



PAPER

Impaired face detection may explain some but not all cases of developmental prosopagnosia

Kirsten A. Dalrymple¹ and Brad Duchaine²

1. Institute of Child Development, University of Minnesota, USA

2. Department of Psychological and Brain Sciences, Dartmouth College, USA

Abstract

Developmental prosopagnosia (DP) is defined by severe face recognition difficulties due to the failure to develop the visual mechanisms for processing faces. The two-process theory of face recognition (Morton & Johnson, 1991) implies that DP could result from a failure of an innate face detection system; this failure could prevent an individual from then tuning higher-level processes for face recognition (Johnson, 2005). Work with adults indicates that some individuals with DP have normal face detection whereas others are impaired. However, face detection has not been addressed in children with DP, even though their results may be especially informative because they have had less opportunity to develop strategies that could mask detection deficits. We tested the face detection abilities of seven children with DP. Four were impaired at face detection to some degree (i.e. abnormally slow, or failed to find faces) while the remaining three children had normal face detection. Hence, the cases with impaired detection are consistent with the two-process account suggesting that DP could result from a failure of face detection. However, the cases with normal detection implicate a higher-level origin. The dissociation between normal face detection and impaired identity perception also indicates that these abilities depend on different neurocognitive processes.

Research highlights

- Individuals with developmental prosopagnosia (DP) have impaired face recognition.
- Impaired face recognition could result from an impaired face detection system.
- We confirmed DP in seven children and tested them with two face detection tasks.
- Four of the seven children were impaired at face detection in some way.
- Poor face detection may explain some cases of DP. Others have higher-level origins.

Introduction

Face processing is an important part of our daily lives that provides our primary means to identify other

individuals so we can form and maintain social relationships. Because of its importance, the development of face processing has received extensive attention. One of the leading developmental theories, the two-process theory of face recognition (Morton & Johnson, 1991), suggests that we are born with an innate tendency to orient to face-like stimuli and that this face orienting system (known as ‘CONSPEC’) causes a second, category-general learning-based system (‘CONLERN’) to develop specialized procedures for face individuation. Both systems are necessary for the development of normal face recognition. Developmentally, the theory posits that face-selective areas in the brain become specialized for processing faces because preferential attention to faces early in life (via CONSPEC) provides input to cortical visual pathways that activate certain cortical areas, making these areas sensitive to faces. Further input strengthens these connections (CONLERN) leading to increased proficiency with face stimuli (Johnson, 2005).

Address for correspondence: Kirsten A. Dalrymple, Institute of Child Development, University of Minnesota, 51 East River Parkway, Minneapolis, MN, USA; e-mail: kad@umn.edu

However, face recognition does not always develop normally, leaving some individuals without this proficiency for faces. Developmental prosopagnosia (DP), sometimes called congenital prosopagnosia, is defined by severe face recognition difficulties due to the failure to develop the visual mechanisms necessary for processing faces (Behrmann, Avidan, Marotta & Kimchi, 2005; Susilo & Duchaine, 2013). However, little is known about why those mechanisms fail to develop, and what stage or stages of face processing are affected (Dalrymple, Corrow, Yonas & Duchaine, 2012a). One straightforward extension of the two-process theory of face recognition is that an impairment early in life affects the ability to rapidly discriminate faces from non-face objects and direct attention to faces, and this impairment may lead to DP. Specifically, orienting to faces and treating them as a special class of object is critical to acquiring the experience necessary for normal recognition, and a failure to do so may result in DP. Similarly, Tsao and Livingstone (2008) suggest that prosopagnosia can be explained by a failure to detect faces: faces are not being treated as a special class of object and are therefore not being processed by a specialized face system. Comparable suggestions have been made to explain face processing deficits in autism spectrum disorders: Schultz (2005) proposed a model where perceptual biases for faces at birth lead to enhanced salience of faces, which leads to increased experience with faces and improved face perception abilities.

Individuals with DP provide the perfect opportunity to test the prediction that impaired face recognition results from impaired face detection. Several reports suggest that face detection is normal in DP, but many of the tests used were categorization tasks (e.g. is this a face or a non-face?) (de Gelder & Rouw, 2000; Duchaine, Nieminen-von Wendt, New & Kulomaki, 2003a; Duchaine, Yovel, Butterworth & Nakayama, 2006; Le Grand, Cooper, Mondloch, Lewis, Sagiv *et al.*, 2006) rather than search tasks that would more closely simulate finding faces in everyday life (Lewis & Ellis, 2003). To address this issue, Garrido, Duchaine and Nakayama (2008) tested a group of adults with DP on two detection tasks that were search-like in nature. One task required participants to find faces among non-faces (objects, scenes, etc.), and another required participants to find two-tone faces among scrambled face parts. Like controls, the individuals with DP showed normal inversion effects on the two tasks, having faster reaction times in upright compared to inverted trials. However, as a group, the DPs were slower than controls at finding the faces in both tasks, suggesting impaired face detection. At an individual level, three of the DPs had normal performance on both tasks, indicating that face detection is

impaired in some, but not all, adults with DP. Only one previous study has assessed face detection in a child with DP, reporting normal performance compared to age-matched controls (Schmalzl, Palermo, Green, Brunson & Coltheart, 2008).

