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What aspects of face processing are impaired in developmental prosopagnosia?

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Abstract

Developmental prosopagnosia (DP) is a severe impairment in identifying faces that is present from early in life and that occurs despite no apparent brain damage and intact visual and intellectual function. Here, we investigated what aspects of face processing are impaired/spared in developmental prosopagnosia by examining a relatively large group of individuals with DP ($n = 8$) using an extensive battery of well-established tasks. The tasks included measures of sensitivity to global motion and to global form, detection that a stimulus is a face, determination of its sex, holistic face processing, processing of face identity based on features, contour, and the spacing of features, and judgments of attractiveness. The DP cases showed normal sensitivity to global motion and global form and performed normally on our tests of face detection and holistic processing. On the other tasks, many DP cases were impaired but there was no systematic pattern. At least half showed deficits in processing of facial identity based on either the outer contour or spacing of the internal features, and/or on judgments of attractiveness. Three of the eight were impaired in processing facial identify based on the shape of internal features. The results show that DP is a heterogeneous condition and that impairment in recognizing faces cannot be predicted by poor performance on any one measure of face processing.

Keywords: Prosopagnosia; Face processing; Global motion; Global form; Face detection; Holistic processing; Configural processing; Featural processing; Attractiveness

1. Introduction

Adults are ‘experts’ in face processing: they can recognize thousands of individual faces rapidly and accurately, and they can easily decipher various cues, such as sex of face, emotional expression, and direction of gaze (see Bruce & Young, 1998, for a review). This proficiency in face recognition is remarkable considering that all 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. While most adults are experts in face recognition (Carey, 1992), there exist rare cases of individuals who are severely impaired in face recognition, a clinical condition known as prosopagnosia. Documenting the pattern of their deficits may increase our understanding of the developmental processes underlying normal face perception.

Most studies have involved individuals who acquired prosopagnosia (AP) after damage to occipital-temporal cortex (e.g., Damasio, Damasio, & van Hoessen, 1982; Sergent & Villemure, 1989). However, there exist individuals that

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have impairment in face recognition all their lives despite no known brain injury. The term developmental prosopagnosia[1] (DP) refers to the absence of any known lesion or neurological condition that could account for the impairment in face recognition, and excludes individuals suffering from visual deprivation, such as congenital cataract, or developmental problems such as autism spectrum disorder. While interest in DP continues to grow, current knowledge of this condition is limited and in general the findings have been contradictory and inconsistent. This may be due to the small number of reported cases, the heterogeneity of the condition, the prevalence of single case studies, and/or the variability in the methods used to examine DP (for reviews see Behrmann & Avidan, 2005; Kress & Daum, 2003a).

Previous studies of individuals with DP typically have involved a single case and a limited number of tasks (Ariel & Sadeh, 1996; Bentin, Deouell, & Soroker, 1999; de Gelder & Rouw, 2000a; Duchaine, 2000; Duchaine, Nieminen-von Wendt, New, & Kulomaki, 2003; Duchaine, Parker, & Nakayama, 2003; Jones & Tranel, 2001; McConachie, 1976; Nunn, Postma, & Pearson, 2001; but see Behrmann, Avidan, Marotta, & Kimchi, 2005, for a more systematic study of 5 cases). These studies have indicated that there is variability in performance across tasks and across individuals with DP. Of course, all DP cases have trouble with facial identity, but tests with familiar faces (celebrities and acquaintances) have shown that some individuals with DP can recognize faces after a large number of exposures (Duchaine et al., 2003; Nunn et al., 2001) whereas others have trouble even with commonly seen faces (Barton, Cherkasova, Press, Intriligator, & O'Connor, 2003; Duchaine, 2000; Duchaine & Nieminen-von Wendt et al., 2003). The use of standardized clinical tests of face recognition, such as the Warrington Recognition Memory for Faces (RMF; Warrington, 1984) and the Benton Facial Recognition Test (BFRT; Benton, Sivan, Hamsher, Varney, & Spreen, 1983), have also revealed inconsistent findings. While some individuals with DP show deficits on these standardized tests (e.g., Ariel & Sadeh, 1996; de Gelder & Rouw, 2000a), others perform within the normal range despite clear impairment on tests of familiar face recognition (e.g., Duchaine, 2000; Nunn et al., 2001). The validity of these standardized measures has been criticized because the photos used in testing contain non-facial cues such as hairstyle and clothing (Duchaine & Weidenfeld, 2003; Kress & Daum, 2003a). In fact, on modified versions of the RMF and BFRT in which facial cues are removed by occluding the inner portion of the test faces, the accuracy of both normal controls and developmental prosopagnosics alike is within the normal range (Duchaine & Nakayama, 2004; Duchaine & Weidenfeld, 2003). Thus, normal performance on the BFRT and RMF by prosopagnosic individuals should be interpreted with caution, especially when reaction time measures are absent (see Delvenne, Seron, Coyette, & Rossion, 2004).

Investigations into the neural bases of DP also have found inconsistencies. Structural studies usually report no obvious abnormalities (Duchaine & Nieminen-von Wendt et al., 2003; Kress & Daum, 2003b; Nunn et al., 2001), but one case (YT) had a significantly smaller right temporal lobe compared to normals (Bentin et al., 1999). Some cases of DP show an abnormally small difference in the ERP response to faces versus objects for the 'N170', which is normally characterized by much greater negativity occurring 170 ms after stimulus onset for faces than for a variety of non-face object categories (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bentin et al., 1999; Kress & Daum, 2003b). In other cases, the N170 is not modulated normally by the inversion of the face or its presentation in the left temporal versus nasal visual field (de Gelder & Stekelenburg, 2005). Most cases of DP who have undergone fMRI have shown normal activation of the 'fusiform face area' or FFA (Avidan, Hasson, Malach, & Behrmann, 2005; Hasson, Avidan, Deouell, Bentin, & Malach, 2003), a region in the occipito-temporal cortex that responds more to faces than to most other stimulus categories (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997). Yet an apparently normal FFA in a prosopagnosic may nevertheless show inefficient interactions with working memory and attention (DeGutis, Sagiv, D'Esposito, & Robertson, 2004). There are also three documented cases of DP without selective activation for faces within the FFA (Hadjikhani & de Gelder, 2002).

Individuals with DP often have impairments with other aspects of face processing, but again some individuals have shown normal abilities while others are impaired. This is true for recognition of facial expressions of emotion (Ariel & Sadeh, 1996; de Haan & Campbell, 1991; Duchaine et al., 2003; Jones & Tranel, 2001; McConachie, 1976; Nunn et al., 2001), and gender discrimination (Ariel & Sadeh, 1996; de Haan & Campbell, 1991; Jones & Tranel, 2001; Nunn et al., 2001). In most cases non-face object processing is intact, and when deficits in object recognition are present they are much less pronounced than face processing impairments (Ariel & Sadeh, 1996; Barton et al., 2003; Behrmann et al., 2005; Bentin et al., 1999; de Haan & Campbell, 1991; Duchaine & Nakayama, 2005; Nunn et al., 2001). In addition, a number of DP cases have severe impairments with navigation (Duchaine et al., 2003), suffer from auditory processing deficits (Duchaine, 2000; McConachie, 1976; Temple, 1992), and show interference between local elements and global shape under conditions in which global shape is dominant in normal controls, as if local details dominate their processing of objects (Behrmann et al., 2005). While there is no conclusive

[1] The terms "congenital prosopagnosia" and "developmental prosopagnosia" have been used interchangeably to refer to a condition involving a severe deficit in face processing in the absence of any observable cortical damage. However, congenital prosopagnosia has the added implication that the deficit was present from birth. While the participants in the present study have no evidence of cortical damage, recall no incident such as meningitis or accident that could have caused the impairment, and remember problems with face recognition all their lives, there is no way to ascertain whether their face processing impairment was in fact present at birth. To be conservative, we refer to these individuals as having developmental prosopagnosia (DP).

evidence that DP represents a disorder that is specific to faces, the general finding is that face recognition problems are disproportionately more severe than other deficits (for a review see Behrmann & Avidan, 2005). Note that the conclusions from the comparisons discussed here should be treated with caution, because almost all are based on comparing the results of different cases assessed with different tests.

The purpose of our study was to examine the face processing skills of a relatively large group of individuals with DP ($n = 8$) using a large battery of well-established tasks. All DP cases complained of significant problems with face recognition throughout their lifetime, and recounted numerous experiences in which they were unable to recognize highly familiar individuals including close friends and family members despite no medical history of brain trauma. The tasks used here were chosen to probe systematically different aspects of face processing and its precursors within the ventral stream. For each task, we had collected data already on normal development and, in most cases, its alteration by early visual deprivation from congenital cataract. That allowed us to evaluate whether the pattern of deficit and sparing in individuals with DP is related to the pattern of normal development, (i.e., are deficits more likely on those aspects of face processing that take more years to develop and/or depend on early visual input). The comprehensiveness of the battery also allowed us to evaluate whether there are hierarchical relationships among the skills, such that a deficit in X (e.g., face detection) always is accompanied by a deficit in Y (e.g., holistic face processing) but not vice versa.

The battery included tests of face detection, holistic face processing (gluing the facial features together into a Gestalt), discrimination of facial identity, detection of the sex of the face, and judgments of attractiveness. In addition, we included two tasks that measure the ability to integrate individual elements into a global signal at intermediary stages of object processing in the ventral and dorsal streams, respectively: (a) perception of global form and (b) perception of global motion. We compared the performance of each individual with developmental prosopagnosia to that of a large age-matched control group. Previously we have tested LH, a well-documented case of acquired prosopagnosia (e.g., de Gelder & Rouw, 2000b), on this assessment battery (Le Grand et al., 2003). LH was found to lack sensitivity to structure in global form, and showed severe impairment on all but one of our tests of face processing—gender discrimination. The findings demonstrate that our assessment battery is capable of identifying face processing deficits in cases of prosopagnosia. In the rest of the *Introduction*, we present the rationale behind each task included in the test battery.

