early visual experience. However, the two hemispheres are not equipotential: only the right hemisphere is capable of using the early input to develop expertise at face processing.

Adults can recognize thousands of faces at a glance and are considered "experts" at processing faces[1]. This ability requires encoding information about subtle differences among individual faces such as the shape of facial features (featural processing), the shape of the face (contour processing) and/or differences in the spacing among facial features, like the distance between the eyes (a type of configural processing commonly referred to as *second-order relational processing*)[2]. Although adults use all three types of information to recognize faces, expertise in processing second-order relations is especially important[3], and continues to improve past 14 years of age[4].

The right hemisphere plays a critical role in processing second-order relations. In adults, areas of the occipito-temporal cortex (including a "fusiform face area") are more active when viewing faces compared to a variety of non-face objects with which adults do not have the same expertise[5,6]. This face-sensitive activation is typically larger in the right than in the left hemisphere[5,6], especially when the task encourages attending to the entire face rather than individual features[7,8]. Lesions involving these areas in both hemispheres, or just the right hemisphere, can lead to impairment in face recognition (prosopagnosia)[9], that is especially severe if faces must be recognized based on second-order relational cues[10]. By 9 months of age, babies provide evidence of similar hemispheric specialization. For example, only when face or non-face stimuli are presented to the right hemisphere do they show sensitivity to spacing information[11,12]. Perhaps as a result, infants learn to discriminate faces more rapidly if the stimuli are presented to the right hemisphere than to the left[13].

Together, these results support the existence of a neural substrate within the right hemisphere that is involved in processing spacing among features from infancy, and that underlies adults' expertise in face processing. Some have argued for the existence of an innate face module that is pre-specified in the genome[14]. However, in a previous study we showed that early visual experience is necessary for the development of expert face processing. Deprivation of early visual input to both hemispheres—by dense bilateral congenital cataract—severely impairs the later development of sensitivity to second-order relations in faces[15].

In the present study we evaluated the degree of plasticity in the lateralization of networks underlying expert face processing by measuring the effects of early visual deprivation to the right versus left hemisphere. To do so, we took advantage of the fact that during infancy, visual input to each eye is predominantly transmitted to the contralateral hemisphere. During the first six months of life, the monocular visual field expands from the center out, and sensitivity to stimuli in the temporal visual field develops much faster than sensitivity to stimuli in the nasal visual field[16]. Images from the temporal visual field are cast on the nasal hemi-retina, and its fibers project to the contralateral cerebral hemisphere. Unlike the adult nervous system, there appears to be no functional integration of visual information across the corpus callosum during early infancy. Cortically mediated transfer of visual information between the hemispheres is not evident prior to 24 months of age[13,17,18,19]. Thus, during early infancy input to the right hemisphere comes primarily from the left eye and input to the left hemisphere comes primarily from the right eye. A similar contralateral bias has been documented in anatomical and electrophysiological studies of infant kittens and ferrets[20,21]. As a consequence of this bias, a unilateral congenital cataract that blocks all patterned input to the left eye causes deprivation of input mainly to the right hemisphere, whereas a unilateral congenital cataract in an infant's right eye causes deprivation of input mainly to the left hemisphere. After treatment by surgical removal of the cataract and fitting with a compensatory contact lens, input to both hemispheres is restored. Here we tested the consequences of the initial period of deprivation affecting mainly the right or left hemisphere on later development.

We tested 20 patients treated for unilateral congenital cataract that blocked all patterned input to either the left eye (LE, n=10) or the right eye (RE, n=10) (see Table 1 for patient details). Testing occurred later in life and after many (at least 8) years of visual experience to allow for recovery from the initial monocular deprivation. Testing was binocular; thus patients were able to use their unaffected eye when performing the task. This design allowed us to evaluate whether initial deprivation affecting mainly the right hemisphere, versus the left hemisphere, prevents the later development of expert face processing, despite years of visual input being available to both hemispheres beginning later in infancy, via both the expanded visual field of the unaffected eye and the recovery of the treated eye.

Patients made same/different judgments about pairs of faces that were presented sequentially and which differed only in the shape of the eyes and mouth (featural set), only in the shape of the external contour (contour set), or only in the spacing among the internal features (spacing set) (see Fig. 1). The three stimulus sets were presented in separate blocks, with all sets first presented in an upright orientation, followed by an inverted orientation (see Methods section). In previous research we showed that the three sets tap different aspects of face processing, which develop at different rates[4,22]. Moreover, inverting the stimuli greatly disrupts visually normal adults' ability to discriminate faces in the spacing set, but not in the featural or contour sets[15,22]. These results are consistent with previous findings that inversion disrupts second-order relational processing but has little or no effect on other types of face processing[22,23]. Because face processing skills continue to improve through adolescence[4], the mean accuracy and reaction time for each patient for each condition were compared to the mean of a group of 36 subjects of the same age with a normal visual history and then converted to z-scores (units of standard deviation above or below the age norm). Thus, normal performance by a patient is indicated by a z-score near zero.

RESULTS

Accuracy. Mean accuracy z-scores for each condition are shown in Figure 2 (see Supplementary Table 1 online for mean accuracy scores). To determine whether either patient group showed a deficit on any condition (performed worse than an expected mean z-score of zero), one sample t-tests were conducted. A Bonferroni correction was applied for the number of comparisons (adjusted alpha = 0.008). For the featural and contour sets, both patient groups performed normally whether the faces were upright or inverted (all Ps > 0.1). For the spacing set, patients in the RE (left hemisphere deprivation) group also performed normally on both orientations (both Ps > 0.1). In contrast, patients in the LE (right hemisphere deprivation) group were severely impaired on distinguishing faces from the upright spacing set (t_9 = -4.94, P < 0.001; see Fig. 2a). The LE group had a mean z-score of -1.78, a value equivalent to the performance of the lowest 4% of the normal population. The second-order relational deficit in the LE group was manifested despite binocular testing (with the non-deprived right eye available), and did not correlate with acuity in either eye (both Ps > 0.1). The deficit was evident even in cases when the initial deprivation lasted as little as 2-3 months (see Fig. 3). The LE group also showed a small but significant impairment of about 0.5 standard deviations on the inverted spacing set (t_9

= -3.45, $P < 0.007$, see Fig. 2b). Similar results for the one-sample t-tests were obtained when accuracy scores were converted to the sensitivity statistic *d-prime* (see Supplementary Results and Fig. 1 online).

An ANOVA with group, stimulus set and orientation as factors confirmed that the LE and RE groups differed only on the spacing set. The ANOVA showed a significant interaction between group and stimulus set ($F_{2,36} = 3.83$, $P < 0.01$) that did not interact with orientation. Analysis of simple effects indicated that the two patient groups did not differ on the featural and contour sets (both $Ps > 0.1$). They differed significantly only on the spacing set ($F_{1,18} = 10.58$, $P < 0.01$), with the LE (right hemisphere deprivation) group performing worse than the RE (left hemisphere deprivation) group. The same results were obtained when analyses were conducted using standardized d-primes as the dependent measure (see Supplementary Results online).