In the present study, we tested a group of children with DP with modified versions of the tasks used by Garrido *et al.* (2008) to test face detection. Little is known about DP in childhood (Dalrymple *et al.*, 2012a), and it is not clear that findings from studies with adult DPs would be replicated in a child sample. For example, a recent study on face perception and face memory in children and adults with DP found that all of the children had impaired face perception and face memory, yet more than half of the adults were normal at face perception despite impaired face memory, indicating key differences in how DP manifests itself in the two age groups (Dalrymple, Garrido & Duchaine, 2014). In addition, studying DP in children is particularly important because unlike adults, children have had less opportunity to develop compensatory strategies that may mask their deficits and they have had less time for neuronal reorganization that may occur when the face processing system is compromised. Given the heterogeneity of DP (Dalrymple *et al.*, 2014; Duchaine & Nakayama, 2005; Harris, Duchaine & Nakayama, 2005; Le Grand *et al.*, 2006) and the findings that some, but not all, adult DPs are impaired on tasks of face detection (Garrido *et al.*, 2008), we tested a group of children with DP and analyzed the data at a single subject level. If children with DP are impaired at face detection, this provides support for the hypothesis that impaired face recognition can result from a failure to detect faces. However, normal face detection in children with DP would indicate that other developmental disturbances led to their impaired face recognition.

Method

Participants

Potential participants were selected from a group of children whose parents reported that their child experiences face recognition difficulties. These parents contacted us through our website, www.faceblind.org. Families who expressed an interest in participating in research completed a preliminary screening questionnaire, which was used to determine whether the children met our inclusion criteria: children were at least 7 years of age, had normal or corrected-to-normal vision, no history of brain trauma, and no diagnosis of autism or Asperger's Syndrome.

The parents of children who met our inclusion criteria were contacted by email to ask if they were interested in having their child participate in an in-home assessment of face recognition. A member of the research team (KAD) traveled to the family homes. Parents and children first signed permission and assent forms to confirm their willingness to volunteer in the study. The tests reported here were part of a larger testing session that included other face processing tasks such as holistic processing, attentional cuing, expression recognition, and gender discrimination, though the exact combination of tasks varied between children. The entire testing session took between 4 and 5 hours depending on the child and the number and duration of breaks. Children were generally motivated by the fact that they were helping with 'an important science project' and working with a 'special visitor who traveled a long distance to see them'. Some children missed a day of school to participate in the study, which also served as motivation. Children were compensated for their participation. This study was approved by the Committee for the Protection of Human Subjects at Dartmouth College.

Assessment

Participating children ($n = 7$, two females) were Caucasian and between 8- and 12-years-old (mean = 9.9, $SD = 1.4$). To avoid possible 'other-race effects' the face stimuli used in the assessments were also Caucasian. Children were assessed for general cognitive functioning (Wechsler Abbreviated Scale of Intelligence – II (WASI–II)), and with two tests of face memory (Cambridge Face Memory Test – Kids (Dalrymple, Gomez & Duchaine, 2012b); Old/New Faces), one test of face perception (Dartmouth Face Perception Test), and two tests of face detection (Faces Among Non-Faces, Faces Among Face Parts). We will first describe and present results from the tests of face memory and perception, and then tests of face detection. Example trials from each test are in Figure 1. The data from each child with DP were compared to data from between 14 and 20 typically developing children of the same age. Accuracy means and standard deviations from typically developing children are provided in Table 1. Data from children with DP can be found in Table 2 and Figure 2.

Analysis

We used two methods to compare the children's scores on each task to scores from age-matched control participants. First, we identified accuracy scores that were more than two standard deviations below the control mean. We then ran Crawford, Garthwaite and

Howell (2009) modified t -tests using SINGLIMS software (Crawford *et al.*, 2009; Sokal & Rohlf, 1995) to compare each child to their age-matched control group. This modified t -test is a more conservative measure of differences between single subjects and control groups with small sample sizes. All t -tests were two-tailed and p -values were compared to $\alpha = 0.05$.

Note that because of the variability in control means and SD s as a function of age, it can be misleading to compare the magnitude of the z -scores of DPs of different ages. For reference, the means and standard deviations from typically developing children that were used to calculate the z -scores are provided in Table 1.

Face memory and face perception

Two tests of face memory and one test of face perception were used to establish that the children are prosopagnosic. These tasks are described briefly here, but are presented in more detail in Dalrymple *et al.* (2014).

The Cambridge Face Memory Test – Kids is based on the adult version of the task (CFMT; Duchaine & Nakayama, 2006), but uses faces of children instead of adults. The task has three sections: (1) target faces are learned and participants are immediately asked to pick the most recently learned target face from a choice of three faces before learning the next target; (2) participants review all targets together and are then asked to identify any of those targets in a series of test items consisting of three choice faces; and (3) a final section that is identical to the second section, but test items are partially masked by visual noise. Children 10 years of age and older learn six target faces and children 9 years of age and younger learn four targets.

The Old/New Faces task consists of 10 target and 30 distractor faces. Participants are asked to memorize the target faces, which are presented one at a time, and then repeated in the same order. In the test phase, trials consist of a target and a similar-looking distractor appearing simultaneously on the screen. Participants must press a key to indicate which face is one of the target faces.