2. Non-face tasks

2.1. Global form

The perception of global form requires the integration of information about local elements into a coherent whole, and such integration may be a prerequisite to identifying that a stimulus is a face and determining facial identity. Local elements can be detected by simple and complex cells in the primary visual cortex, the output of which is then integrated by cells with larger receptive fields in higher cortical areas, especially extrastriate area V4v in the ventral visual pathway (reviewed in Lewis et al., 2004; Wilson, 1999). Single cell recordings of the monkey have identified a type of cell in area V4v responsive primarily to global concentric structure (Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Kobatake & Tanaka, 1994; Pasupathy & Connor, 1999). The global concentric units in V4 may be a critical link between the processing of local detail by cells in V1 and the extraction of information about face identity in IT, to which V4 provides a major input (Wilkinson et al., 2000). Glass (1969) patterns are ideal stimuli for studying sensitivity to structure in global form. When a pattern of random dots is superimposed over an identical pattern and rotated a critical amount about the central axis, a compelling perception of concentric swirls arises. These concentric Glass patterns can be used to assess sensitivity to global form by varying the ratio of paired signal dots to unpaired noise dots in the signal pattern until the subject can no longer discriminate accurately between the signal pattern and a pattern comprised solely of noise dots (see Fig. 1). Previously we have shown that adults detect the signal pattern accurately when it is carried by only 12% of the dot pairs (Lewis et al., 2004). This sensitivity becomes adult-like by 9 years of age (Lewis et al., 2004) and is impaired after early visual deprivation (Lewis et al., 2002).

2.2. Global motion

To compare the ability of individuals with prosopagnosia to integrate local signals in the ventral pathway with their ability to integrate local signals in the dorsal pathway, we also measured sensitivity to global motion—an aspect of vision that requires extrastriate regions of the visual cortex including the middle temporal (MT) area (Maunsell & Van Essen, 1983; Morrone et al., 2000; Newsome & Paré, 1988). The display consists of dots moving

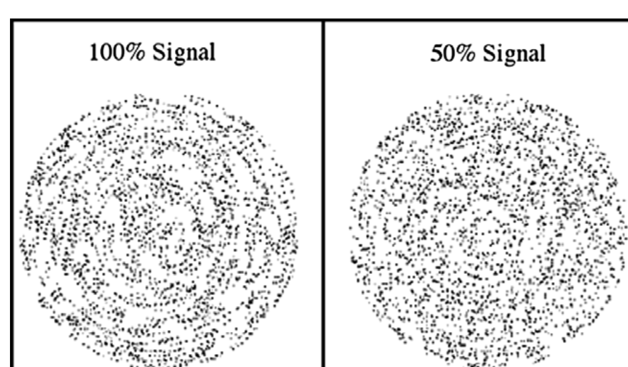

Fig. 1. Global form stimuli. Example of stimuli used to test sensitivity to global form. Pattern on the left has 100% of the dots paired to form a global swirl and pattern on the right has 50% paired signal dots and 50% randomly placed noise dots.

in random directions except for a percentage of signal dots moving in the same direction (see Fig. 2). These stimuli ensure that any percept of overall direction of motion arises from the integration of local motion cues. Visually normal adults can detect the direction of global motion accurately even when it is carried by less than 10% of the moving dots. Previously we have shown that sensitivity to global motion, as measured by our version of the task, is adult-like by 6 years of age and is impaired after early visual deprivation (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002).

3. Face tasks

Adult expertise in face perception is attributed to enhanced sensitivity to configural information in faces (that arises from years of experience identifying faces). 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, Le Grand, & Mondloch, 2002). It is contrasted with *featural processing*—processing information related to the individual features of the face such as the shape or colour 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; (3) sensitivity to *second-order relations*—encoding the spacing among facial features, like the distance between the eyes. While all three types of configural processing require sensitivity to the relations among facial featural components, differences in their rate of development (Mondloch, Le Grand, & Maurer, 2003) as well as differential impairment in prosopagnosia (de Gelder & Rouw, 2000b) and in children and adults with a history of early visual deprivation (Mondloch et al., 2003) suggest that these aspects of face processing involve, at least in part, separate underlying neural mechanisms. In the present study, we included a measure of each of the three types of configural processing and a measure of featural processing.

3.1. Face detection

Face detection refers to the ability to detect that a visual stimulus is a face. It is facilitated by the fact that all faces share the same ordinal (first-order) relations of features: the two eyes are positioned above the nose, which is above the mouth (Diamond & Carey, 1986). Adults have a remarkable ability to detect that a stimulus is a face based on first-order relations. 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, & Behrmann, 1997) and when presented with a two-tone Mooney stimulus (see Fig. 3) in which the perception of individual local features has been degraded by transforming all luminance values to black or white (Kanwisher, Tong, & Nakayama, 1998; Mondloch et al., 2003)—at least when the stimuli are upright. Upright, but not inverted Mooney faces activate the 'fusiform face area' (FFA), an area that normally responds more to faces than to most other stimulus categories (Kanwisher et al., 1998). While several measures of face detection exist (Lewis & Ellis, 2003), we employed Mooney images because they preclude focusing on local features. On each trial either a Mooney face or a scrambled Mooney face was presented briefly, and the participant decided whether the stimulus was a face or non-face. Performance on this task is not adult-like in visually normal 8-year-olds (Maurer, unpublished data), but is normal in older children with a history of early visual deprivation (Mondloch et al., 2003). While deficits on this task could be caused by impairments in visual closure rather than in face detection, *normal* performance provides strong evidence of intact sensitivity to first-order relations.

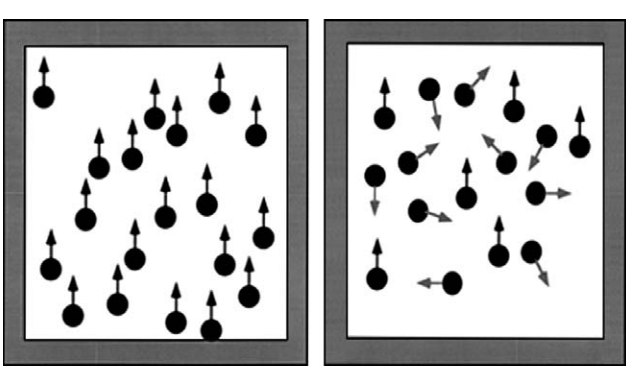

Fig. 2. Global motion stimuli. Example of stimuli used to test sensitivity to global motion. Pattern on the left has 100% coherent motion (all the dots are moving upwards) and pattern on the right has 37% coherent signal (6 of 16 dots are moving upward and the remaining dots are moving in random directions).

Fig. 3. Mooney stimuli. Example of stimuli used to measure face detection based on sensitivity to first-order relations. The image on the left is a two-tone Mooney face and the image on the right is a scrambled Mooney face.

3.2. Holistic face processing

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 (Young, Hellawell, & Hay, 1987). A similar effect occurs when adults are asked to make same/different judgments about the top halves of unfamiliar faces (see Fig. 4) (Hole, 1994; Le Grand, Mondloch, Maurer, & Brent, 2004). Holistic processing, as measured by the composite face effect, is adult-like by 6 years of age (Mondloch, Pathman, Le Grand, & Maurer, 2003) but is abnormal in children and adults with a history early visual deprivation caused by bilateral congenital cataract (Le Grand et al., 2004).

3.3. Recognition of individual faces

Because all faces share the same first-order relations, recognition of individual faces requires sensitivity to subtle differences in the shape of individual internal features (e.g., eyes, mouth), in the shape of the external contour (e.g., chins), and in the spacing among internal features (called second-order relations—e.g., the distance between the eyes). Recognition based on the first two types of cues depends on featural processing, whereas recognition based on spacing depends on second-order relational processing. Because under some conditions featural and contour processing of faces do not provide reliable cues for recognition (e.g., they change with 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. Sensitivity to second-order relations as a cue to facial identity is especially slow to develop (Freire & Lee, 2001; Mondloch, Le Grand, & Maurer, 2002), is most affected by inversion (Collishaw & Hole, 2000; Freire, Lee, & Symons, 2000; Leder & Bruce, 2000; Mondloch et al., 2002; Mondloch et al., 2003; Rhodes, Brake, & Atkinson, 1993) and, unlike featural processing, is abnormal in children and adults with a history of early visual deprivation—a pattern of results suggesting a qualitative difference between the underlying processes (Le Grand, Mondloch, Maurer, and Brent, 2001, 2003), at least when the variations in the spacing of features stay within natural limits (see Yovel & Kanwisher, 2004 for a different pattern of inversion effects when the spacing changes are much larger—4.5 *SD*s beyond the normal mean). To measure sensitivity to each of these cues to facial identity, participants made same/different judgments for pairs of faces that differed either in the shape of internal features (featural set), the shape of the external contour (contour set), or the spacing of internal features (spacing set) (see Fig. 5). The task was designed to avoid floor and ceiling effects and to sample most of the natural variation among adult Caucasian female faces in the spacing of internal features (Farkas, 1994).

Fig. 4. Composite faces. Example of stimuli used to measure holistic face processing. Two face pairs from the misaligned condition are in the top row, and two face pairs from the aligned condition are in the bottom row. In this example, the top halves are identical and the bottom halves are different.

3.4. Judgments of attractiveness

Despite innate influences that attract infants' attention to attractive over unattractive faces (Langlois et al., 1987; Rubenstein, Kalakanis, & Langlois, 1999; Slater et al., 1998), several lines of evidence indicate that postnatal experience with faces affects our judgments of attractiveness. One demonstration is that adults' preference for the eye colour, hair colour, (Little, Penton-Voak, Burt, & Perrett, 2003), and age (Perrett et al., 2002) of their romantic partner is correlated with these characteristics in their parents. Experiential influences may also explain why computer-generated average faces (created from a number of individual component faces) are generally rated as more attractive than the component faces used in their creation (Langlois & Roggman, 1990; Perrett, May, & Yoshikawa, 1994; Rhodes & Tremewan, 1996). An experiential hypothesis suggests that average faces are attractive because they resemble internal face prototypes that are formed from the sum of an individual's experience with faces (Langlois & Roggman, 1990; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; but see Rhodes et al., 2005, for evidence inconsistent with an experiential explanation). The similarity

Fig. 5. The Jane stimuli. Stimuli used to measure facial identity. (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 eyes and between the eyes and mouth.

of average faces to the internal prototypes leads to greater ease of processing and a sense of familiarity, and may result in average faces being judged as more attractive. This experiential hypothesis is supported by the finding that adults' judgments of attractiveness can be changed systematically by short-term adaptation to altered faces in the lab (Rhodes et al., 2003; Webster, Kaping, Mizokami, & Duhamel, 2004) and the finding that the preference for average faces appears to develop sometime after infancy (Rhodes, Geddes, Jeffery, Dziurawiec, & Clark, 2002). Additional evidence for an effect of experience comes from developmental changes in the perceived attractiveness of faces with the internal features at different heights. Throughout development from 5 months to 12 years of age, children look longer at, or judge as more attractive, faces with the proportions most similar to their accumulated experience (Cooper & Maurer, 2002; Geldart, Maurer, & Henderson, 1999). For example, young children with high levels of peer interaction rate faces with child-like proportions as "more pretty" than other faces (Geldart, 2003), and older children develop the adult preference for faces with average adult proportions only when the faces of their peers have developed those adult proportions (Cooper & Maurer, 2002).