Previously we documented a deficit in sensitivity to second-order relations of faces in patients treated for bilateral congenital cataract[15]. To compare the effect of early visual deprivation to both hemispheres versus the right hemisphere only, a planned comparison was conducted between 10 patients treated for bilateral cataract (BE - both eyes group) and the LE group on z-scores from the spacing set for both orientations. The LE and BE groups were equally impaired on the spacing set (see Fig. 3), and both showed larger deficits for the upright than the inverted orientation. This was shown by a significant effect of orientation on the size of the deficit for the spacing set ($F_{1,18} = 22.76$, $P < 0.001$) but no significant effect of group or interaction (both Ps > 0.1). The analyses showed similar results for standardized d-primes (see Supplementary Results online).

Reaction times. For each patient in each condition, median reaction times on correct trials were calculated and converted to standardized z-scores based on age norms. One sample t-tests revealed that both the LE and RE groups had normal response times on the three stimulus sets for both orientations (all Ps > 0.2). These data demonstrate that the LE (right hemisphere deprivation) groups' impairment on second-order relational processing (as shown by accuracy scores) cannot be attributed to a speed-accuracy trade-off (see Table 2).

Discussion

Our findings indicate that neural networks in the right hemisphere are not pre-specified for second-order relational processing: this expert ability will not develop if patterned visual input is missing during early infancy. Deprivation of early visual input to the right hemisphere (LE group) leads to impairment in second-order relational processing that is as severe as the deficit following early deprivation to both hemispheres (BE group). In contrast, deprivation of early visual input to the left hemisphere (RE group) has no apparent effect on expert face processing. These results show that early visual input restricted mainly to the right hemisphere is adequate to set up or maintain the neural substrate responsible for expert face processing, while early input restricted mainly to the left hemisphere is insufficient. Thus, the two hemispheres are not created equal. Networks in the right hemisphere might be affected by early visual input because they are biased to respond to stimuli that are more face-like, because relevant regions of the temporal cortex become functional earlier in the right hemisphere than do homologous regions in the left hemisphere[24], and/or because they are better tuned to the low spatial frequencies that the infant can perceive and that specify the spacing among features but provide little information about feature details[25].

Deficits in second-order relational processing following early right hemisphere deprivation cannot be attributed to poor visual acuity because the size of the face processing deficit was not correlated with visual acuity and because patients could use their non-deprived eye, which had normal or nearly normal acuity, to do the task (see Table 1). It also cannot be attributed to patients in the LE group performing poorly on any difficult perceptual task. There were no baseline differences between the upright spacing and contour sets for visually normal adults[15,22], or in the normative groups to which the patients were compared (see Supplementary Table 1 online). Both patient groups were normal on the contour set while only the RE group performed normally on the spacing set (see Fig. 2a).

Other results from the same cohort indicate that the deficit is not in object perception per se nor in all higher level visual capabilities that are mediated by the right hemisphere. Children treated for bilateral congenital cataract perform normally when asked to make judgments about the spacing among features in a simple pattern of five shapes[26], discriminations for which there is evidence of lateralization favoring the right hemisphere in infants as young as 4 months old[12]. When tested monocularly with either eye, patients treated for unilateral congenital cataract are normal at matching geometric shapes even when the target and matching shape differ in luminance, size, contour, or the presence of masking lines[27]. They do have small deficits in linking local elements into a global form, but unlike the results reported here, the deficit is only in the previously deprived eye, and does not depend on whether the left or right eye was deprived[28]. Regardless of which eye is tested, children treated for unilateral congenital cataract perform normally on measures of visual spatial attention[29] (for paradigm details see[30,31]), another function mediated largely by networks in the right hemisphere[32,33]. Nevertheless, it is possible that early visual input to the right hemisphere is necessary not only for the later development of normal processing of second-order relations in faces, but for other types of expertise that depend on the same or similar networks in the right hemisphere. For example, it may be a prerequisite for the development of later expertise in differentiating among individual members of other homogeneous classes such as car experts' ability to differentiate among similarly shaped cars[34].

Visually normal adults show a large inversion effect for the spacing set. This pattern is consistent with previous studies that demonstrate that inversion disrupts second-order relational processing[22,23]. However, inversion does not completely eliminate sensitivity to the spacing among features, as adults' accuracy for the inverted spacing set is low but above chance. This finding may account for the LE groups' severe deficit on the upright spacing set (almost 2 standard deviations below normal), and slight impairment (0.5 standard deviations below normal) on the inverted spacing set. For the upright spacing set, the impairment was pronounced compared to normal individuals with intact second-order relational processing (Fig. 2a). For the inverted spacing set, the LE patients' deficits were minimal when compared to visually normal individuals who also have difficulty processing spacing information when these faces are inverted (Fig. 2b).

Clearly not all face-processing abilities require early visual experience. Featural processing of faces emerges early in life and becomes lateralized to the left hemisphere by 9 months of age[11], yet our results indicate that early deprivation to either or both hemispheres does not prevent it from developing to a normal level. Contour face processing is also spared following early visual deprivation[4] although it too emerges during infancy[35]. Individuals treated for bilateral congenital cataract can lip-read, match facial expression, and decode direction of eye gaze[36]. These results suggest that many aspects of face processing can develop normally even when visual input is absent during early infancy. They reinforce the conclusion that second-order relational processing is unique—it continues to improve long after other face processing skills are adult-like[4,22], but only if its development was initiated by visual input to the right hemisphere during early infancy.

METHODS

Participants.

Deprived Patients. The two patient groups consisted of 10 patients treated for left eye (LE) unilateral congenital cataract (2 male; 10 Caucasian), and 10 patients treated for right eye (RE) unilateral congenital cataract (2 male; 9 Caucasian). Patient details are summarized in Table 1. All patients were right-handed and were at least 8 years of age at test. Patients were included in the sample only if they had a dense central cataract that blocked all patterned visual input to the affected eye on their first eye exam, which was always before 6 months of age. Duration of deprivation was defined as the period extending from birth until the age of first optical correction following surgery to remove the cataract (i.e., the first time the infant received focused visual input onto the retina of the affected eye). From this point, input to the treated eye was only nearly normal because the contact lens focused input perfectly for only one distance and the eye could not accommodate for other distances. The amount of patching of the non-deprived eye (from treatment until age 5) did not differ significantly between the groups and was not correlated with accuracy in any condition. Detailed inclusion and exclusion criteria for the patients have been described elsewhere[36,37].

Bilateral Patients. To compare the effects of unilateral deprivation to bilateral deprivation, the 10 bilateral patients that most closely matched the two unilateral patient groups on age, race, and duration of deprivation were chosen from among a larger group of 14 bilateral patients whose results have been reported previously[15].

Normative Group. Norms were based on five groups of 36 right-handed Caucasian subjects: 8-year-olds (± 3 months), 10-year-olds (± 3 months), 12-year olds (± 3 months), 14-year olds (± 3 months), and adults (aged 18-28 years). Half of the participants in each group were female. None of the normal participants had a history of eye problems, and all met our criteria on a visual screening exam[22]. Results for each normative age group are reported elsewhere[4,22]. Patients aged 17 years and older were compared to the normal adults; patients under 17 years were compared to the closest normative group of a younger age.