The Dartmouth Face Perception Test presents a face at the top of the screen facing 30° to the viewer's left. Below the target face are three choice faces (frontal views). Choice faces were created by morphing targets with a distractor face of the same gender and therefore vary systematically in their similarity to the target. Participants are asked to choose the face that looks the most like the target face. Because target and choice faces remain on the screen until a response is given, the memory demands of the task are minimal. Chance-level performance for this test is 33.3%.

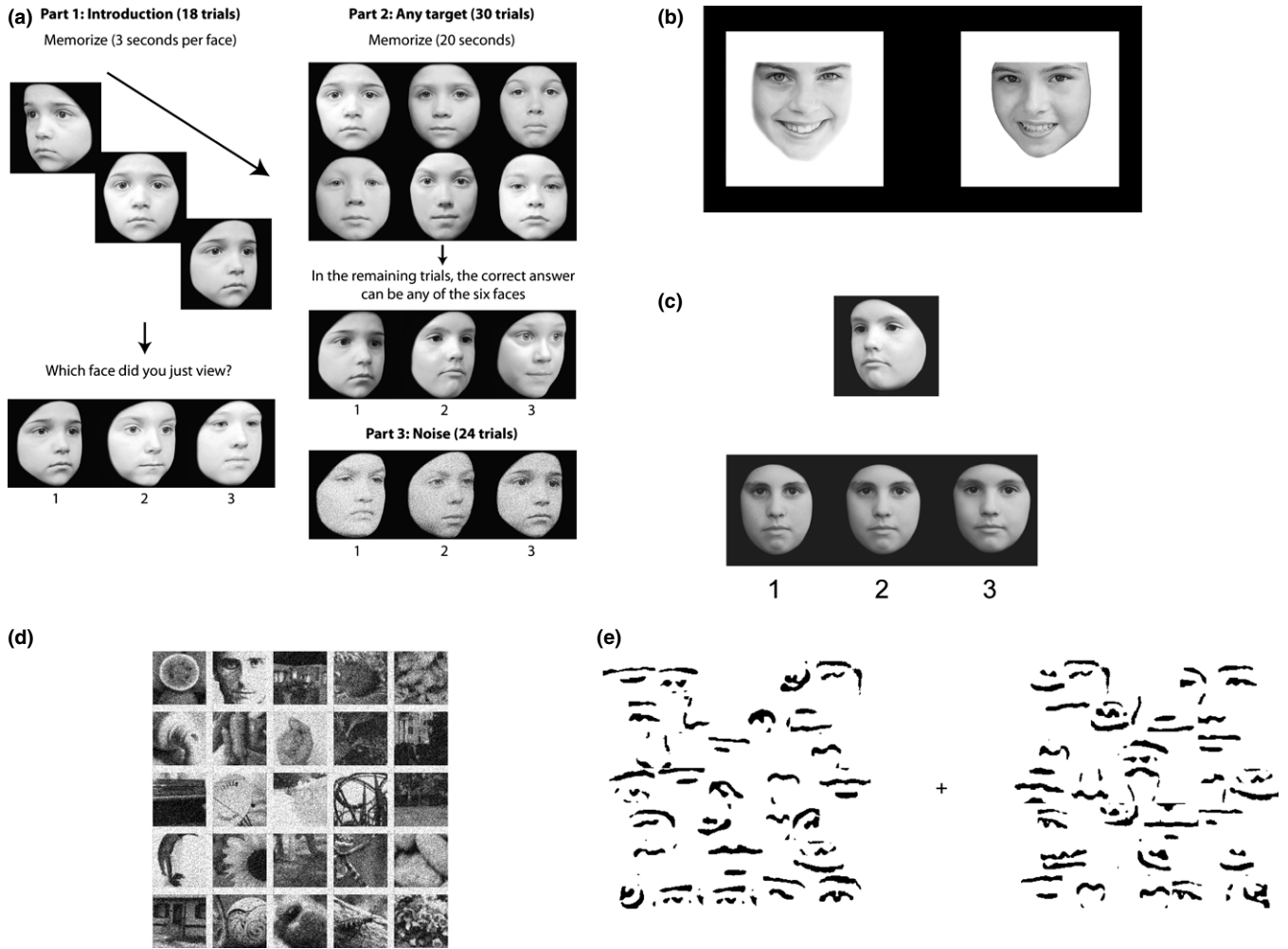


Figure 1 Examples from children's tasks: (a) Cambridge Face Memory Test- Kids (CFMT-K), (b) Old/New Faces, (c) the Dartmouth Face Perception Test (DFPT), (d) Faces Among Non-Faces, and (e) Faces Among Face Parts.

Object memory

Two tests of object memory were used to determine whether the children's deficits are face-specific or domain-general (i.e. also included non-face objects). The Cambridge Bicycle Memory Test is matched in format and difficulty to the CFMT-Kids, but uses bicycles instead of faces. Similarly, the Old/New Flowers task is matched in format and difficulty to the Old/New Faces task, but uses flowers instead of faces.

Results

Accuracy, *t*-values, and *p*-values are presented in Table 2. Data are plotted as *z*-scores in Figure 2. All but one child was 2 standard deviations (*SD*) below the control mean for the CFMT-K (BG: $z = -1.48$) and all but one was 2 *SD* below the control mean on the Old/New

memory test (HPH: $z = -0.44$). Modified *t*-tests (Crawford *et al.*, 2009; Sokal & Rohlf, 1995) determined that five of the children were significantly below the control mean on the CFMT-K (all except AO: $p = .062$; BG: $p = .173$). Similarly, five of the children were significantly below the control mean on the Old/New test (all except AO: $p = .065$; HPH: $p = .677$).