We included two measures of attractiveness: one involving faces with different heights of internal features (see Fig. 6A), and a second task involving comparisons of individual and average faces (see Fig. 6B). We hypothesized that participants with prosopagnosia might be abnormal in their judgments of attractiveness as a result of their abnormal experience with faces during development.

3.5. Sex of face

Despite diminished capacity to recognize faces, individuals with prosopagnosia often retain the ability to judge the sex of a face (e.g., Nunn et al., 2001). To capture this preserved ability, we included a test of sex of face. Despite the ease with which visually normal adults judge the sex of a face, the discrimination requires the detection of subtle differences on multiple dimensions, and this skill is not fully developed in children until sometime after 4 years of age (Newell, Strauss, Best, & Gastgeb, 2004).

4. Methods

This study was approved by the Research Ethics Board of McMaster University. Prior to testing, the procedures were explained and informed written consent was obtained from the participant. For all experiments, the participant sat in a dimly lit room and the stimuli were presented on an

Fig. 6. Facial attractiveness stimuli. Example of stimuli used to measure judgments of facial attraction. (A) Features placed (left) lower, (middle) average, and (right) higher than the population mean. (B) Computer-generated average female (left) and unaltered individual female (right).

Apple 21-in. "Cinema Display" LCD computer monitor controlled by an Apple Macintosh G4 Cube. All testing was binocular.

5. Participants

5.1. Developmental prosopagnosic group

The DP group consisted of 8 individuals (4 male) ranging in age from 20 to 71 years, with no overt brain damage or neurological disease that could account for their face recognition impairment. All participants report having severe difficulty in identifying familiar faces from an early age (including close family members), and show severe impairment on tests of face recognition despite no traumatic brain injury in their medical history. Their impairment recognizing faces was evident despite intact visual acuity, normal visual processing, object recognition and intellectual functioning.

Because no single established diagnostic measure of prosopagnosia exists, we employed several tasks to document the DP's face recognition deficits. In addition to every DP case reporting severe difficulty recognizing familiar faces throughout their lifetime, we tested their ability to recognize familiar faces using at least one test of famous face recognition, and when possible, the ability to recognize a recently studied face (the One in Ten test). These tests have previously been used to diagnose developmental prosopagnosia and are discussed in detail elsewhere (see Duchaine, 2000; Duchaine & Nieminen-von Wendt et al., 2003). For the famous face recognition tests, participants were presented with the faces of well-known celebrities drawn primarily from entertainment and politics (e.g., Bill Clinton, Madonna). Answers were considered correct if the participant provided the celebrity's name or some other uniquely identifying information about the person (e.g., political office held, movie role). For the One in Ten test, participants first viewed 15 images of a target face that varied in luminance and were then asked to recognize the target face from a variety of non-target faces. The performance of each DP case was compared to established norms from an age-matched group. The results for each DP participant on these measures of face recognition are shown in Table 1. Note that individuals with DP can develop effective compensatory strategies for face recognition including reliance on diagnostic facial features (e.g., Robert De Niro's mole) and/or non-facial cues (e.g., Pope's white zucchetto). Such strategies likely account for normal performance on certain tests of face recognition (despite severe deficits on others), and highlights the need for a conventional standardized clinical measure of prosopagnosia.

To compare our DP cases with previously documented cases, when available we also report their performance on the Warrington (RMF) and Benton (BFRT) standardized tests of face recognition. Similar to previous studies of DP (e.g., Behrmann et al., 2005; Duchaine et al., 2003), we did not rely on the RMF or BFRT to diagnose face processing impairments because individuals with severe impairments can achieve normal scores on these tests (see Section 1; Duchaine & Weidenfeld, 2003; Duchaine & Nakayama, 2004).

[AS:] AS is a 21-year-old right-handed college student majoring in mathematics. She reports trouble with recognizing familiar faces throughout her life. She has severe difficulty in recognizing familiar faces and showed severe impairment on our famous face recognition test and in learning new faces on the One in Ten Face test.

Table 1
Performance of the developmental prosopagnosics on measures of face recognition

Participant	Famous faces (10 items)		Famous faces (25 items)		One in ten face test	
	%	*z* score	%	*z* score	*d′*	*z* score
AS	—	—	16	**−13.90**	1.87	**−3.55**
BC	40	**−3.64**	24	**−12.48**	2.15	**−2.98**
DJ	0	**−6.67**	—	—	—	—
EN	30	**−4.39**	52	**−7.52**	3.30	0.84
HH	60	**−2.12**	—	—	—	—
JH	10	**−5.91**	24	**−13.90**	2.5	**−2.27**
MT	90	0.2	76	**−3.26**	2.1	**−3.08**
NM	—	—	60	**−6.10**	1.66	**−3.98**
Controls	88	—	94	—	3.61	—

The data from prosopagnosic participants were converted into *z* scores using the mean and standard deviation for a group of age-matched control participants. The cutoff for normal performance was set at a *z* score of −1.65, which corresponds to the lowest 5% of the normal population. Numbers in bold (red) represent impaired performance. All prosopagnosic participants were severely impaired on at least one measure of face recognition. (For interpretation of the references to colour in this table legend, the reader is referred to the web version of this paper.)

AS has normal object perception as measured by the perceptual tests in the Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993) and recognition of common objects from Snodgrass and Vanderwart's corpus of line drawings (1980). Her Snellen acuity with optical correction is 20/20 in each eye.

[BC:] BC is an ambidextrous 54-year-old retired engineer who has a degree in electrical engineering as well as a law degree. He has a family history of prosopagnosia and has suffered with a lifelong face perception problem. BC has great difficulty recognizing individuals whom he has known for years. He performs normally on tests of object recognition (Duchaine, 2000), but has severe deficits in several face processing tests. He also showed severe impairment on our famous face recognition tests and learning novel faces in the One in Test Face test (see also Duchaine, 2000). He performed within the normal range on the both the RMF and BFRT, however his response time were extremely slow (Duchaine, 2000). As with other cases of DP showing auditory deficits (e.g., McConachie, 1976; Temple, 1992), BC has been diagnosed with Central Auditory Processing Deficit, which is characterized by difficulty understanding speech in noisy settings. An extensive website is devoted to his prosopagnosia (www.choisser.com/faceblind). His Snellen acuity with optical correction is 20/20 in each eye.

[DJ:] DJ is a right-handed 36-year-old engineer. He reports frequent difficulties recognizing other people, including close friends and family members. He often recognizes familiar people who approach him only after a short conversation, and was severely impaired on our test of famous face recognition. Consistent with several other reported cases of prosopagnosia (e.g., Duchaine & Nakayama, 2004), DJ performed within the normal range on the BFRT and was slightly impaired on the RMF (response times were not measured). His Snellen acuity with optical correction is 20/20 in each eye. Electrophysiological findings in DJ have been reported by Sagiv, Barnes, Swick, and Robertson (2001). DJ showed an abnormal response pattern similar to the one reported by Bentin et al. (1999) in the developmental case YT (i.e., an abnormally small N170 differentiation between faces and other stimuli). A structural MRI scan conducted by Sagiv in 2001 showed no evidence of brain damage.

[EN:] EN is a 31-year-old right-handed female house painter. She received a B.A. in psychology, and she has reported problems with face recognition throughout her life. EN performed within the normal range on the One in Ten Face test, but showed severe impairment on the two tests requiring recognition of famous faces. She performed normally on the perceptual tests in Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993) and had no difficulty recognizing common objects drawn from Snodgrass and Vanderwart's corpus of line drawings (1980). Her Snellen acuity with optical correction is 20/20 in each eye.

[HH:] HH is a right-handed 71-year-old physician. Since childhood he has reported difficulty recognizing people except by their voice or gestures. In the laboratory, he failed to recognize pictures of close relatives including his wife and even himself (L. Barnes, L.C. Robertson, personal communication), and performed poorly on our test of famous face recognition. HH performed within the normal range on the RMF and was mildly impaired on the BFRT (response times were not measured). Earlier testing (R. Efron, personal communication) showed normal colour vision, stereo vision, and visual search for letter stimuli. Similar to other cases of prospagnosia, he also reports right-left confusion and other spatial confusions (e.g., Duchaine et al., 2003). His Snellen acuity with optical correction is 20/25 in the right eye and 20/30 in the left eye. Like the developmental cases DJ and YT, electrophysiological testing showed that HH has an abnormal N170 response that does not differentiate between faces and other stimuli (Sagiv et al., 2001).

[JH:] JH is a 20-year-old right-handed college student majoring in education. He has had lifelong face perception difficulties, and others in his family also have problems with face perception (Duchaine, Le Grand, Nakayama, & Maurer, 2003). JH performs normally on tests of object recognition, and like other cases of DP, reports severe navigational difficulties. He has severe difficulty leaning new faces (as measured by the One in Ten Face test), and performed poorly on our tests of famous face recognition. His Snellen acuity with optical correction is 20/20 in each eye.

[MT:] MT is a 60-year-old right-handed self-employed woman. Her problems with face recognition have caused serious social problems, and fears of social interaction have led this personable woman to become reclusive. She had severely impaired performance on the One in Ten Face test and problems on one of our two tests of famous face recognition. A website has been devoted to her prosopagnosia (http://prosopagnosia.homestead.com/index.html). MT performed normally on the perceptual tests in Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993) and had no difficulty recognizing common objects drawn from Snodgrass and Vanderwart's corpus of line drawings (1980). Her Snellen acuity with optical correction is 20/25 in the right eye and 20/20 in the left eye.

[NM:] NM is a 40-year-old left-handed female English teacher. She has severe difficulty recognizing facial identity, but she recognizes facial expressions normally (Duchaine et al., 2003). Similar to several other cases of prosopagnosia, she also reports difficulties with navigation. NM reports using various strategies for person recognition including hair, body shape, voice, and characteristic facial expressions. She is severely impaired on our test of recognizing famous faces and learning new faces as measured by the One in Ten Face test (see also Duchaine & Nieminen-von Wendt et al., 2003). Her performance on the WRMF was in the severely impaired range. NM performs normally on several tests of object recognition (Duchaine et al., 2003). Her Snellen acuity with optical correction is 20/20 in each eye, and she has normal contrast sensitivity.

5.2. Control group

Because of the wide range in age of the participants with prosopagnosia (20–71 years), we tested a control group of 28 right-handed Caucasian control subjects aged 20–73 years, with normal or corrected-to-normal vision. There were five participants in each of the age ranges from 20 to 29, 30 to 39, 40 to 49, 50 to 59, and 60 to 69, and three participants aged 70 to 75. Control participants received either course credit or a gift certificate in appreciation for their time.