Stimuli and Procedure.

A detailed description of the stimuli and procedure has been reported elsewhere[22]. Briefly, a single face was modified to create three sets of face stimuli with four faces in each set (see Fig. 1). Faces in the featural set were created by replacing the original female's eyes and mouth with the features of different females. Features of the same length were chosen to minimize resulting changes in the spacing among features. Faces in the contour set were created by combining the internal portion of the original face with the outer contour of four different females. Faces in the spacing set were created by moving both the eyes and mouth relative to the original face. The eyes were moved either 4 mm. up, down, closer together or farther apart, and the mouth was moved either 2mm. up or down. On fourteen of the fifteen different trials in the spacing set, the two faces differed in both the spacing of the eyes and the mouth; on the one remaining different trial the two faces differed in the spacing of the eyes but shared the same mouth position. All stimuli were 10.2 cm. wide and 15.2 cm. high (5.8 x 8.7 visual degrees from the testing distance of 100 cm.).

The participant sat 100 cm. from a monochrome Radius 21-GS monitor on which the faces were presented by a Macintosh LC-475 computer and Cedrus Superlab software. When necessary, patients wore an additional optical correction so that the eyes were focused at the testing distance. Testing was binocular. Participants judged whether two faces presented sequentially were the same or different. The first face appeared for 200 ms., and following an inter-stimulus interval of 300 ms., the second face appeared until the subject signaled a response with a joystick. The correct response was "same" for half of the 30 trials within each of the three blocks. The three blocks were presented in the same order (spacing-featural-contour) to all patients, with the upright condition tested first. Previous work has shown that accuracy is not affected by the order in which the face sets are presented[22].

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Competing interests statement

The authors declare that they have no competing financial interests.

Figure Captions

Fig.1. The face stimuli.

(a) Featural stimulus set - variation in individual features (eyes and mouth). **(b)** Contour stimulus set – variation in the external contour of the face. **(c)** Spacing stimulus set - variation in spacing of the eyes and between the eyes and mouth.

Fig.2. The effect of early left vs. right hemisphere deprivation on face processing **(a)** upright orientation and **(b)** inverted orientation. Plotted are the mean accuracy z-scores, which represent the difference between patients and age norms, for detecting featural, contour and spacing changes. Data are shown for the patient groups with deprivation affecting mainly the right hemisphere (LE Group = ◆), and mainly the left hemisphere (RE Group = ◆). A value of zero represents the normal mean, and negative values indicate deficits in units of standard deviation from the normal mean. The area outside the shaded portion (± 1.3 standard deviations) represents the highest and lowest 10% of the normal population.

Fig.3. The effect of duration of visual deprivation on second-order relational processing.

Individual z-scores for accuracy on the upright spacing set for patients with deprivation affecting mainly the right hemisphere (LE Group = ◆) are plotted as a function of the duration of visual deprivation from birth. For comparison, z-scores are shown for patients (n = 10) with deprivation affecting both hemispheres (BE

Group = ◆). Negative scores represent deficits in units of standard deviation from the norm for the patient's age.

SUPPLEMENTARY ONLINE RESULTS

D-Primes. For each patient, d-prime scores in each condition were calculated and then converted to standardized z-scores based on age norms. Mean d-prime z-scores for each condition are shown in Supplementary Figure 1 online. To determine whether either patient group showed a deficit on any condition (performed worse than an expected mean z-score of zero), one sample t-tests were conducted. A Bonferroni correction was applied for the number of comparisons (adjusted alpha = 0.008). For the featural and contour sets, both patient groups performed normally whether the faces were upright or inverted. For the spacing set, patients in the RE (left hemisphere deprivation) group also performed normally on both orientations. In contrast, patients in the LE (right hemisphere deprivation) group were severely impaired on distinguishing faces from the upright spacing set ($t_9 = -7.03$, $P < 0.001$). The LE group also showed a small but significant impairment of about 0.5 standard deviations on the inverted spacing set ($t_9 = -3.36$, $P = 0.008$).

The contribution of early visual input to the right versus left hemisphere towards the development of face-processing strategies was measured by an ANOVA with group, stimulus set and orientation as factors. The results showed that the two deprived groups differed only on the spacing set. The ANOVA showed a significant interaction between stimulus set and group ($F_{2,36} = 6.12$, $P < 0.01$) that did not interact with orientation. Analysis of simple effects showed that the deprived groups did not differ on the featural and contour sets (both Ps > 0.1). They differed significantly on the spacing set only ($F_{1,18} = 10.65$, $P < 0.01$; all other Ps > 0.1) with the LE (right hemisphere deprived) performing worse than the RE (left hemisphere deprived) group.

Previously we documented a deficit in sensitivity to second-order relations for faces in patients treated for bilateral congenital cataract[1]. To compare the effect of early visual deprivation to the right hemisphere versus both hemispheres, a planned comparison between the LE group, and 10 comparably aged patients treated for bilateral cataract (BE - both eyes group) was conducted on z-scores from the spacing set for both orientations. The LE and BE groups were equally impaired on the spacing set, and both showed larger deficits on the upright orientation. This was shown by a significant effect of orientation on the spacing set ($F_{1,18} = 22.99$, $P < 0.001$) but no significant effect of group or interaction between group and orientation (both $Ps > 0.1$).

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

Fig.1. Supplementary Online The effect of early left vs. right hemisphere deprivation on face processing **(a)** upright orientation and **(b)** inverted orientation. Plotted are the mean d-prime z-scores, which represent the difference between patients and age norms, for detecting featural, contour and spacing changes. Data are shown for the patient groups with deprivation affecting mainly the right hemisphere (LE Group = ⬖), or mainly the left hemisphere (RE Group = ⬗). A value of zero represents the normal mean, and negative values indicate deficits in units of standard

deviation from the normal mean. The area outside the shaded portion (± 1.3 standard deviations) represents the highest and lowest 10% of the normal population.