All seven children were more than 2 *SD* below the control mean on the Dartmouth Face Perception Test. These results were largely in line with results from the modified *t*-tests (Crawford *et al.*, 2009; Sokal & Rohlf, 1995), which identified six of the seven children as scoring significantly below the control mean (all except BG: $p = .068$).

Note that floor effects in the younger control groups make it difficult to detect scores that were significantly below the mean. Therefore, although the younger DPs

Table 1 Mean scores (%) by age for typically developing children on tests of face memory, face perception, and face detection

Test	Chance	Age (years)						
		7	8	9	10	11	12	
Object Memory								
CBMT ^a	33%	72.5 (16.2) <i>n</i> = 15	80.2 (9.7) <i>n</i> = 16	79.9 (14.8) <i>n</i> = 15	68.0 (9.4) <i>n</i> = 15	71.6 (9.6) <i>n</i> = 16	75.6 (8.7) <i>n</i> = 16	
Old New Flowers	50%	81.7 (9.8) <i>n</i> = 14	85.0 (8.2) <i>n</i> = 16	87.6 (14.4) <i>n</i> = 14	88.4 (8.0) <i>n</i> = 15	89.6 (6.9) <i>n</i> = 15	90.5 (8.6) <i>n</i> = 15	
Face Memory								
CFMT-Kids ^a	33%	59.0 (18.5) <i>n</i> = 15	70.2 (16.1) <i>n</i> = 20	80.2 (12.0) <i>n</i> = 16	84.7 (7.2) <i>n</i> = 15	78.4 (13.7) <i>n</i> = 15	79.4 (8.6) <i>n</i> = 14	
Old New Faces	50%	72.3 (13.5) <i>n</i> = 15	77.8 (10.2) <i>n</i> = 15	81.5 (11.0) <i>n</i> = 17	88.7 (6.3) <i>n</i> = 15	87.0 (8.8) <i>n</i> = 16	90.0 (5.9) <i>n</i> = 15	
Face Perception								
DFPT	33%	72.7 (10.3) <i>n</i> = 14	75.8 (16.2) <i>n</i> = 15	82.2 (13.3) <i>n</i> = 15	84.8 (7.7) <i>n</i> = 15	88.1 (7.9) <i>n</i> = 16	89.8 (6.4) <i>n</i> = 14	
Face Detection								
Faces Among Non-Faces	% RT(ms)	50%	93.2 (6.4) 1661.0 (362.1) <i>n</i> = 14	93.9 (4.2) 1619.5 (400.6) <i>n</i> = 15	96.2 (3.1) 1508.5 (283.7) <i>n</i> = 15	97.8 (2.2) 1275.2 (317.1) <i>n</i> = 15	97.6 (3.3) 1204.5 (237.5) <i>n</i> = 15	98.2 (2.6) 1001.0 (136.4) <i>n</i> = 15
Faces Among Face Parts	50%	65.8 (13.8) <i>n</i> = 14	67.7 (9.0) <i>n</i> = 16	77.6 (8.7) <i>n</i> = 14	77.7 (11.9) <i>n</i> = 19	83.1 (9.9) <i>n</i> = 17	81.1 (12.7) <i>n</i> = 15	

Note: CBMT = Cambridge Bicycle Memory Test; CFMT-K = Cambridge Face Memory Test – Kids; DFPT = Dartmouth Face Perception Test. Standard deviation in parentheses. ^aFor the CBMT and CFMT-K children aged 7–9 years memorized 4 targets, children aged 10–12 years memorized 6 targets.

(AO, BG, and HPH) performed poorly on the face memory tasks, their scores were not necessarily significantly below those of controls. However, these children experience difficulties in daily life and their scores on face tests were extremely poor. In contrast, their IQ and object memory scores were relatively high (see Table 2), suggesting that they are capable of performing well on similar tests.

Face detection

The first detection task was a modified version of the ‘Faces Among Non-Faces’ task used in Garrido *et al.* (2008). Participants are presented with arrays of 25 images in a 5 × 5 grid (see Figure 1d). Images are greyscale, covered with 15% Gaussian noise, and include photographs of scenes, objects, food, and animals. On target-present trials, one of the 25 images shows a face. Half of the targets are adult faces, and half are children’s faces. Target-absent trials have no faces. The participant is instructed to find the face as quickly as possible and indicate that a face has been found by key-press. Participants have 8 seconds to find the face. Target-absent trials require that the participant withhold a response. If a key-press is made, the next trial begins immediately. If no key-press is made, the image remains on the screen for 8 seconds, at which point the next trial begins. There are 24 target-present trials and 12 target-absent trials, for a total of 36 trials. The primary

dependent measure for this task is mean reaction time, which is calculated using correct target-present trials only. The version of this task that was used by Garrido *et al.* (2008) generated large inversion effects in adults, suggesting that it engages face processing mechanisms. To be sure that these inversion effects also exist for children, we tested a group of 12 control participants between the ages of 8 and 13. Like the adults from Garrido *et al.*, these children showed large inversion effects on this task both in terms of reaction time, Upright mean = 1118.8 ms, *SD* = 316.0, Inverted mean = 1566.8 ms, *SD* = 467.3, $t(11) = 6.63$, $p < .001$, $d = 1.12$, and accuracy, Upright mean = 98.6%, *SD* = 2.8, Inverted mean = 93.7%, *SD* = 4.6, $t(11) = 5.01$, $p < .001$, $d = 1.29$. Reaction time data from another 89 typically developing children between the ages of 7 and 12 years indicates that this task has strong split-half reliability, Spearman-Brown corrected split-half correlation, $r_{SB} = 0.78$.