6. Non-face tasks

6.1. Global form

A prerequisite for face processing is the perception of the global structure of an object. This requires that the local elements be integrated into a coherent whole. In the present task, thresholds for detecting global form were measured by having participants discriminate concentric Glass patterns from noise patterns (see Fig. 1).

6.1.1. Stimuli and procedure

The stimuli and procedure were identical to those reported by Lewis et al. (2002), except that the stimuli were 37% larger. Briefly, participants viewed an array of white "dots" (2.7 arc min squares) on a grey background contained within a 17.6° circle centred on the computer monitor. The array formed either coherent "signal patterns" or noise patterns. For signal patterns, pairs of dots were placed at random within the pattern, but the orientation of the pair was always tangent to a circle centred on the pattern. Signal patterns were degraded to varying degrees by replacing a percentage of the signal dot pairs with an equal number of randomly spaced noise dots that were the same size and shape as the signal dots. To measure thresholds for detecting global structure in Glass patterns, subjects discriminated signal patterns from noise patterns in a two-alternative temporal forced choice procedure where the task was to indicate whether the pattern with the signal had appeared in the first or second 1500 ms interval.

After completing criterion and practice trials, each participant received four signal values that were each presented 20 times in a random order. The values selected were designed to bracket the expected threshold, based on the results from the practice run. The percentage of correct responses was plotted as a function of signal value and the data were fit by a Quick (1974) or Weibull (1951) function using a maximum likelihood procedure. Thresholds were defined as the percent signal necessary to obtain 75% correct responses. Reaction time data were not recorded because an experimenter entered the participant's response on each trial.

6.1.2. Results and discussion

6.1.2.1. Control group. For each participant, we calculated a threshold representing the percentage of signal dots necessary for correct detection of the signal pattern at an accuracy of 75%. When the thresholds of the control group were analyzed in a one-way ANOVA with age as a between subjects factor (six levels), there was a main effect of age ($p < .01$). Fisher's post-tests revealed that the main effect was driven by the significantly worse performance of the participants in the 70 to 75 age-range compared to that of all other age groups ($ps < .01$). As the performance of the single DP participant in the 70 to 75 age range (HH threshold = 14%) was much better than controls of the same age (mean threshold = 27%), we excluded control data from that age range. When that age group was excluded, there was no longer a significant effect of age, and therefore we collapsed the control data across the remaining ages. Mean threshold of the 20- to 60-year-olds was 12.4%, virtually identical to the threshold of 12.3% that we obtained in a previous study of visually normal adults (17 to 29 years of age) using the same procedure (Lewis et al., 2004).

6.1.2.2. Prosopagnosic participants. To simplify comparison across tasks, the data from prosopagnosic participants were converted into z scores using the mean and standard deviation for the thresholds of the control participants (excluding participants in the 70 to 75 age range). The cutoff for normal performance was set at a z score of −1.65, which corresponds to the lowest 5% of the normal population.

All DP participants performed within the normal range for sensitivity to global form (mean normalized threshold: −0.08, range: −1.10 to 0.47). Their mean threshold of 14.53% did not differ from the mean of 14.01% in the control group. The results rule out impairment in the perception of global form (a precursor of face processing) as a potential explanation for their difficulty in recognizing faces. To our knowledge, there have been no previous studies that measured sensitivity to global form in individuals with DP.

6.2. Global motion

The purpose of this experiment was to examine the ability of individuals with prosopagnosia to integrate local signals for the perception of global motion. Thresholds for detecting global motion were measured by having participants discriminate the direction of motion in displays with a varying percentage of dots moving coherently in the same direction amongst dots moving in random directions (see Fig. 2).

6.2.1. Stimuli and procedure

The stimuli and procedure were identical to that of Ellemberg et al. (2002) except that thresholds were tested with the method-of-constant stimuli rather than with a staircase procedure. Briefly, participants viewed random-dot-kinematograms (RDKs): patterns of dots moving randomly except for a proportion that moved coherently either up or down. Each trial contained 300 limited-lifetime black dots (diameter = 30 arc min; density = 0.75/deg) within a 20° × 20° square against a white background. The percentage of the dots moving coherently varied across trials and the task on each trial was to say whether the overall direction of motion was upwards or downwards. Reaction time data were not recorded because an experimenter entered the participants' responses.

6.2.2. Results and discussion

6.2.2.1. Control group. For each participant, we calculated a coherence threshold: the minimum percentage of coherently moving dots necessary for correct discrimination of the direction of global motion with an accuracy of 75%. The data from three participants (one in the 20–29 and two in the 30–39 age groups) were excluded because their psychometric functions were unsystematic. For the remaining 27 controls, a one-way ANOVA with age as a between subjects factor revealed no effect of age ($p > .5$). The mean coherence threshold of 14.4% is like that of our previous study of visually normal 18- to 28-year-olds tested monocularly with similar stimuli (Ellemberg et al., 2002). z Scores were calculated using the mean and standard deviation for the thresholds of the control participants from all age groups.

Table 2
Prosopagnosic performance on the non-face tasks

Participant	Global form		Global motion	
	Threshold	z score	Threshold	z score
AS	11.70	0.14	10.19	0.63
BC	12.61	−0.04	13.97	0.19
DJ	13.64	−0.24	8.45	0.82
EN	9.24	0.63	7.66	0.92
HH	13.96	−0.31	13.69	0.22
JH	6.88	1.10	10.89	0.55
MT	13.03	−0.12	14.32	0.15
NM	14.78	−0.47	—	—

Percent signal thresholds and normalized thresholds for the measures of global form and global motion. All DP participants performed within the normal range on the non-face tasks.

6.2.2.2. Prosopagnosic group. Thresholds of the prosopagnosic participants were converted into z scores based on the mean and standard deviation of the entire control group. Overall the prosopagnosics performed normally at discriminating the direction of motion. Seven of the eight participants in the DP group had a threshold that was within normal limits. We do not report the threshold of one developmental case (NM), whose psychometric function was too unsystematic to calculate an accurate threshold (see Table 2). The results show normal function of dorsal visual stream in the DP cases, and that their face processing deficits are not due to a general visual impairment.

7. Face processing tasks

7.1. Face detection

The purpose of this task was to measure face detection based on sensitivity to first-order relations. Participants made face/nonface discriminations between Mooney faces and scrambled Mooney images (see Fig. 3).

7.1.1. Stimuli and procedure

The stimuli comprised thirteen black-and-white Mooney faces and a scrambled version of each of these faces. The stimuli were created using photographs of frontal views of female faces 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 were 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. 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. All stimuli were 10.2 cm wide and 15.2 cm high (5.8° × 8.7° visual degrees from the testing distance of 100 cm). The experiment was run using Cedrus Superlab software and participants signaled their responses via a game pad.

Participants were told that they would see a series of ambiguous stimuli—Mooney faces and scrambled Mooney faces—and that they would be asked to classify each stimulus as a face or non-face. The experimenter showed one practice trial with a Mooney face and one practice trial with a scrambled stimulus. Trials were initiated once the experimenter judged that the participant was fixating a central fixation cross. The fixation cross was then replaced by a stimulus, and the participant indicated using a game pad whether it was a face or a scrambled image. Each stimulus was presented for 100 ms, and the 24 trials were presented in a different random order to each participant. Mean accuracy and reaction time for correct trials were recorded.

7.1.2. Results and discussion

7.1.2.1. Control group. Consistent with previous findings from adults performing the identical task (Mondloch et al., 2003), participants in the control group were highly accurate at detecting faces in Mooney stimuli (mean = 91%). There was no effect of age on accuracy (ANOVA with Age group as a between subject factor, $p > .2$). The results support the notion that adults have a remarkable ability to detect faces rapidly based on their first-order relations, and can do so even when individual features are absent (e.g., Kanwisher et al., 1998; Moscovitch et al., 1997).

There was a significant effect of age on reaction time (ANOVA with Age group as a between subject factor, $p < .05$). Fisher's post-tests revealed that the main effect was due to significantly slower response times in the 60 to 69 year-old age group and the 70 to 75 year-old age group relative to the other ages ($ps < .01$). As a result, we separated the reaction time data from control participants into two age groups: a younger age group (20–59 years) and an older age group (60–75 years). The data from prosopagnosic participants were converted into *z* scores using the mean and standard deviation of the age-appropriate control subgroup (either younger or older). In a separate analysis using the entire control group to calculate *z* scores, the results for the prosopagnosic participants were identical to those reported below.

7.1.2.2. Prosopagnosic participants. All eight of the participants in the DP group were highly accurate and performed within the normal range at classifying Mooney images as faces or scrambled stimuli (mean accuracy = 91%; mean *z* score = 0.013; range = −1.1 to 0.6; see Table 3), and their reaction times were within normal limits. The DP group's normal performance cannot be due to a speed/accuracy trade-off or a ceiling effect. None of the DP individuals were 100% accurate, and only 2 of the 28 control participants obtained 100% accuracy. The results suggest that not all

Table 3
Prosopagnosic performance on measures of face detection and holistic face processing

Participant	Mooney stimuli		Composite face effect	
	%	*z* score	Difference score (%)	*z* score
AS	96	0.6	29	0.1
BC	92	0.1	15	−1.3
DJ	88	−0.4	12	−1.6
EN	96	0.6	4	**−2.4**
HH	83	−1.1	38	1.0
JH	96	0.6	19	−0.9
MT	88	−0.4	27	−0.1
NM	92	0.1	50	2.2

Numbers in bold (red) represent abnormal performance (*z* score < −1.65). Performance as indexed by reaction time showed that all participants were normal on the Mooney task. EN failed to show the composite effect as measured by both reaction time and accuracy. (For interpretation of the references to colour in this table legend, the reader is referred to the web version of this paper.)

types of configural processing are impaired in developmental prosopagnosia (for a review of the different types of configural processing see Maurer et al., 2002). That every DP participant performed within the normal range on both accuracy and reaction time on this task suggests they are normal both at detecting a face based on first-order relations and at the visual closure required to see an object in a Mooney stimulus. The results suggest that the impaired processing of face identity in DP is not caused by deficits in encoding the first-order relations of faces. These findings are consistent with a previous study of two cases of DP who show good performance on a speeded face detection task, but who are impaired on other measures of configural processing (de Gelder & Rouw, 2000a). Previously, a DP case (EP) has been reported who is impaired at making gender discriminations with Mooney face stimuli (Nunn et al., 2001). The discrepancy could represent a difference between cases and/or a difference between normal face detection and impaired gender discrimination with impoverished stimuli requiring visual closure.