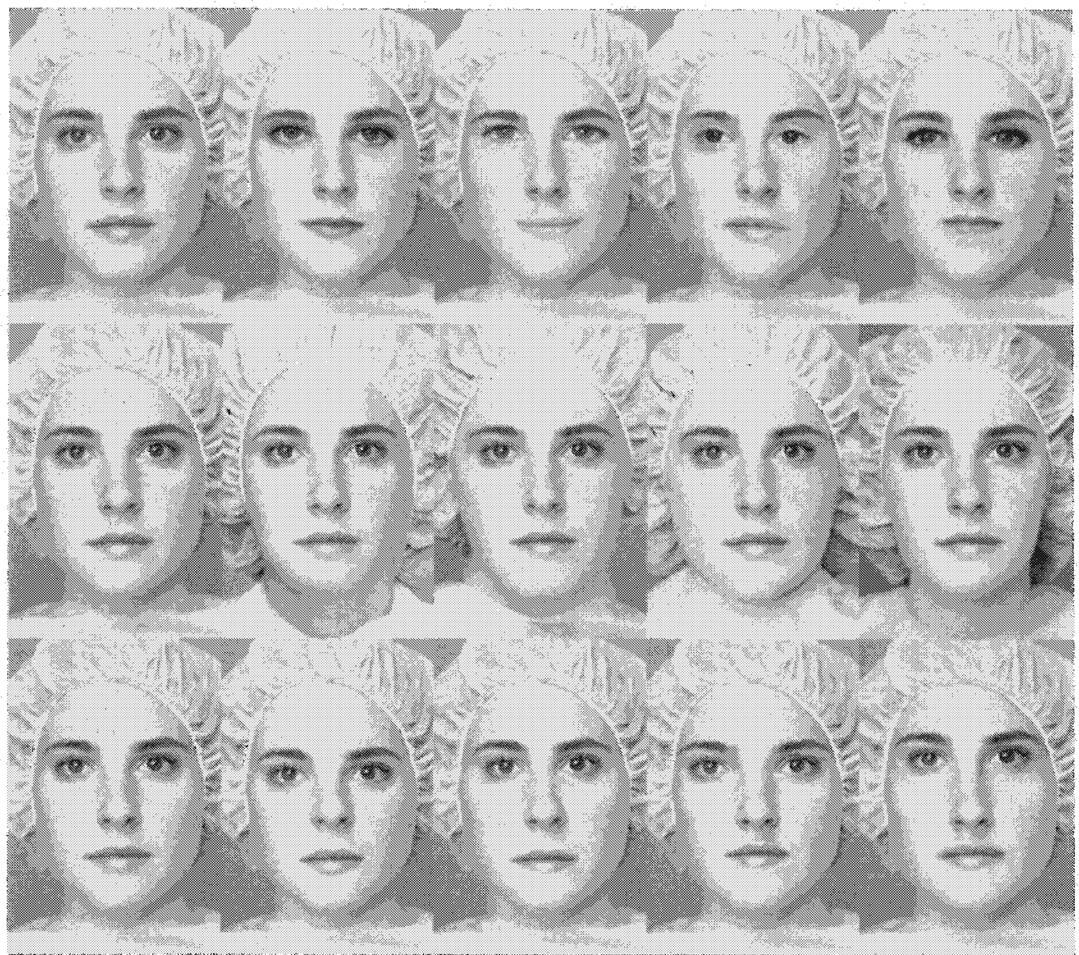

Fig.1. The face stimuli.

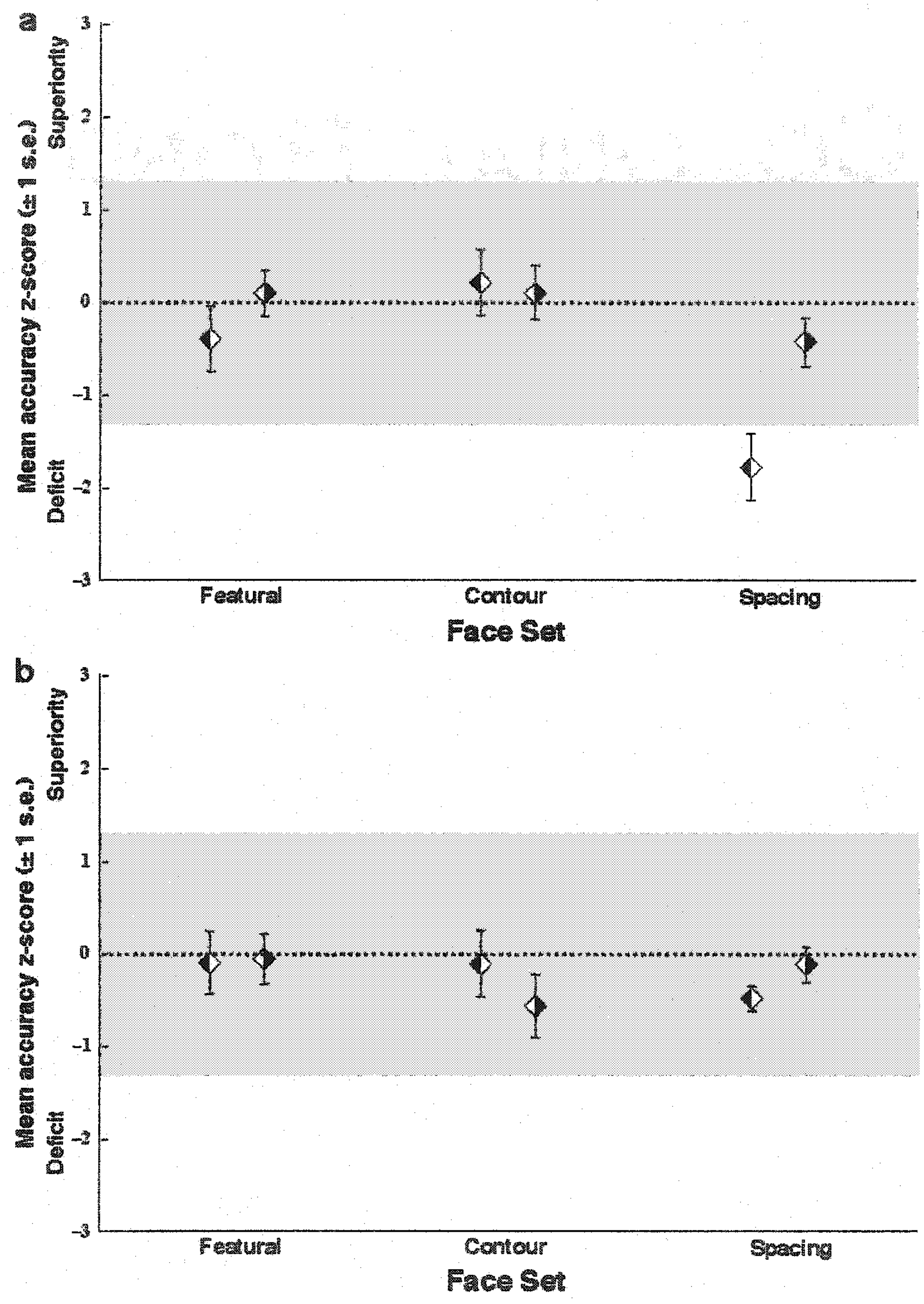

Fig.2. Mean accuracy z-scores for the left eye and right eye group on the upright (a) and inverted (b) stimulus sets.