The second task was a modified version of the ‘faces among face parts’ task used in Garrido *et al.* (2008). This task requires participants to find faces among distractors. Faces are black and white images generated by increasing the contrast of greyscale photos of real faces. These two-tone faces are accompanied by distractors that are scrambled elements of other two-tone faces (Figure 1e). The task begins with example trials in which participants are asked if they can see a face among the distractors.

Table 2 Data from children with developmental prosopagnosia on tests of object memory, face memory, face perception, and face detection

Child (age/gender)								
Test	Chance	AO (8M)	BG (9F)	HPH (9M)	DD (10M)	NL (10M)	SWJ (11M)	MF (12F)
WASI-II								
VIQ	N/A	132	123	134	113	120	154	91
PIQ	N/A	122	105	102	105	117	126	86
Object Memory								
CBMT	33%	79.2 $t(15) = -0.10$ $p = .922$	91.7 $t(14) = 0.77$ $p = .453$	84.7 $t(14) = 0.31$ $p = .758$	68.1 $t(14) = 0.01$ $p = .992$	84.7 $t(15) = 1.72$ $p = .107$	59.7 $t(15) = -1.20$ $p = .248$	72.2 $t(15) = -0.38$ $p = .710$
Old New Flowers	50%	90.0 $t(15) = 0.59$ $p = .563$	76.7 $t(13) = -0.73$ $p = .478$	66.7 $t(13) = -1.40$ $p = .184$	76.7 $t(14) = -1.42$ $p = .179$	90.0 $t(14) = 0.19$ $p = .849$	73.3* $t(14) = -2.29$ $p = .038$	86.7 $t(14) = -0.43$ $p = .675$
Face Memory								
CFMT-Kids	33%	37.5 $t(19) = -1.98$ $p = .062$	62.5 $t(15) = -1.43$ $p = .173$	52.0* $t(15) = -2.28$ $p = .038$	56.9* $t(14) = -3.74*$ $p = .002$	34.7* $t(14) = -6.72*$ $p < .001$	44.4* $t(14) = -2.40*$ $p = .031$	51.4* $t(13) = -3.15*$ $p = .008$
Old New Faces	50%	56.7 $t(14) = -2.00$ $p = .065$	53.3* $t(16) = -2.49$ $p = .024$	76.7 $t(16) = -0.42$ $p = .677$	73.3* $t(14) = -2.37*$ $p = .033$	33.3* $t(14) = -8.51*$ $p < .001$	60.0* $t(15) = -2.98*$ $p = .009$	56.7* $t(14) = -5.47*$ $p < .001$
Face Perception								
DFPT	33%	40.0* $t(14) = -2.14*$ $p = .050$	55.0 $t(14) = -1.98$ $p = .068$	42.5* $t(14) = -2.89$ $p = .012$	65.0* $t(14) = -2.49*$ $p = .026$	30.0* $t(14) = -6.89*$ $p < .001$	35.0* $t(15) = -6.52*$ $p < .001$	47.5* $t(13) = -6.40*$ $p < .001$
Face Detection								
Faces Among Non-Faces %	50%	94.4 $t(14) = 0.12$ $p = .910$ $A' = 0.94$	94.4 $t(14) = -0.56$ $p = .583$ $A' = 0.94$	94.4 $t(14) = -0.56$ $p = .583$ $A' = 0.96$	97.2 $t(14) = -0.26$ $p = .796$ $A' = 0.97$	91.7* $t(14) = -2.69$ $p = .018$ $A' = 0.95$	91.7 $t(14) = -1.73$ $p = .105$ $A' = 0.94$	97.2 $t(14) = -0.37$ $p = .715$ $A' = 0.97$
RT (ms)		2418.4 $t(14) = 1.93$ $p = .074$	2175.2* $t(14) = 2.28$ $p = .039$	1643.0 $t(14) = 0.46$ $p = .653$	1788.7 $t(14) = 1.57$ $p = .139$	1177.0 $t(14) = -0.30$ $p = .769$	1960.0* $t(14) = 3.07$ $p = .008$	1077.6 $t(14) = 0.54$ $p = .595$
Faces Among Face Parts	50%	36.7* $t(15) = -3.34$ $p = .004$	56.7* $t(13) = -2.31$ $p = .038$	73.3 $t(14) = -0.48$ $p = .642$	80.0 $t(18) = 0.19$ $p = .853$	63.3 $t(18) = -1.18$ $p = .254$	46.7* $t(16) = -3.58$ $p = .003$	83.3 $t(14) = 0.17$ $p = .872$

Note: WASI-II = Wechsler Abbreviated Scale of Intelligence – II; VIQ = Verbal IQ; PIQ = Performance IQ; CBMT = Cambridge Bicycle Memory Test; CFMT-K = Cambridge Face Memory Test – Kids; DFPT = Dartmouth Face Perception Test. For the CBMT and CFMT-K children 7–9 years memorized 4 targets, children 10–12 years memorized 6 targets. Bold indicates scores > 2SD below the control mean. *Indicates scores significantly different than age-matched control group based on Crawford and colleagues' modified *t*-tests, two-tailed, $\alpha = 0.05$ (Crawford & Garthwaite, 2002; Crawford & Howell, 1998).