Similar findings of spared face detection have been reported in another population with face processing deficits—individuals who were initially deprived of early visual experience due to congenital cataract (Mondloch et al., 2003). Despite years of compensatory visual input after treatment for the initial deprivation, these patients show deficits later in life on a variety of face processing tasks (Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002; Le Grand et al., 2003, 2001, 2004). However, they perform normally on the same face detection task as reported in the current study (Mondloch et al., 2003). Together, these results indicate that sensitivity to first-order facial relations is not sufficient for normal encoding of facial identity. We cannot conclude from these behavioural results, however, that the DP cases are recruiting the same neural mechanisms to detect that a stimulus is a face as are normal controls. That possibility is underscored by a previous report of a developmental case (YT) who has an abnormal N170—an EEG component that is believed to reflect the neural processing involved in face detection (e.g., Bentin et al., 1996).

7.2. Holistic face processing

To examine whether prosopagnosia affects the normal tendency to integrate facial features into a gestalt-like representation, the participants were tested on a measure of holistic processing, the Composite Face Task, in which it is difficult to recognize that the top halves of two faces are the same when they are aligned with different bottom halves (see Fig. 4).

7.2.1. Stimuli and procedure

A detailed description of the stimuli and procedure has been reported elsewhere (Le Grand et al., 2004). We created face composites by splitting face images in half horizontally, and then recombining the top and the bottom halves of different individuals. The top and bottom face segments were either properly aligned or misaligned by shifting the bottom half horizontally to the right. On each trial, participants judged whether the top halves of two sequentially presented faces were the same or different; the bottom halves were always different. Each face was presented for 200 ms. The two conditions were blocked, with the participants receiving the misaligned condition first and the aligned condition second ($n = 48$ trials per block). Previous work has shown that performance is not affected by the order in which the conditions are presented (Le Grand et al., 2004). The experiment was run using Cedrus Superlab software and participants signaled their responses via a game pad. Stimuli in the aligned condition were 9.8 cm wide and 14 cm high ($5.6° \times 8°$ of visual angle from a distance of 100 cm). Stimuli in the misaligned condition were 14.7 cm wide and 14 cm high ($8.4° \times 8°$ from a distance of 100 cm). Mean accuracy and correct response times for each condition were recorded.

7.2.2. Results and discussion

7.2.2.1. Control group. Consistent with previous results with this task in normal adults (e.g., Le Grand et al., 2004), the control group showed a large composite face effect. They were slower and much less accurate on same/aligned trials (mean = 780 ms and 63%) than on same/misaligned trials (mean = 616 ms and 91%).

An ANOVA on accuracy revealed significant main effects for Condition (aligned versus misaligned; $F(1,22) = 59.69$, $p < .001$), and Correct Response (same versus different; $F(1,22) = 20.13$, $p < .001$), but no significant effect of Age Group ($p > .2$). There was also a significant 2-way interaction between Condition and Correct Response ($F(1,22) = 26.24$, $p < .001$). The analysis of simple effects revealed a significant effect of Condition for *same* trials ($F(1,27) = 55.18$, $p < .001$), but not for *different* trials ($p > .1$).

An ANOVA on reaction time revealed a similar pattern of results. The effect of Age Group was not significant ($p > .2$), and there was a significant 2-way interaction between Condition and Correct Response ($F(1,22) = 18.75$, $p < .01$). The analysis of simple effects revealed a significant effect of Condition for *same* trials ($F(1,27) = 28.08$, $p < .001$), but not for *different* trials ($p > .1$).

This is the pattern predicted by holistic processing: in the aligned condition, processing the faces holistically creates the impression that the top halves are always different, despite the fact that on half the trials the two top halves are identical and only the bottom halves differ. When holistic processing is disrupted by misaligning the face halves, performance on same trials is significantly faster and more accurate.

The size of the composite face effect for each control participant was represented as the difference between the two critical conditions (same/misaligned trials minus same/aligned trials) using both accuracy and reaction time measures. Because there was no effect of age in the control group, the z score calculations for the prosopagnosic group were based on the mean and standard deviation of the entire control group's difference scores.

7.2.2.2. Prosopagnosic participants. Seven of the eight participants in the DP group showed the normal composite face effect (see Table 3). They were faster and much more accurate at recognizing that the top halves of two faces were the same when the faces were misaligned rather than aligned. The exception was EN who demonstrated an impairment in holistic processing by performing much better than controls on the critical condition where holistic processing impairs performance, same/aligned trials on both accuracy (EN = 92% vs. Controls = 63%: $z = -2.40$) and reaction time (EN = 437 ms vs. Controls = 683 ms: $z = -1.83$).

Despite the overall heterogeneity of DP cases, the current findings suggest that this subtype of prosopagnosia is not characterized by a deficit in holistic processing. Thus, like the findings for sensitivity to first-order relations, the impaired recognition of face identity in DP cannot be accounted for by a failure to process faces holistically. The discrepant results from one case, EN, indicate the variability within the DP group and establish that sensitivity to first-order relations (which were normal) and holistic processing (which was abnormal) likely involves different underlying mechanisms.

7.3. Discrimination of facial identity

To determine what types of information the DP participants are able to use for recognizing facial identity, we tested their ability to discriminate faces on the “Jane Task.” In this task, faces differ either in the individual features, the spacing of the features, or the global contour of the face (see Fig. 5).

7.3.1. Stimuli and procedure

A detailed description of the stimuli and procedure has been reported elsewhere (Mondloch et al., 2002). Briefly, a single face was modified to create three sets of face stimuli with four faces in each set (see Fig. 5). Faces in the featural set were created by replacing the eyes and mouth with the features of different females. Faces in the contour set were created by combining the internal portion of the original face with the outer contour of different females. Faces in the spacing set were created by moving the features in/out (eyes) and up/down (eyes; mouth) relative to the original face. Care was taken to ensure that the size of the spacing changes did not exceed normal limits and to avoid ceiling and floor effects. On each trial, participants judged whether two faces were the same or different. The first face appeared for 200 ms., and after a 300 ms. inter-stimulus interval, the second face appeared until the participant responded. The three blocks ($n = 30$ trials per block) were presented in the same order (spacing–featural–contour) to all participants; previous work has shown that performance is not affected by the order in which the face sets are presented(Mondloch et al., 2002). After the three blocks in which the stimuli were upright, each participant was tested on three blocks in which the stimuli were inverted. The experiment was run using Cedrus Superlab software and participants signaled their responses via a game pad. Mean accuracy and reaction time on correct trials were calculated for each condition.

7.3.2. Results and discussion

7.3.2.1. Control group. An ANOVA on accuracy with Face Set (featural, spacing, contour) and Orientation (upright, inverted) as the within-subject factors and Age Group as the between subject factor revealed significant main effects for Face Set ($p < .001$), and Orientation ($p < .01$), but no significant effect of Age Group. There was also an interaction of Face Set and Orientation ($p < .01$). Tukey's post-tests revealed that accuracy on all three face sets was affected by inversion. In the upright condition, performance on the featural set was significantly higher (mean = 90%) than on the spacing set (mean = 78%) and the contour set (mean = 77%) (both ps < .001). In the inverted orientation, all three face sets differed significantly from one another (featural > contour > spacing) (all ps < .001).

To measure the size of the inversion effect for each face set, we calculated the difference in accuracy between upright and inverted conditions. An ANOVA for difference scores revealed a significant main effect of Face Set ($p < .001$). Tukey's post-tests revealed that the size of the inversion effect was significantly larger for the spacing set (mean = 21%) than for the contour set (mean = 9%) or the featural set (mean = 9%) (both ps < .001). These results are consistent with previous findings that when stimulus sets are blocked and variations stay within natural limits, inversion affects the processing of second-order relations more than the processing of features (Freire et al., 2000; Le Grand et al., 2001; Mondloch et al., 2002).

An ANOVA on reaction time with Face Set (featural, spacing, contour) and Orientation (upright, inverted) as the within-subject factors and Age Group as the between subject factor revealed a significant main effect of face set ($F(2,22) = 13.87$, $p < .01$). No other effects (including Age Group) were significant (all ps > .1). Fisher tests revealed that participants were significantly slower on the spacing set compared to the featural and contour sets (both ps > .001). Examination of the individual means suggested that the effect was driven by much longer reaction times for the inverted spacing set (an index of the typical inversion effect).

7.3.2.2. Prosopagnosic participants. z Scores were based on the entire control group's mean and standard deviation (for both accuracy and reaction) for each upright condition, and the mean and standard deviation of the size of the inversion effect for accuracy for each face set. All DP participants had reaction times within normal limits on the upright face sets (mean $z = -0.34$; range = −1.28 to 1.34). Seven of the eight participants in the developmental group performed abnormally in differentiating faces from at least one of the three face sets (see Table 4). However, there was no uniformity in the pattern of abnormalities: three (AS, HH, JH) were impaired for the face set involving differences in the shape of internal features; five (AS, HH, JH, MT, NM) were impaired for the face set involving differences in the shape of the external contour, and four (BC, DJ, JH,

Table 4
Prosopagnosic performance on the measure of face identity

Participant	Upright						Difference score (Upright − inverted)					
	Spacing		Feature		Contour		Spacing		Feature		Contour	
	%	z score	%	z score	%	z score	%	z score	%	z score	%	z score
AS	70	−1.14	67	**−3.29**	63	**−2.33**	20	−0.10	4	−0.50	−7	−1.60
BC	73	−0.71	90	0	70	−1.17	−4	**−2.50**	3	−0.60	10	0.10
DJ	80	0.29	83	−1.0	80	0.50	−7	**−2.80**	3	−0.60	10	0.10
EN	73	−0.71	100	1.43	90	2.17	20	−0.10	7	−0.20	40	3.10
HH	67	−1.57	70	**−2.86**	63	**−2.33**	17	−0.40	10	0.10	−4	−1.30
JH	50	**−4.0**	77	**−1.86**	63	**−2.33**	−7	**−2.80**	4	−0.50	−4	−1.30
MT	67	−1.57	100	1.43	60	**−2.83**	7	−1.40	23	1.40	10	0.10
NM	60	**−2.57**	83	−1.0	63	**−2.33**	0	**−2.10**	2	−0.60	−4	−1.30

Numbers in bold (red) represent abnormal performance (z score < −1.65). All participants were within the normal limits for reaction time on the upright condition. (For interpretation of the references to colour in this table legend, the reader is referred to the web version of this paper.)

NM) were impaired for the face set involving differences in the spacing of features and/or showed an abnormally small inversion effect for this set. One participant in the DP group (EN) performed within normal limits on all three face sets.