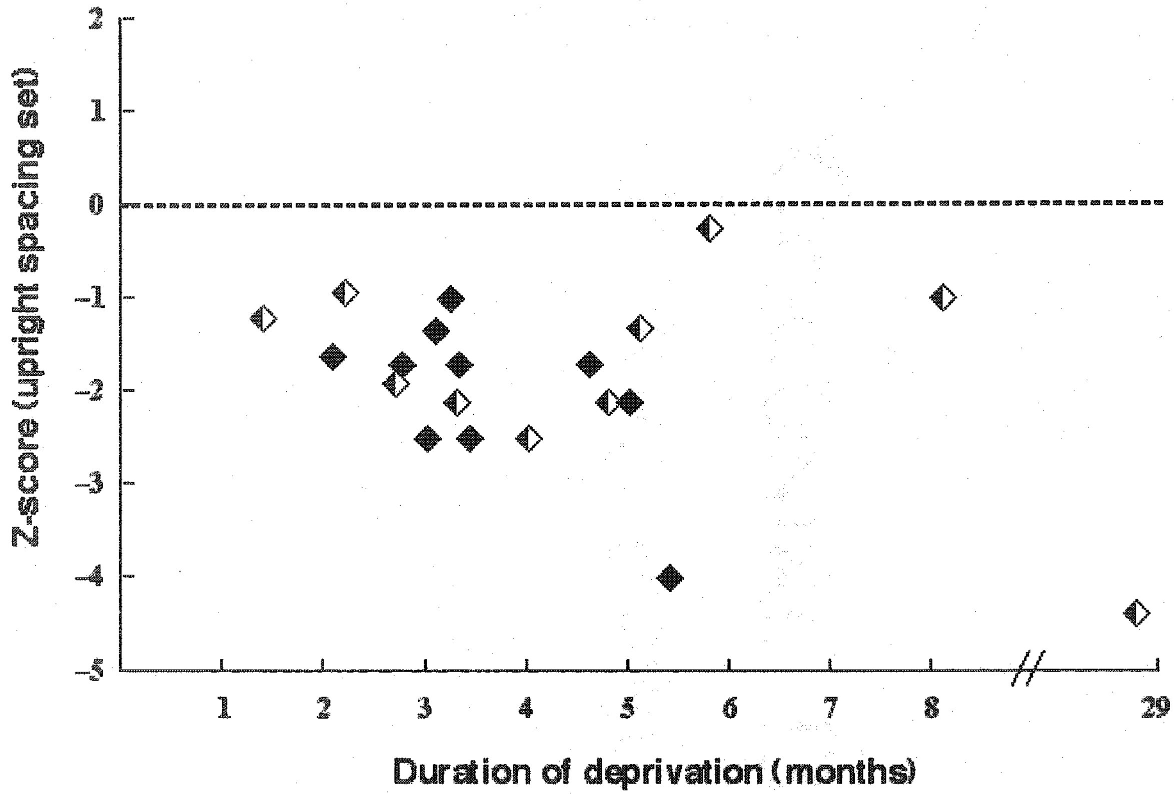

Fig. 3. Individual *z*-scores for accuracy on the upright spacing set plotted as a function of the duration of visual deprivation from birth.

Table 1 Supplementary Online Material.
Mean Accuracy (percent correct) for each stimulus set.

Face Set	Deprived Group		Normative Group	
	LE	**RE**	**For LE patients**	**For RE patients**
UPRIGHT				
Featural	84	86	87	86
Contour	80	78	78	77
Spacing	60	72	77	75
INVERTED				
Featural	81	80	81	80
Contour	70	63	69	69
Spacing	56	58	61	60

LE = left eye deprived group (right hemisphere deprivation)
RE = right eye deprived group (left hemisphere deprivation)

Table 2. **Deprived patients' reaction time z-scores (mean, standard error) for each stimulus set.**

GROUP	UPRIGHT			INVERTED		
	FEATURAL	SPACING	CONTOUR	FEATURAL	SPACING	CONTOUR
LE	–0.12 (0.38)	0.43 (0.39)	–0.47 (0.41)	0.09 (0.40)	0.27 (0.42)	–0.42 (0.34)
RE	0.02 (0.52)	–0.12 (0.41)	0.27 (0.54)	–0.09 (0.48)	0.95 (0.74)	–0.15 (0.49)

LE = left eye deprived group (right hemisphere deprivation)
RE = right eye deprived group (left hemisphere deprivation)

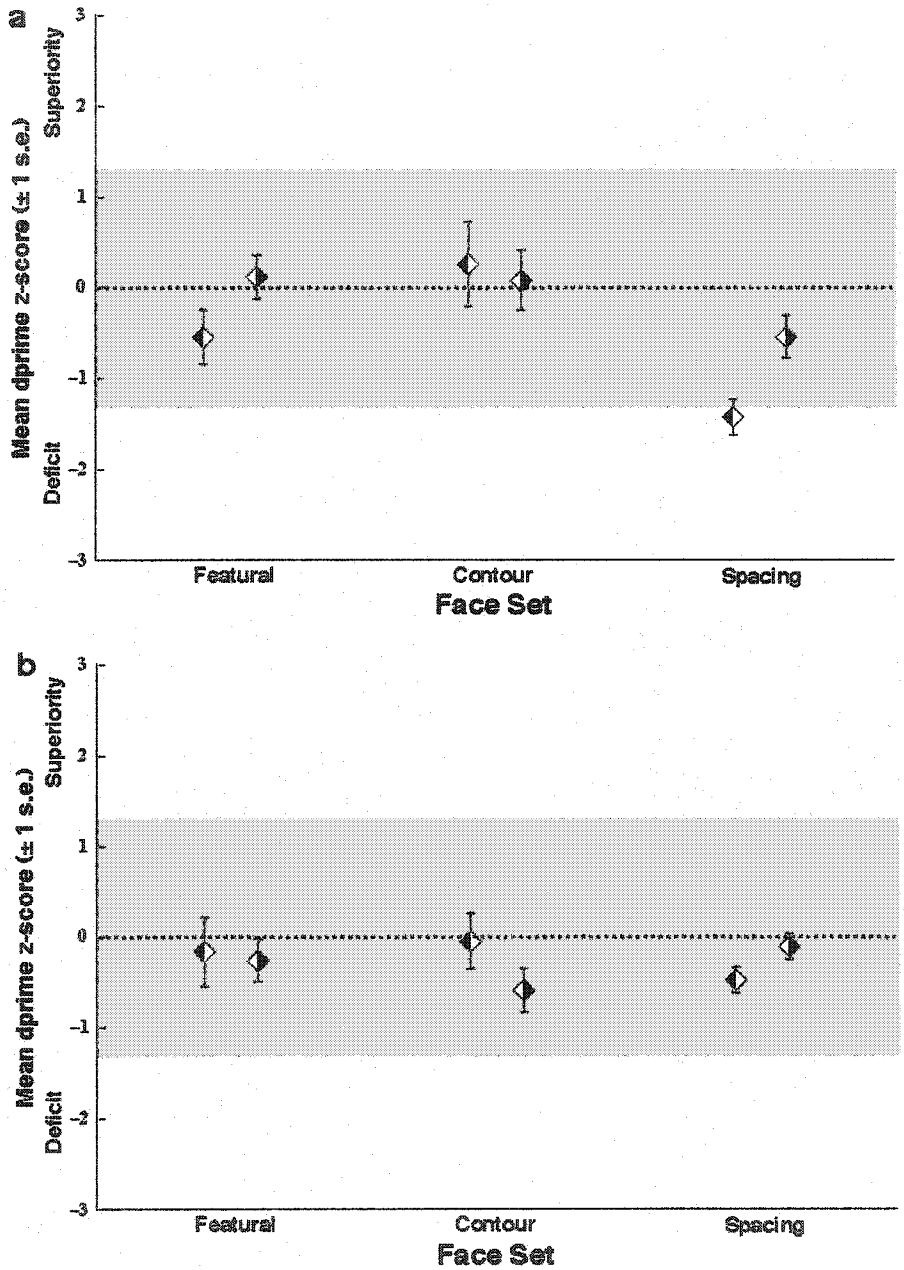

Fig.1. Supplementary Online. Mean d-prime z-scores for the left eye and right eye group on the upright (a) and inverted (b) stimulus sets.