If they cannot find the face, the experimenter presses a key and the face is highlighted. Participants view five example images. In the actual task, two images are presented on either side of a fixation cross. One image contains a face among face parts, the other contains only face parts. Participants must indicate by key-press whether the face is in the image that appears on the left or right of fixation. If they do not respond within 5 seconds, the images disappear and the participant is prompted to give a response. There are 30 experimental trials. The primary dependent measure for this task is accuracy. Chance-level performance is 50%. The version

of this task that was used by Garrido *et al.* (2008) generated large inversion effects in adults, so it also appears to engage face processing mechanisms. To be sure that these inversion effects also exist for children, we tested a group of 12 control participants between the ages of 8 and 13. Like the adults from Garrido *et al.*, these children showed large inversion effects on this task, Upright mean = 86.7%, $SD = 11.7$, Inverted mean = 52.5%, $SD = 9.1$, $t(11) = 7.83$, $p < .001$, $d = 3.26$. Data from another 97 typically developing children between 7 and 12 years indicates that this test has acceptable internal consistency, Cronbach's $\alpha = 0.65$.

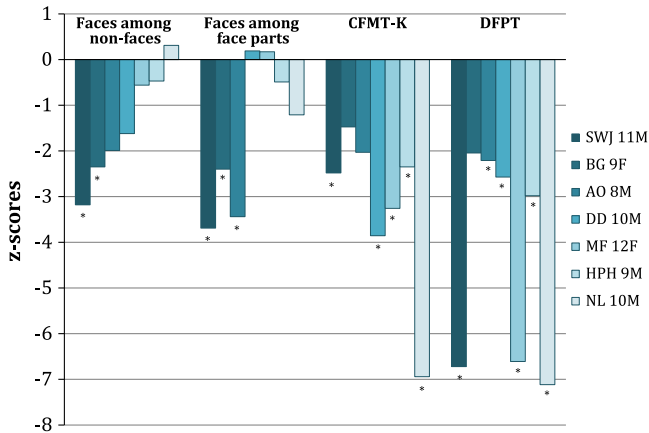


Figure 2 Face detection, face memory, and face perception data for children with developmental prosopagnosia. Data are presented in z-scores. Faces Among Non-Faces data are reaction times, multiplied by -1 so that negative z-scores indicate slower than average performance. Faces Among Face Parts, Cambridge Face Memory Test – Kids (CFMT-K), and Dartmouth Face Perception Test (DFPT) data are measured in accuracy. *significantly different from age-matched controls according to Crawford and colleagues' modified *t*-tests (two-tailed, $\alpha = 0.05$).

Results

Accuracy, A' , and *t*- and *p*-values are presented in Table 2. Data are plotted as z-scores in Figure 2. Four of the seven children (AO, BG, NL, and SWJ) were impaired on one or both of the face detection tasks. The remaining three children (HPH, DD, and MF) performed normally on both tasks.

Performance by controls on the Faces Among Non-Faces task was high, so reaction time was the main dependent measure. Accuracy scores for all but one of the DP children were normal; NL was the only child whose accuracy was more than 2 *SD* below the mean (91.7%, due to failing to detect the face in three arrays). Two children (BG and SWJ) were more than 2 *SD* slower than age-matched controls on this task and AO was 1.99 *SD* slower than other 8-year-olds. Modified *t*-tests (Crawford & Garthwaite, 2002; Crawford & Howell, 1998) corroborated these results: NL's accuracy was significantly lower than that of other 10-year-olds, $t(14) = -2.69$, $p = .018$, though his reaction time was normal, $t(14) = -0.30$, $p = .769$. BG and SWJ were significantly slower than controls, BG: $t(14) = 2.28$, $p = .039$; SWJ: $t(14) = 3.07$, $p = .008$, and AO's reaction time was borderline: $t(14) = 1.93$, $p = .074$.

For the Faces Among Face Parts task, the accuracy scores of BG, SWJ, and AO were more than 2 *SD* below the mean, while the other four children were in the

normal range. These results were supported by modified *t*-tests, AO: $t(15) = -3.34$, $p = .004$; BG: $t(13) = -2.31$, $p = .038$; SWJ: $t(16) = -3.58$, $p = .003$.