A previous study of three individuals with DP has reported impairment in processing both the details of facial features (i.e., eye colour) and their spatial relations (Barton et al., 2003).[2] Our findings indicate that the pattern of impaired processing of internal features and their spatial relations is not general to all individuals with DP. In fact, only one case (JH) performed abnormally on both the featural and spacing sets. In addition, our findings document for the first time that individuals with DP are also often impaired at processing the external contour of the face. In fact, an impairment in contour processing was the most common deficit. This was an unexpected outcome because processing of the external contour appears to underlie the initial face processing of infants (Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grenet, 1995), because children as young as 6 years are as accurate as adults on the contour set used here (Mondloch et al., 2002), and because early visual deprivation from cataracts does not lead to impairments on this set (Le Grand et al., 2003).

The impairment on the contour set in the five participants in the DP group may be related to a perceptual deficit reported in acquired prosopagnosia in encoding smooth curved surfaces. The acquired case GA is unable to discriminate among curved lines and surfaces (Kosslyn, Hamilton, & Berstain, 1995). Similarly, the acquired case RP is severely impaired in discriminating among geometric objects with smoothly curved surfaces (Laeng & Caviness, 2001). In the present contour task, information about curvature may be useful for discriminating subtle differences in the shape of the external contour. Thus, problems in encoding the curvature of faces may be a factor contributing to both acquired and developmental prosopagnosia.

One DP case (EN) showed a pattern different from the other seven cases: she performed within normal limits on all three-face sets. She was also the single DP case with abnormal holistic processing as measured by the composite face task. Together, the results indicate that problems with processing facial identity can arise from (1) abnormal processing of facial contour, features or their spacing *or* (2) from the failure to integrate the features into a holistic Gestalt. Apparently spared holistic processing (true of seven DP cases), spared featural processing (true of five DP cases), and/or spared processing of spacing (second-order relations) (true of four DP cases) is not sufficient to support normal processing of facial identity. Nor does there appear to be a hierarchical relationship among these skills, such that an impairment in featural processing always leads to an impairment in processing of the spacing among features (see Section 9 for elaboration of this point). Of course, these conclusions apply to processing as measured by the specific tasks we used. Nevertheless, the results indicate considerable heterogeneity in the pattern of deficits among DP cases.

8. Facial attractiveness

To examine judgments of facial attractiveness in prosopagnosia, we tested the participants on two tasks: the Feature Placement task involved rating the attractiveness of faces with different heights of internal features (see Fig. 6A), and the Averaged Faces task involved rating the attractiveness of individual faces and computer-generated average faces (see Fig. 6B).

8.1. Feature placement

8.1.1. Stimuli and procedure

The stimuli and procedure were the same as in a previous study of adults (Geldart et al., 1999). Participants rated the attractiveness of 18 faces on a 5-point Likert scale (1 = Very Unattractive, 5 = Very Attractive). The 18 stimuli comprised three versions of six adult Caucasian female faces created by digitally repositioning the facial features of the six images to the average vertical location of features, 2 *SD*s lower, and 2 *SD*s higher than the population mean according to anthropometric measurements of facial proportions (Farkas, 1994). The stimuli were presented in a random order. Reaction time data were not recorded because an experimenter entered the participants' responses.

8.1.2. Results

To eliminate individual differences in overall judgments of attractiveness, we normalized the ratings using z scores that represented the variation in ratings across the three feature heights. First, for each participant we calculated the mean rating of attractiveness of each feature height and the overall mean and standard deviation of the ratings across all the faces. We then used these values to convert each participant's mean ratings for the six faces at each feature height to z scores, based on deviations from their individual overall mean.

8.1.2.1. Control group. An ANOVA of the z scores with height of features as a within subject factor and age group as a between subject factor revealed a significant main effect of height of features ($p < .01$), but no significant effect of age group or interaction ($p > .2$). Fisher's post tests revealed that the control participants judged the Average face set as significantly more attractive than both the Low ($p < .01$) and High face sets ($p < .01$), and the Low face set as significantly more attractive than the High face set ($p < .01$). The group data indicated that the faces with features at an average height were on average rated as 0.51 *SD*s more attractive than the others; the faces with high features were on average rated as 0.66 *SD*s less

[2] Because these cases also had abnormal sensitivity to contrast, luminance, and saturation, the deficits may have arisen from low-level visual deficits, rather than specific impairments in face processing.

Table 5
Performance of the prosopagnosics on measures of facial attractiveness and gender discrimination

Participant	Feature height attractiveness	Averaged faces		Sex of face	
		Male z score	Female z score	%	z score
AS	Normal	0.17	**−2.58**	95	−0.21
BC	Normal	1.76	0.02	94	−0.77
DJ	**Abnormal**	−0.76	−0.45	94	−0.77
EN	Normal	0.83	0.18	97	0.35
HH	**Abnormal**	−0.76	−0.37	95	−0.21
JH	**Abnormal**	**−1.98**	**−1.80**	92	−1.33
MT	**Abnormal**	3.07	1.05	98	0.90
NM	Normal	−0.76	−1.32	92	−1.33

Bold (red) represents abnormal performance. (For interpretation of the references to colour in this table legend, the reader is referred to the web version of this paper.)

attractive than the others; and the faces with low features were rated in between (0.14 *SD*s above the mean). This pattern is identical to that found in a previous study using the same stimuli with normal adults (Geldart et al., 1999). The normalized data from each prosopagnosic case were compared to this pattern.

8.1.2.2. Prospagnosic participants. Four of the participants in the DP group showed a normal pattern of rating the faces with features in an average location as most attractive and the faces with high features as least attractive. The remaining individuals with prosopagnosia did not show this pattern. Two cases (DJ and MT) had essentially flat functions, and two cases (HH and JH) rated faces with low features as equal to, or less attractive than, faces with high features (see Table 5).

8.2. Averaged faces

8.2.1. Stimuli and procedure

Participants rated the attractiveness of 34 colour photographs of faces on a 5-point Likert scale (1 = Very Unattractive, 5 = Very Attractive). Thirty-two stimuli were comprised of unaltered photographs of 16 men and 16 women between the ages of 18 and 30. The remaining two faces were computer-generated morphs: an averaged male face created by morphing all 16 males faces together and an average female face created by morphing all 16 female faces together (Rowland & Perett, 1995). Because the resulting morphs have unnaturally smooth skin and look as if they are in "soft-focus," a wavelet-based algorithm was used to calculate an average skin texture from the component faces with which to replace the unnaturally smooth skin (Tiddeman, Burt, & Perrett, 2001).

The faces were presented in a unique random order to each subject. Stimuli remained on the screen until the experimenter entered the participant's response, at which point the face was replaced immediately. Participants were instructed that if they recalled any face from earlier in the experiment they were to judge it as if they had not seen it before. Reaction time data were not recorded because an experimenter entered the participants' responses.

8.2.2. Results and discussion

For each participant, attractiveness ratings were collapsed into four values: the mean of the 16 individual males faces, the mean of the individual 16 female faces, the rating of the averaged male face, and the rating of the averaged female face.

8.2.2.1. Control group. Data from the control participants were analyzed with an ANOVA with sex of face and stimulus set (average versus individual) as within-subject factors and age of participant as a between-subject factor. Consistent with the large body of research demonstrating that average faces are rated as being more attractive than most of the individual faces used in their creation (Langlois & Roggman, 1990; Rhodes & Tremewan, 1996), the main effect of stimulus set was significant ($p < .01$), with average faces being rated significantly more attractive than individual faces. Both the main effects of age of subject and sex of face, and all interactions were non-significant ($ps > .05$). For comparison to prosopagnosic cases, we calculated z scores based on the difference in rating for the average and individual faces of each sex using the data of the entire control group.

8.2.2.2. Prosopagnosic participants. Most of the prosopagnosic participants performed normally in making judgments of attractiveness: six of the eight DP participants rated the average face as more attractive than the individual faces for both male and female faces and the magnitude of the effect was within normal limits (see Table 5). One case (JH) did not rate the average faces as more attractive for faces of either sex; a second developmental case (AS) did not rate the average face as more attractive for female faces (Table 5).

The results indicate that developmental prosopagnosia interferes with normal judgments of attractiveness. Five of the eight participants with DP failed to perform normally on at least one of the two measures of judgments of attractiveness. The findings do not show one-to-one correspondences between their impairments in face processing abilities and their performance on the attractiveness tasks. For example, of the four DP cases with impaired sensitivity to second-order relations, two preformed normally on both attractiveness tasks and two showed impairments. Of the four cases with normal sensitivity to second-order relations, three performed abnormally on at least one of the attractiveness tasks. There is a similar pattern of non-correspondence between normality of attractiveness judgments and normality of processing of facial identity based on internal features or external contour. We speculate that abnormalities in face processing during development prevented experience from having its normal influence on judgments of attractiveness and led to these deficits. It is also possible that in the absence of sensitivity to information upon which attractiveness judgments may normally be based, prosopagnosics may employ different compensatory strategies (whether implicitly or explicitly). Consequently, their ratings of attractiveness may not necessarily agree with normal judgments.

8.3. Sex of face

8.3.1. Stimuli and procedure

The stimuli were the same 32 photographs of 16 men and 16 women used for the judgments of attractiveness (see section above on attractiveness ratings for individual and average faces). After completing the judgments of attractiveness (see above), participants saw the same faces again and judged whether each face was male or female. Reaction time data were not recorded because an experimenter entered the participants' responses.

8.3.2. Results and discussion

When the percentage correct for the control group was analyzed in a one-way ANOVA with age as a between subjects factor, there was a significant main effect of age ($p < .05$). Fisher's post-tests revealed that the main effect was driven by the significantly worse performance of the participants in the 70 to 73 year age range compared to all other age groups ($ps < .05$). As the performance of the single DP participant in his seventies (HH) (95% accuracy) was better than controls of the same age (mean = 87.5%), we excluded the three control participants from that age range. When those participants were excluded, the effect of age was no longer significant ($p > .2$), and the remaining control data were collapsed across ages. The mean accuracy of the control participants was 95.3%. All prosopagnosic participants performed normally (mean accuracy = 94.6%; mean z score = −0.42, range: −1.31 to 0.90; see Table 5). Such normal accuracy in judging sex of face is consistent with previous findings for DP (e.g., Nunn et al., 2001).

9. General discussion

To examine perceptual encoding of different types of information used for face processing in individuals with developmental prosopagnosia, we administered a battery of eight tasks to a relatively large group of individuals with this condition ($n = 8$). Overall, the individuals with developmental prosopagnosia performed within the normal range on several of the face processing tasks including: detecting faces based on first-order relations, encoding faces holistically, and judging the sex of a face. They also performed well on the two non-face tasks (sensitivity to global form and global motion). The normal sensitivity to global form, global motion, and first-order relations of a face, as well as normal holistic face processing, suggest that their deficit in face recognition cannot be accounted for by a general impairment in visual processing or in integrating information about local features into a global percept.