Table 1. **Details of the two patient groups**

Group	N	Age at test (mean; range)	Duration of deprivation (mean; range)	Acuity of non-deprived eye [1] (median; range)	Acuity of deprived eye [1] (median; range)	Patching [2] (mean; range)
LE Group	10	17 yrs (8-29)	199 days (43 - 863)	20/20 (20/20 - 20/25)	20/200 (20/50 - 20/200)	4 hours/day (0.5 - 7)
RE Group	10	15 yrs (9-23)	201 days (56 - 483)	20/25 (20/16 - 20/32)	20/200 (20/32 - 20/200)	3 hours/day (0 - 5)

LE = left eye deprived group (right hemisphere deprivation)
RE = right eye deprived group (left hemisphere deprivation)

[1] acuity measured at time of test
[2] mean hrs/day of patching the non-deprived until the age of 5 years

CHAPTER 6

GENERAL DISCUSSION

This thesis examined the role of early visual experience in the development of expert face processing. Previous research has shown that visual input during infancy is necessary for some, but not all, aspects of face processing (Geldart et al., 2002). Based on the pattern of deficits in face processing skills following early visual deprivation, Geldart et al. hypothesized that visual input during infancy is necessary for face processing skills that require the ability to encode the spatial relations among facial features (configural processing), but is not necessary for skills that require the ability to encode information about the individual facial features (featural processing). This thesis directly examined the influence of early visual input on the later development of configural processing versus featural processing. Because there are different components of configural processing, separate tasks were used to evaluate the deprived patients' ability to detect faces based on each of these components: face detection based on first-order relations, the tendency to process faces holistically, and sensitivity to second-order relational information.

The research reported in Chapter 2 investigated the role of early visual experience in the development of second-order relational versus featural processing of faces, and allowed for an evaluation of various theories of the development of face processing. It provided a direct test of the hypothesis that early visual experience is necessary for second-order relational processing, an ability that is associated with expertise in face recognition. The findings demonstrated that featural processing can develop even in the absence of early visual experience. The deprived patients performed normally at differentiating faces that varied in the shape of individual features (featural processing). In contrast, early visual experience was found to be necessary for the normal development of processing second-order relational information, a type of configural processing. The deprived patients were severely impaired at differentiating faces that varied only in the spacing among the features (second-order relational processing). Because early visual input may also be required for the development of other components of configural face processing, the studies reported in Chapters 3 and 4 evaluated the role of early visual experience in the development of holistic face processing (Chapter 3), and the ability to detect faces based on first-order relations (Chapter 4). The findings of these studies demonstrate that visual input during infancy is required for the later development of some, but not all types, of configural face processing.

The research reported in Chapter 3 demonstrated that the tendency to process faces holistically requires early visual experience. The deprived patients failed to provide evidence of integrating facial features into a whole. Unlike visually normal individuals, the deprived patients did not show a composite face effect, a measure of holistic processing. This impairment in holistic processing may have also led to their deficit in processing the spacing among facial features (second-order relational processing) that was documented in Chapter 2. Deprived patients may perceive faces as an assortment of independent features, and as a result, they may be less sensitive to the spatial relations among those features. Visually normal adults' expertise in face processing is based heavily on their ability to process faces holistically and recognize individual faces based on second-order relational information. The impairment in these abilities following early visual deprivation suggest that visual input during infancy is essential for the later development of expert face processing.

The research reported in Chapter 4 explored the role of early visual experience in the development of face detection based on the first-order relations that define all faces. Although even newborns appear to be able to detect the first-order relations of a face, an initial study on infants' face preferences immediately following treatment for early visual deprivation suggests that the more sophisticated preferences for face-like stimuli that occur later in infancy require early visual experience (Mondloch, Lewis, Maurer, & Levin, 1998). Thus, visual experience during early infancy may be required for the later ability to detect complex face stimuli such as Mooney faces. The findings reported in Chapter 4 showed that although early visual experience is necessary for various face preferences to emerge at the normal rate during infancy, the ability to detect faces based on first-order relations later in life does not require early visual input. The deprived patients performed normally at classifying Mooney stimuli as a face/non-face, a task that cannot be solved based on processing the individual features. Thus, not all components of configural processing require early visual input. This finding suggests that impairment in holistic and second-order relational processing following early visual deprivation cannot be the result of a failure to process the first-order relations of faces.

Previous studies suggest that the right hemisphere plays an important role in face processing, and may be especially important for processing configural information. The research presented in Chapter 2 demonstrated that a lack of visual input to both hemispheres during infancy prevents the normal development of sensitivity to second-order relational information. The research reported in Chapter 5 investigated directly the contribution of early visual input to each hemisphere to the normal development of expert face processing. The study involved patients treated for unilateral congenital cataract that affected mainly the contralateral hemisphere because of slow growth of the nasal visual field and lack of functional integration of visual input across the corpus callosum during infancy. The findings demonstrated that it is not visual deprivation per se that disrupts the normal development of second-order relational processing, but deprivation of input to the right hemisphere. Patients whose early visual deprivation affected mainly the right hemisphere were severely impaired at discriminating faces that differed in the spacing among the facial features. In contrast, patients whose early deprivation affected mainly the left hemisphere had no apparent deficits. Previous research suggests that the right hemisphere may also play an important role in holistic face processing (Rossion, Dricot, et al., 2000). Thus, patients treated for congenital left eye cataract (that affected mainly the right hemisphere), may also have deficits in holistic face processing. To establish whether early visual input to the right hemisphere is necessary to set up the neural networks that will become specialized for holistic face processing, future studies could use the composite face task (a measure of holistic processing) to test patients treated for unilateral congenital cataract affecting either the left or right hemisphere.

Alternative Explanations

It is important to rule out possible alternate explanations for the findings reported in this thesis other than the effect of early visual deprivation. It is unlikely that poor acuity can account for the present findings. Visual acuity was not correlated with performance on any of the tasks. Furthermore, patients treated for unilateral left eye cataract showed deficits on processing second-order relations despite binocular testing that allowed the use of their non-deprived eye (Chapter 5). Although patients treated for bilateral congenital cataract also showed deficits on second-order relational processing, despite their poor acuity they performed normally at making fine feature discriminations (Chapter 2). Visual acuity also cannot account for the bilaterally deprived patients' impairment in holistic processing, as their deficit was shown by *superior* performance compared to normal controls on the critical condition (Chapter 3).