Discussion

The two-process theory of face recognition (Morton & Johnson, 1991) implies a potential etiological account of developmental prosopagnosia (DP): a failure to detect faces normally could lead to deficits with facial identity recognition. Similarly, Tsao and Livingstone (2008) propose that prosopagnosia may be explained by a failure to differentiate faces from non-face objects, and Schultz (2005) suggests that face recognition deficits in autism may be explained by a failure to orient to faces. To investigate the possible link between impaired face detection and impaired identity recognition, we tested seven children with DP to determine whether they have face detection impairments. Two of these children (BG and SWJ) were impaired on both face detection tasks, and one child (AO) was in the impaired range for one task, and borderline-impaired on the other. Furthermore, one additional child (NL) had abnormally low accuracy on the Faces Among Non-Faces task. Inspection of NL's responses indicates that all of his errors were due to failure to find the face in the time allowed. Taken together, these results suggest that three of the seven children with DP were impaired at face detection and that an additional child, NL, may be impaired. In contrast, the remaining three children had normal face detection despite clear deficits with face recognition. These varied profiles are consistent with a number of other studies that suggest that DP is a heterogeneous condition (Dalrymple *et al.*, 2014; Duchaine & Nakayama, 2005; Eimer, Gosling & Duchaine, 2012; Harris *et al.*, 2005; Le Grand *et al.*, 2006) that may have different etiologies.

The two-process theory of face recognition (Morton & Johnson, 1991) suggests that infants are born with an innate system (CONSPEX) that predisposes them to detect and orient to face-like stimuli over non-face stimuli. This tendency to fixate on faces allows a second, category-general learning-based system (CONLERN) to build special procedures for face recognition. The theory suggests that without preferential orienting to faces from a young age, one cannot accumulate the experience needed for processing faces normally. Johnson (2005) applied this model to propose a developmental mechanism by which face-selective areas, such as the fusiform face area (FFA), become specialized for processing faces. He proposed that preferential attention to faces early in life ensures input to cortical visual pathways that activate certain cortical areas, making these areas sensitive to

faces. Further input strengthens these connections and generates stimulus-specific activation in response to face stimuli. Though agnostic as to the precise location of processing, Bentin, Deouelle and Soroker (1999) similarly reasoned that poor discrimination between faces and objects could lead to disorganization within the face processing system, and that if this disruption occurs early in development, then the face processing system will not become optimally tuned to face stimuli. The present finding that some children with DP are impaired with face detection is consistent with the prediction that some cases of DP may be explained by a failure to detect faces. Specifically, a lack of preferential orienting to face stimuli may restrict face-specific input to areas that normally become specialized face processors. However, the present findings also reveal that a failure to detect faces cannot necessarily explain all cases of DP: our finding that some children with DP have normal face detection suggests that impaired face recognition may be explained by higher-level failures in the system in some cases. Although it is possible that these children had impaired face detection at a young age and have since adopted compensatory strategies for this ability, the dissociation between normal detection and impaired identity recognition in these individuals implies that different processes underlie these two abilities.

Why might face detection be impaired in some, but not all, cases of DP? One explanation is suggested by a proposal about the developmental events leading to another selective developmental disorder. Following Galaburda's seminal work on dyslexia (Galaburda & Kemper, 1979; Galaburda, Sherman, Rosen, Aboitiz & Geschwind, 1985), Ramus has proposed that ectopias, localized areas of cortical disorganization caused by neural migration disturbances, could underlie dyslexia and other selective developmental disorders (Giraud & Ramus, 2013; Ramus, 2004, 2006). According to this account, the location of ectopias would dictate the resulting behavioral deficits, with particular cognitive functions disrupted by cortical abnormalities in areas that normally underlie those functions. Ramus therefore argues that a cognitive outcome (e.g. face recognition) mediated by multiple areas could be affected by an abnormality or abnormalities in a number of different areas, and that the precise location of the abnormalities would dictate the cognitive effects. Moreover, disruptions due to ectopias in one region could lead to problems in others areas dependent on the normal functioning of the disrupted region. In the context of the present findings, ectopias in areas mediating face detection could lead to DP because higher-level face processing mechanisms needed for identity recognition do not receive normal input and so fail to develop properly. Similar abnormal-

ities in higher-level occipital and temporal regions that contribute to face perception and/or face memory but not to face detection could lead DP with normal face detection. A third possibility is that in some cases developmental abnormalities are more widespread, leading to problems with face perception and face memory that are concurrent with, but not necessarily a downstream repercussion of, impaired face detection.

Some of the children in our study showed normal detection despite being impaired at facial identity perception and memory. This dissociation suggests that face detection relies on different cognitive processes from facial identity and is consistent with findings from adults with developmental prosopagnosia (Garrido *et al.*, 2008) and a case of acquired prosopagnosia (Dricot, Busigny & Rossion, 2008). Bruce and Young (1986) omitted face detection from their cognitive model because there was no evidence at the time that faces required special analysis, and because the relative timing of face detection versus face recognition was unclear. There is now considerable evidence that faces are processed separately from objects: face-selective responses have been recorded at a single cell level (Foldiak, Xiao, Keyser, Edwards & Perrett, 2004; Tsao, Moeller & Freiwald, 2008), as well as through neuroimaging (Kanwisher, McDermott & Chun, 1997; Liu, Harris & Kanwisher, 2002; McCarthy, Puce & Gore, 1997) and event-related potentials (Bentin, Allison, Puce, Perez & McCarthy, 1996; Botzel, Schulze & Stodieck, 1995; Jeffreys, 1989). Evidence from transcranial magnetic stimulation (Pitcher, Charles, Devlin, Walsh & Duchaine, 2009) and neuropsychology (Duchaine *et al.*, 2006; Moscovitch, Winocur & Behrmann, 1997) further supports the view that face processing and object processing are dissociable. However, it is still unclear at what point face processing and object processing dissociate. On the one hand, it is possible that faces and objects are detected by a common mechanism that carries out basic-level object recognition. On the other hand, Tsao and Livingstone (2008) argue that it is more efficient to have a domain-specific filter (i.e. a detection process) to extract faces from objects, allowing the recognition process to operate on a restricted set of stimuli. The unusual case of CK, a severe object agnostic with normal face recognition, supports this view. In a detection task, CK was faster than age-matched controls at detecting faces among objects. In contrast, he is severely impaired with basic-level object recognition and he was impaired at detecting objects that competed with faces (Moscovitch *et al.*, 1997). Thus, CK's results indicate that face detection can occur independently of object detection. It will be valuable in future to examine whether face detection can be impaired while object recognition is normal.