Every DP case showed deficits on at least one aspect of face processing tested here, and some cases were impaired on several face perception tasks. The pattern of impairment in the DP group diverged from predictions based on differential rate of normal development for different face processing skills and from the pattern of impairment after early visual deprivation from cataracts. Half or more of the DP cases were impaired in discriminating individual faces based on the spacing of internal features (4 cases out of 8) and/or on the shape of the external contour (5 cases out of 8). Sensitivity to spacing information in faces takes many years to develop and is not yet adult-like at 14 years of age when measured by this task (Mondloch et al., 2002, 2003). On the other hand, sensitivity to the external contour of a face emerges very early in infancy (Pascalis et al., 1995), and is adult-like by six years of age on the same task used here (Mondloch et al., 2002, 2003). After visual deprivation during early infancy, accuracy for the spacing set that measures second-order relational processing is severely impaired but accuracy for the set measuring external contour processing is not (Le Grand et al., 2003, 2001). Similarly, the pattern of deficits and sparing in developmental prosopagnosia for non-face tasks cannot be predicted from other indices of plasticity. Individuals with DP all had normal sensitivity to global form and global motion whereas individuals deprived by cataracts during early infancy show marked deficits on both tasks (Ellemberg et al., 2002; Lewis et al., 2002).

The finding of normal holistic processing in seven of the eight DP cases suggests that they follow a different pattern of development from individuals deprived of early vision by cataract, who perform abnormally when tested with the same task (Le Grand et al., 2004). Note, however, that we cannot be sure that holistic processing in these seven cases was normal throughout development. Signs of holistic processing are evident as early as 3 months of age in normal infants (Cashon & Cohen, 2004): they react to the face as a composite of the internal features and external contour, rather than as a collection of independent elements. 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 et al., 2003). Normal asymptotic performance in the DP cases may reflect recovery from an initial deficit.

The pattern of impairments highlights the complexities underlying the development of face processing. The data suggest that normal sensitivity to first-order relations (as assessed with the Mooney face task) and normal holistic processing (as measured by the composite face effect) are not sufficient for the development of normal sensitivity to second-order relations. Each of the eight participants in the DP group performed normally at detecting faces based on first-order relations and only one participant showed an absence of holistic face processing. Yet four of the DP cases showed impaired sensitivity to second-order relations as measured by the Jane spacing set. The data also raise the possibility that normal holistic face processing may not be necessary for normal sensitivity to second-order relations: EN is impaired in holistic face processing, but has normal sensitivity to second-order relations as measured by the spacing set. While sensitivity to second-order relations and the ability to integrate the facial features are likely related, the current findings demonstrate that they are separable. Under normal conditions, face processing likely follows a hierarchical system in which the features of faces are first fused into a whole and subsequently the spatial relations of the features are processed. However, there may be circumstances when processing of second-order relations can occur in the absence of holistic processing (and vice versa). For example, adults are as accurate at processing the distance between the eyes when viewing the entire face (that is, the spacing of features in the context of the whole face) or the eye region only (that is, without the possibility of holistic processing) (Leder, Candrian, Huber, & Bruce, 2001). Thus, second-order relational processing consists at least in part of the processing of local relations between facial features. We speculate that sensitivity to the spacing information in a face can occur without integrating the features into a holistic representation and this could account for EN's pattern of results.

Although every DP case was impaired on at least one face processing task, their performance on tasks designed to tap specific skills (e.g., the ability to discriminate faces based on the spacing of features) could not predict the ability to recognize facial identity in the real world. Unlike DP cases, individuals deprived of early visual input by cataracts show a more consistent pattern of deficits in face processing tasks, and those deficits are more severe than those seen in participants with DP. Cataract patients perform normally on our face detection task (Mondloch et al., 2003), but have severe impairments in holistic processing (Le Grand et al., 2004) and sensitivity to second-order relations (Le Grand et al., 2003, 2001). Nonetheless, individuals deprived of early vision do not report any difficulty in recognizing familiar faces. This contrast raises questions about the nature of prosopagnosia. Developmental prosopagnosia may reflect deficits in forming a visual percept of a face and/or associating that percept with individual identity (see Bruce & Young's (1986) functional model of face processing). In contrast, the problem in patients treated for early deprivation from cataract may be limited to perceptual encoding.

The deficits seen in DP cases are not restricted to face discrimination and the ability to associate visual percepts with individual identity. Several individuals had deficits in judging facial attractiveness. We speculate that the abnormalities in judgments of attractiveness result from the abnormal experience that the participants with DP had with faces earlier in their development—because they processed those faces abnormally. This hypothesis is consistent with previous research demonstrating that the development of both the preference for faces with features in an average location and the preference for averaged faces may depend on normal experience (Cooper & Maurer, 2002; Geldart et al., 1999). This may also explain why individuals with prosopagnosia perform normally on non-identity face judgments along dimensions such as age, sex, and emotional expression (Bruce & Young, 1998). Unlike judgments of attractiveness, judgments of age, sex, and emotional expression can be based on explicit cues in the stimulus. Judgments of attractiveness may instead rely upon the implicit comparison of a target face to an internal face prototype, a cognitive representation of the mean of all faces experienced in the environment (Langlois & Roggman, 1990). The impairments in face processing that define DP may compromise the formation of this internal face prototype and subsequently lead to abnormal judgments of attractiveness.

10. Conclusion

Over the last few decades a variety of approaches have been employed to better understand face processing and the neural mechanisms underlying this ability. These include studies of normal development, the effects of early visual deprivation, impairment following brain damage (acquired prosopagnosia), and more recently developmental prosopagnosia. In the present study, we examined impairment of various face processing skills in developmental prosopagnosia. There was no systematic pattern of deficits found among the DP participants. Although every DP case showed impairment on at least one aspect of face processing tested here, their pattern of performance bore no clear relationship to the pattern during normal development or to the pattern after early visual deprivation. Performance on measures of specific face processing skills could not predict ease of face recognition in the real world. Our findings demonstrate the need for caution in generalizing from single cases of DP. It also illustrates the complexity of the face processing system, the intricate process by which humans become so adept at recognizing faces, and the variety of ways in which normal face processing can go awry in a minority of individuals.

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References

Ariel, R., & Sadeh, M. (1996). Congenital visual agnosia and prosopagnosia in a child: A case report. *Cortex, 32*, 221–240.

Avidan, G., Hasson, U., Malach, R., & Behrmann, M. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 2. Functional neuroimaging findings. *Journal of Cognitive Neuroscience, 17*, 1150–1167.

Barton, J. J. S., Cherkasova, M. V., Press, D. Z., Intriligator, J. M., & O'Connor, M. (2003). Developmental prosopagnosia: A study of three patients. *Brain and Cognition, 51*, 12–30.

Behrmann, M., & Avidan, G. (2005). Congenital prosopagnosia: Face-blind from birth. *Trends in Cognitive Sciences, 9*, 180–187.

Behrmann, M., Avidan, G., Marotta, J. J., & Kimchi, R. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 1. Behavioral findings. *Journal of Cognitive Neuroscience, 17*, 1130–1149.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*, 551–565.

Bentin, S., Deouell, L. Y., & Soroker, N. (1999). Selective visual streaming in face recognition: Evidence from developmental prosopagnosia. *Neuroreport, 10*, 827–832.

Benton, A. L., Sivan, A. B., Hamsher, K., Varney, N. R., & Spreen, O. (1983). *Contribution to neuropsychological assessment*. New York: Oxford University Press.

Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology, 77*, 305–327.

Bruce, V., & Young, A. W. (1998). *In the eye of the beholder: The science of face perception*. London: Oxford University Press.

Carey, S. (1992). Becoming a face expert. In A. Cowey & V. Bruce (Eds.), *Processing the face image* (pp. 95–103). New York: Oxford University Press.

Carey, S., & Diamond, R. (1994). Are faces perceived as configurations more by adults than by children? *Visual Cognition, 1*, 253–274.

Cashon, C. H., & Cohen, L. B. (2004). Beyond U-shaped development in infants' processing of faces: An information-processing account. *Journal of Cognition and Development, 5*, 59–80.

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

Cooper, P. A., & Maurer, D. (2002). Influence of visual familiarity on developmental changes in judgments of attractiveness. In *Annual meeting of the International Society for the Study of Behavioural Development, August, Ottawa, Canada*.

Damasio, A., Damasio, H., & van Hoessen, G. (1982). Prosopagnosia: Anatomical basis and behavioral mechanisms. *Neurology, 32*, 331–341.

de Gelder, B., & Rouw, R. (2000a). Configural face processes in acquired and developmental prosopagnosia: Evidence for two separate face systems? *Neuroreport, 11*, 3145–3150.

de Gelder, B., & Rouw, R. (2000b). Paradoxical configuration effects for faces and objects in prosopagnosia. *Neuropsychologia, 38*, 1271–1279.

de Gelder, B., & Stekelenburg, J. J. (2005). Naso-temporal asymmetry for the N170 for processing faces in normal viewers but not in developmental prosopagnosia. *Neuroscience Letters, 376*, 40–45.

DeGutis, J. M., Sagiv, N., D'Esposito, M., & Robertson, L. (2004). The fusiform face area in prosopagnosia: Inefficient interactions during attention and working memory tasks. In *11th Annual meeting of the Cognitive Neuroscience Society, April, San Francisco*.

de Haan, E. H., & Campbell, R. (1991). A fifteen year follow-up of a case of developmental prosopagnosia. *Cortex, 27*, 489–509.

Delvenne, J.-F., Seron, X., Coyette, F., & Rossion, B. (2004). Evidence for perceptual deficits in associative visual (prosop)agnosia: A single-case study. *Neuropsychologia, 42*, 597–612.

Diamond, R., & Carey, S. (1986). Why faces are and not are special: An effect of expertise. *Journal of Experimental Psychology: General, 115*, 107–117.

Duchaine, B. (2000). Developmental prosopagnosia with normal configural processing. *Neuroreport, 11*, 79–83.

Duchaine, B., & Nakayama, K. (2004). Developmental prosopagnosia and the Benton Facial Recognition Test. *Neurology, 62*, 1219–1220.

Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience, 17*, 249–261.

Duchaine, B., & Weidenfeld, A. (2003). An evaluation of two commonly used tests of unfamiliar face recognition. *Neuropsychologia, 41*, 713–720.