It is also unlikely that the deficits in face processing occurred because of abnormal visual-spatial attention. Previous research has shown that patients treated for bilateral congenital cataracts have impairments in shifting attention to the upper visual field (Goldberg, Maurer, Lewis, & Brent, 2001). Despite their attentional impairments, the deprived patients had normal performance on some face processing tasks such as differentiating faces that differ only in the features or the external contour. Impairment in holistic processing cannot be explained by abnormal visual-spatial attention. For the composite face task (Chapter 3), the deprived patients performed well at making same/different judgments for the top halves of faces, an area of visual space where their attention is abnormal, and were in fact better than normal on trials where the same top halves were aligned with different bottom halves. Abnormal visual-spatial attention also cannot explain the deficits in second-order relational processing. The results of Chapter 5 demonstrated that impairment in processing second-order relational information was similar in patients treated for bilateral congenital cataracts and patients treated for unilateral left eye cataract (Chapter 5). While bilateral cataract patients have impairments in visual-spatial attention, patients treated for unilateral congenital cataract perform normally on measures of visual spatial attention (Goldberg, 1998).

The finding of impairment in face processing following early visual deprivation cannot be accounted for by poor performance on any difficult task, rather than a specific type of visual processing. This is important because the deprived patients performed normally on two tasks that normal controls were highly accurate at – featural processing and face detection, and the patients performed poorly on a more difficult task – second-order relational processing. The research reported in Chapter 5 showed that there were no baseline differences between the upright spacing and contour sets for visually normal individuals. While the bilateral and left eye cataract patients performed normally on the contour set, they were severely impaired on the spacing set. The deprived patients' impairment in holistic processing was demonstrated in Chapter 3 by enhanced performance relative to the control group on the critical condition. Thus, the deficits in holistic processing and second-order relational processing following early visual deprivation cannot be explained by task difficulty.

Contribution to Our Knowledge of the Development of Face Processing

Not all face-processing skills follow the same developmental pattern and reach maturity at the same time. By 6 years of age, some aspects of face processing are adult-like while others are not. Six-year-old children show an adult-like composite face effect for both familiar faces (Carey & Diamond, 1994), and unfamiliar faces (Mondloch et al., 2003). They also show the whole/part advantage for unfamiliar faces (Tanaka et al., 1998), and the size of the effect is as large as in 11-year olds (the oldest age compared) (Joseph & Tanaka, 2003). Together these findings suggest that holistic face processing is adult-like by 6 years of age. Contour face processing is also mature by this age. Six-year-old children (the youngest age tested) are as accurate as adults at discriminating faces that differ only in the shape of the external contour (Mondloch et al., 2002). Unlike these skills, both 6-year-olds and 8-year-olds are slower and less accurate than adults at detecting that a Mooney stimulus is a face (see Chapter 4). This finding suggests that the ability to detect faces based on their first-order relations takes more than 8 years to become adult-like. By 10 years of age, featural face processing is mature. Ten-year-old children are as accurate as adults at discriminating faces that differ only in the shape of the facial features (e.g., the eyes and mouth) (Mondloch et al., 2002). Second-order relational processing of faces is an ability that is especially slow to mature, and is not adult-like until later in adolescence. For example, even 14 year olds (the oldest age tested) make more errors than adults at discriminating faces that differ in the spacing among the features (e.g., the distance between the eyes) (Mondloch, Le Grand, et al., in press) – at least as tested by these methods.

The deprived patients' pattern of deficits on these aspects of face processing suggests that there is no clear relationship between the effect of early visual deprivation and the normal development of these skills. Visual deprivation affects the development of a skill that is mature relatively early in childhood (holistic face processing) as well as a skill that is especially slow to mature (second-order relational processing). Furthermore, early visual deprivation does not have the same effect on skills that reach maturity at the same age. For example, holistic face processing and contour face processing are both adult-like by 6 years of age. While visual deprivation prevents the normal development of holistic processing, it has no apparent effect on the development of contour face processing. Early visual deprivation also does not prevent the eventual development of featural face processing and face detection, skills that follow different developmental patterns. Together these findings suggest that the effects of deprivation on face processing do not follow the same general principle as that of visual functions mediated by the geniculo-striate pathway. For visual functions mediated by lower level visual areas, the abilities that are most adversely affected by deprivation are those that are immature at birth and develop slowly during childhood (Maurer et al., 1989). In contrast, several aspects of face processing are immature at birth and continue to develop into later childhood, but these skills are not affected equally by visual deprivation. Thus, for the various components of expert face processing that rely on extrastriate ventral processing, the relationship between the development of these skills and the role of early visual experience do not follow the same pattern as visual functions mediated by the geniculo-striate pathway.

The term "configural processing" has been used to refer to a variety of phenomena in the literature on face processing. For example, it has been used to represent the spatial relations among the parts of a face (e.g., Diamond & Carey, 1986), the tendency to process the face as a whole (e.g., Tanaka & Farah, 1993), and the propensity to encode a face in terms of its deviation from a prototype or norm (e.g., Rhodes, Brennan, & Carey, 1987). In this thesis, I have argued that configural processing can be subdivided into three separate, but related, components: first-order relational processing, holistic processing, and second-order relational processing. Evidence for their separability is based on behavioral marker tasks, their sensitivity to experimental manipulations, and their patterns of normal development (reviewed in Maurer et al., 2002). The research reported in this thesis provides further evidence for the separability of the different types of configural processing. Although the deprived patients have deficits in holistic and second-order relational processing, they are able to detect faces based on first-order relations normally. This pattern of performance demonstrates that first-order relational processing can be dissociated from the other two components of configural processing. The research presented in this thesis has also provides insight into how the three components of configural processing relate to one another. Previous research has shown that holistic face processing is the first component of configural processing to become mature (e.g., Mondloch et al., 2003). The present research demonstrates that even in the absence of normal holistic processing, first-order relational processing can nevertheless occur. Thus, for expert first-order relational processing to develop, the ability to process faces holistically is not a precondition. In contrast, for expert second-order relational processing to develop normally, the ability to processing faces holistically might be required. In normal development, second-order relational processing develops later in childhood than holistic processing. The results from this thesis showed that both holistic processing and second-order relational processing were abnormal following early visual deprivation.

Contribution to Theories of Face Processing

Visual deprivation lasting as little as the first two months after birth was sufficient to prevent the normal development of holistic and second-order relational face processing, despite the fact that adult-like expertise in face processing takes several years to develop (e.g., Mondloch et al., 2002). During the first few months after birth, infants receive an abundance of experience with faces, and face-processing skills begin to emerge. The finding that early visual experience is necessary for the development of the ability to encode configural information in faces provides support for prominent developmental theories of face processing. All of the patients tested in this thesis were deprived of visual input for at least the first two months after birth. According to Johnson and Morton (1991), it is during this early period of infancy that the Conspec mechanism biases newborns' attention to faces and provides Conlern with input from faces that is necessary for setting up the cortical circuits that will become responsible for expert face processing. A lack of exposure to faces during these first few weeks after birth may result in a failure of Conlern to become sensitive to the spatial relations among facial features.