Duchaine, B., Le Grand, R., Nakayama, K., & Maurer, D. (2003). Neuropsychological dissociations in family members with face recognition impairments. In *10th Annual meeting of the Cognitive Neuroscience Society, April, New York*.

Duchaine, B., Nieminen-von Wendt, T., New, J., & Kulomaki, T. (2003). Dissociations of visual recognition in a developmental prosopagnosic: Evidence for separate developmental processes. *Neurocase, 9*, 380–389.

Duchaine, B., Parker, H., & Nakayama, K. (2003). Normal emotion recognition in a prosopagnosic. *Perception, 32*, 827–838.

Ellemberg, D., Lewis, T. L., Maurer, D., Brar, S., & Brent, H. P. (2002). Better perception of global motion after monocular than after binocular deprivation. *Vision Research, 42*, 169–179.

Farkas, L. G. (1994). *Anthropometry of the head and face in medicine*. New York: Elsevier.

Freire, A., & Lee, K. (2001). Face recognition in 4- to 7-year-olds: Processing of configural, featural, and paraphernalia information. *Journal of Experimental Child Psychology, 80*, 347–371.

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

Gallant, J. L., Connor, C. E., Rakshit, S., Lewis, J. W., & Van Essen, D. C. (1996). Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey. *Journal of Neurophysiology, 76*, 2718–2739.

Geldart, S. (2003). Experiential influences on the development of face perception. Doctoral Thesis, McMaster University, Canada.

Geldart, S., Maurer, D., & Henderson, H. (1999). Effects of the height of internal features of faces on adults' aesthetic ratings and 5-month-olds' looking times. *Perception, 28*, 839–850.

Geldart, S., Mondloch, C. J., Maurer, D., de Schonen, & Brent, H. P. (2002). The effect of early visual deprivation on the development of face processing. *Developmental Science, 5*, 490–501.

Glass, L. (1969). Moire effect from random dots. *Nature, 223*, 578–580.

Hadjikhani, N., & de Gelder, B. (2002). Neural basis of prosopagnosia: An fMRI study. *Human Brain Mapping, 16*, 176–183.

Hasson, U., Avidan, G., Deouell, L., Bentin, S., & Malach, R. (2003). Face-selective activation in a congenital prosopagnosic subject. *Journal of Cognitive Neuroscience, 15*, 419–431.

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

Jones, R. D., & Tranel, D. (2001). Developmental prosopagnosia in a child with superior intellect. *Journal of Clinical and Experimental Neuropsychology, 23*, 265–273.

Kanwisher, N., McDermott, J., & Chun, M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for the perception of faces. *Journal of Neuroscience, 17*, 4302–4311.

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

Kobatake, E., & Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *Journal of Neurophysiology, 71*, 2269–2280.

Kosslyn, S. M., Hamilton, S. E., & Berstain, J. H. (1995). The perception of curvature can be selectively disrupted in prosopagnosia. *Brain and Cognition, 27*, 36–58.

Kress, T., & Daum, I. (2003a). Developmental prosopagnosia: A review. *Behavioural Neurology, 14*, 109–121.

Kress, T., & Daum, I. (2003b). Event-related potentials reflect impaired face recognition in patients with congenital prosopagnosia. *Neuroscience Letters, 352*, 133–136.

Laeng, B., & Caviness, V. S. (2001). Prosopagnosia as a deficit in encoding curved surface. *Journal of Cognitive Neuroscience, 13*, 556–576.

Langlois, J. H., & Roggman, L. A. (1990). Attractive faces are only average. *Psychological Science, 1*, 115–121.
Langlois, J. H., Roggman, L. A., Casey, R. J., Ritter, J. M., Rieser-Danner, L. A., & Jenkins, V. Y. (1987). Infant preferences for attractive faces: Rudiments of a stereotype? *Developmental Psychology, 23*, 363–369.
Leder, H., & Bruce, V. (2000). When inverted faces are recognized: The role of configural information in face recognition. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 53A*, 513–536.
Leder, H., Candrian, G., Huber, O., & Bruce, V. (2001). Configural features in the context of upright and inverted faces. *Perception, 30*, 73–83.
Le Grand, R., Maurer, D., Mondloch, C., Duchaine, B., Sagiv, N., & de Gelder, B. (2003). What types of configural processing are impaired in prosopagnosia? (Abstract).. *Journal of Vision, 3*(9), 827a.
Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Early visual experience and face processing. *Nature, 410*, 890 Correction: (2001). *Nature, 412*, 786.
Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2003). Expert face processing requires visual input to the right hemisphere during infancy. *Nature Neuroscience, 10*, 1108–1112.
Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Science, 15*, 762–768.
Lewis, M. B., & Ellis, H. D. (2003). How we detect a face: A survey of psychological evidence. *International Journal of Imaging Systems and Technology, 13*, 3–7.
Lewis, T. L., Ellemberg, D., Maurer, D., Dirks, M., Wilkinson, F., & Wilson, H. R. (2004). A window on the normal development of sensitivity to global form in Glass patterns. *Perception, 33*, 409–418.
Lewis, T. L., Ellemberg, D., Maurer, D., Wilkinson, F., Wilson, H. R., Dirks, M., et al. (2002). Sensitivity to global form in Glass patterns after early visual deprivation in humans. *Vision Research, 42*, 939–948.
Little, A. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2003). Investigating an imprinting-like phenomenon in humans: Partners and opposite-sex parent have similar hair and eye colour. *Evolution and Human Behaviour, 24*, 43–51.
Maunsell, J. H., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey: I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology, 49*, 1127–1147.
Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Science, 6*, 255–260.
McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 9*, 605–610.
McConachie, H. R. (1976). Developmental prosopagnosia: A single case report. *Cortex, 12*, 76–82.
Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception, 31*, 553–566.
Mondloch, C. J., Pathman, T., Le Grand, R., & Maurer, D. (2003). Can children's insensitivity to spacing among facial features be attributed to immaturity in holistic processing? In *Annual meeting of the Brain, Behavior and Cognitive Sciences Society, July, Hamilton, Ontario Canada*.
Mondloch, C. J., Le Grand, R., & Maurer, D. (2003). Early visual experience is necessary for the development of some—but not all—aspects of face processing. In O. Pascalis & A. Slater (Eds.), *The development of face processing in infancy and early childhood: Current perspectives* (pp. 99–117). New York: Nova Science Publishers.
Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience, 3*, 1322–1328.
Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience, 9*, 555–604.
Newell, L., Strauss, M., Best, C., & Gastgeb, H. (2004). Gender categorization abilities of preschoolers: The effects of typicality and hair. In *Annual Meeting of the International Society on Infant Studies, April, Chicago*.
Newsome, W. T., & Paré, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience, 8*, 2201–2211.
Nunn, J. A., Postma, P., & Pearson, R. (2001). Developmental prosopagnosia: Should it be taken at face value? *Neurocase, 7*, 15–27.
Pascalis, O., de Schonen, S., Morton, J., Deruelle, C., & Fabre-Grenet, M. (1995). Mother's face recognition by neonates: A replication and an extension. *Infant Behavior and Development, 18*, 79–85.
Pasupathy, A., & Connor, C. E. (1999). Responses to contour features in macaque area V4. *Journal of Neurophysiology, 82*, 2490–2502.
Perrett, D. I., May, K. A., & Yoshikawa, S. (1994). Facial shape and judgments of female attractiveness. *Nature, 368*, 239–242.
Perrett, D. I., Penton-Voak, I. S., Little, A. C., Tidderman, B. P., Burt, D. M., Schmidt, N., et al. (2002). Facial attractiveness judgments reflect learning of parental age characteristics. *Proceeding of the Royal Society of London B, 269*, 873–880.
Quick, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik, 16*, 65–67.
Rhodes, G., Brake, S., & Atkinson, A. P. (1993). What's lost in inverted faces? *Cognition, 47*, 25–57.
Rhodes, G., Geddes, K., Jeffery, L., Dziurawiec, S., & Clark, A. (2002). Are average and symmetric faces attractive to infants? Discrimination and looking preferences. *Perception, 31*, 315–321.
Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W. G., & Nakayama, K. (2003). Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychological Science, 14*, 558–566.
Rhodes, G., Lee, K., Palermo, R., Weiss, M., Yoshikawa, S., Clissa, P., et al. (2005). Attractiveness of own-race, other-race, and mixed-race faces. *Perception, 34*, 319–340.
Rhodes, G., & Tremewan, T. (1996). Averageness, exaggeration, and facial attractiveness. *Psychological Science, 7*, 105–110.
Riddoch, M. J., & Humphreys, G. W. (1993). *Birmingham object recognition battery*. Sussex: Lawrence Erlbaum.
Rowland, D. A., & Perett, D. I. (1995). Manipulating facial appearance through shape and color. *IEEE Computer Graphics and Applications, 15*, 70–76.
Rubenstein, A. J., Kalakanis, L., & Langlois, J. H. (1999). Infant preferences for attractive faces: A cognitive explanation. *Developmental Psychology, 35*, 848–855.
Sagiv, N., Barnes, L., Swick, D., & Robertson, L. C. (2001). The neurophysiology of face blindness. In *8th Annual meeting of the Cognitive Neuroscience Society, March 25–27, New York*.
Sergent, J., & Villemure, J. G. (1989). Prosopagnosia in a right hemispherectomized patient. *Brain, 112*, 975–995.
Slater, A., Von der Schulenburg, C., Brown, E., Badenoch, M., Butterworth, G., Parsons, S., et al. (1998). Newborn infants prefer attractive faces. *Infant Behaviour and Development, 21*, 345–354.
Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 160 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Perception and Performance, 6*, 174–215.
Temple, C. M. (1992). Developmental memory impairment: Faces and patterns. In R. Campbell (Ed.), *Mental lives: Case studies of cognition*. Oxford: Blackwell.
Tiddeman, B., Burt, D., & Perrett, D. I. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications, 21*, 42–50.
Warrington, E. K. (1984). *Recognition memory test*. Windsor, UK: NFER-Nelson.
Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature, 428*, 557–561.

Weibull, W. A. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics, 18*, 292–297.

Wilkinson, F., James, T. W., Wilson, H. R., Gati, J. S., Menon, R. S., & Goodale, M. S. (2000). An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. *Current Biology, 10*, 455–458.

Wilson, H. R. (1999). Non-fourier cortical processes. In P. S. Ulinski (Ed.), *Cerebral cortex* (Vol. 13, pp. 445–477). New York: Plenum Publishers.

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

Yovel, G., & Kanwisher, N. (2004). Face perception: Domain specific, not process specific. *Neuron, 44*, 889–898.