The present research also provides support for de Schonen and Mathivet's (1989) theory that specialization of the right hemisphere for second-order relational processing is set up by visual experience during early infancy. According to their theory, because visual acuity and contrast sensitivity are immature during early infancy, information about faces is limited to low spatial frequency information that specifies the spatial relations among features but provides little information about feature details. Based on this input, regions of the rapidly developing right hemisphere begin to form stable networks that will become specialized for processing configural information. Later in infancy, regions of the left hemisphere begin to develop and become specialized for processing featural information. It is during this period of infancy that acuity and contrast sensitivity have improved sufficiently to provide information about feature details. The research reported in Chapter 5 demonstrated that early deprivation of visual input to specifically the right hemisphere impairs the later development of sensitivity to second-order relational information. However, these studies did not provide support for early specialization of featural processing by the left hemisphere. Patients deprived of early visual input performed normally at identifying faces based on featural information. These results are consistent with previous findings that deprived patients are able to process facial expressions, eye gaze and sound being mouthed – abilities that can be solved based on featural processing. Together these findings suggest that delayed visual experience is sufficient for the development of normal featural face processing.

Future Studies

The studies presented in this thesis used behavioral measures to determine that early visual deprivation causes large and permanent deficits in holistic and second-order relational face processing, but does not cause permanent deficits in the ability to detect faces based on first-order relations and processing featural information. This research also established that early input to the right hemisphere is especially important for the cortical specialization of expert face processing. However, the neural correlates of the deficits and of the spared visual capabilities following early visual deprivation are unknown. Studies using neuroimaging techniques such as fMRI and electrophysiological techniques such as ERP are necessary to study the neural basis of the behavioral findings reported here. Studies using fMRI could be used to explore activity in the FFA, a region of the lateral fusiform gyrus that is highly responsive to faces in visually normal individuals. Early visual deprivation may alter the response properties of the FFA – perhaps in the absence of early visual experience, this cortical area will not respond preferentially to faces. In support of this hypothesis, a recent neural model of the development of face processing suggests that the FFA matures rapidly and becomes specialized for face processing during early infancy as a result of receiving input about faces from lower visual areas (Acerra et al., 2002). Previous studies using ERP have identified a face-specific negative component, the N170, that is larger for faces than for many other stimuli. This face-sensitive component likely emerges in early infancy, as a putative infant N170 has been identified in infants as young as 3 months of age (de Haan et al., 2002). The N170 takes many years to fully develop and is not adult-like until adolescence (Taylor et al., 1999, 2001). Although early visual deprivation does not prevent the eventual development of face detection, the response properties of the N170 may nevertheless be altered as a result of the deprivation. Studies using these techniques could be used to assess whether the neural mechanisms underlying various face processing skills are affected by early visual deprivation. The absence of early visual experience may affect the timing of the neural response to faces, the pattern of lateralization for various face processing skills, and/or the source of these neural signals.

While the findings from the studies reported in this thesis suggest that visual experience from the beginning of life is critical for the normal development of expert face processing, research is required to determine whether the development of expertise for non-face objects also requires early visual experience. Visually normal adults tend to process faces based on second-order relational information because: 1) all faces share the same basic arrangement of features; 2) adults tend to differentiate faces at the individual level; and 3) it is possible to individuate faces on the basis of the distinctive relations between features. Second-order relational information is also relied upon for processing non-face objects provided that these three conditions are met. Previous studies have shown that adults can be trained to become experts at identifying exemplars from a class of homogeneous non-face stimuli (Greebles). Following extensive training, adults show some evidence of processing these non-face stimuli based on configural information (e.g., under some conditions they show an inversion effect, whole/part advantage, and composite effect for Greebles; Gauthier & Tarr, 1997, 2002). To investigate the role of early visual experience in the development of non-face expertise, deprived patients could undergo a similar training procedure. Following training, testing could determine whether deprived patients have reached the criterion set for stimulus expertise. Various tests could also be conducted to determine whether the patients' configural processing deficits extend to non-face object categories. For example, deprived patients could be tested on their ability to recognize an individual Greeble from different viewpoints, or a composite task that requires recognizing the top halves of Greebles that are either aligned or misaligned with different bottom halves. These studies would help determine whether the impairments in configural processing following early visual deprivation reported here are restricted to faces.

The research in this thesis demonstrates that early visual input is necessary to setup the neural networks that will become responsible for expert face processing. However, visual experience after infancy may also be necessary to consolidate these neural connections. Research is required to determine the duration of the sensitive period during which visual experience is necessary for face processing to develop normally. Studies with individuals who had normal visual input during early infancy, but were deprived of visual experience later in life due to developmental bilateral cataracts could be conducted to investigate the role of visual experience at different points in development. If the duration of the sensitive period for face processing is limited to the first few months of infancy, deprivation of visual input occurring after this time should not impair the normal development of face processing. If visual experience is influential after infancy, then impairment in face processing should be observed in individuals who were deprived of visual input after infancy. To determine the sensitive periods for various face processing skills, individuals deprived of visual input after infancy could be tested using the same behavioral measures that were used in the experiments reported in this thesis, and their results could be compared to those of individuals who were deprived of visual input during infancy. Such studies would provide a comparison of the types and degree of deficits in face processing following early versus later deprivation. Neuroimaging techniques would also be valuable to examine the neural mechanisms underlying face processing following visual deprivation that occurred after infancy.

Although I have argued in this thesis that early visual experience in necessary for the development of expert face processing, all the patients tested in the studies reported here were deprived of visual input for at least the first two months of life. It is not known whether visual deprivation limited to only the first few weeks after birth would have an effect on the development of face processing. To examine the role of visual experience during the first few weeks after birth, it is necessary to test individuals who were deprived of early visual input for only a short time after birth.

Conclusion

The findings from the studies reported in this thesis demonstrate that the development of face processing is dependent on visual experience during infancy. The face processing tasks included capabilities that are considered attributes of adults' expertise in face processing, such as integrating the facial features into a gestalt, and encoding the spatial relations among those features. The present findings show that visual deprivation during infancy prevents the development of expert face processing.

Previous studies have shown that expertise in face processing takes many years to mature, and is only adult-like in adolescence. Yet visual deprivation lasting as little as the first two months during infancy is sufficient to prevent its normal development. The role of early visual experience is likely to set up the neural networks that will become responsible for the later development of holistic and second-order relational processing of faces. Individuals who did not receive visual experience during infancy likely experience difficulty in recognizing individual faces later in life, especially in situations in which face recognition based on featural information is ineffective. Such conditions occur in everyday life and include recognizing a face from a distance, or from a novel point of view.

This research contributes to knowledge about the development of various aspects of face processing including face detection based on first-order relational processing, holistic processing, second-order relational processing and featural processing. The findings provide support for developmental theories of face processing, and offer insight into the neural organization of various face processing skills.

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