The neural areas responsible for face detection are unclear, but the existence of individuals with DP with and without detection impairments provides a possible means to investigate the neural basis of face detection. In Haxby, Hoffman and Gobbini's model of face processing (2000, 2002), the Occipital Face Area (OFA) is the first face processing area, preceding activation in the Fusiform Face Area (FFA) and the Superior Temporal Sulcus (STS). Gauthier, Tarr, Moylan, Skudlarski, Gore *et al.* (2000) proposed that the OFA is responsible for face detection while some have proposed that both OFA and FFA may play a role (Nestor, Vettel & Tarr, 2008). The possibility of a subcortical basis for face detection has also received extensive discussion (Cauchoix & Crouzet, 2013; Johnson, 2005). Johnson (2005) cites neuropsychological, electrophysiological, and cognitive evidence in support of a subcortical face processing route that is described as rapid and tuned to low-spatial frequency information. Others have similarly assigned face detection to subcortical areas, such as the superior colliculus and amygdala (de Gelder, Frissen, Barton & Hadjikhani, 2003). Although the present study cannot speak to either side of this debate, cortical and subcortical views of face detection lead to different testable hypotheses about the neural profiles of individuals with and without face detection problems. A cortically mediated view of face detection predicts that individuals with face detection deficits will have more posterior atypicalities, whereas individuals with normal face detection, but abnormal face recognition, will have more anterior atypicalities (Barton, 2008; Barton & Cherkasova, 2003; Barton, Press, Keenan & O'Connor, 2002; Damasio, Tranel & Damasio, 1990; Davies-Thompson, Pancaroglu & Barton, 2014; Haxby *et al.*, 2000). In contrast, a subcortical view of face detection (e.g. de Gelder *et al.*, 2003; Johnson, 2005) predicts that individuals with face detection deficits will have subcortical abnormalities while those with normal face detection will not.

Are face detection tasks appropriate for testing whether a failure of CONSPEC may lead to impaired face identity processing? Discussions of the two-process theory are unclear about this point. In the original report, Morton and Johnson (1991) suggest that the CONSPEC mechanism can be investigated through behaviors such as approach, allocation of attention, or looking preferences. Their primary example is evidence that newborn infants track faces to a greater extent than non-faces (Goren, Sarty & Wu, 1975; Morton & Johnson, 1991). Morton and Johnson (1991) suggest that because young infants are incapable of smooth pursuit, face-tracking behavior can be interpreted as repeated orienting. However, it is difficult to know whether infants are engaging in a degraded form of

smooth pursuit (endogenously following the target), or in fact repeatedly reorienting (exogenously). More recently, Johnson (2005) discussed CONSPEC in terms of a preference for face stimuli that '... served to bias the visual input to developing cortical circuits to ensure the development of a specialization for faces' (p. 768), and Johnson (2011) defined the innate bias for faces as 'the minimum necessary for picking out faces from a natural environment,' (p. 124), which seems to describe face detection. Indeed, Johnson, Senju and Tomalski (in press) imply that CONSPEC is synonymous with face detection. In sum, there is no definitive behavior or paradigm that can be used to test for the existence of a CONSPEC mechanism, but based on the descriptions in the literature, face detection is a reasonable starting point for investigations into the claims of this theory. It would be valuable in future studies to test the theory using other behavioral paradigms with children with DP, such as attentional orienting to faces.

One limitation of the tasks used in the present study is that they did not allow us to determine whether face detection deficits in these children are accompanied by more general visual search deficits. However, general early stage processing deficits that include face detection deficits could still affect later face processing abilities and, given the sensitivity of the face processing system to early visual experience (Le Grand, Mondloch, Maurer & Brent, 2001; Pascalis, Scott, Kelly, Shannon, Nicholson *et al.*, 2005; Sugita, 2008), it would not be surprising if higher-level face processing abilities are disproportionately affected by early domain-general visual processing deficits. Furthermore, unlike with face processing, there is no theoretical reason to suggest that normal object processing requires special orienting to objects early in life (i.e. one would not likely predict that general visual agnosias would result from general visual search deficits).

Future research is needed to determine whether other face processing abilities may be affected by poor face detection. That is, if one predicts that a failure to orient to face stimuli at a young age can lead to difficulties with identity processing, then a similar prediction should follow for face processing abilities such as expression recognition and gender discrimination. However, facial expression recognition has been reported to be normal in DP (Duchaine, Germine & Nakayama, 2007; Duchaine, Parker & Nakayama, 2003b; Humphreys, Avidan & Behrmann, 2007), a finding consistent with cognitive models that suggest that these abilities are mediated by separate neural mechanisms (Bruce & Young, 1986; Haxby *et al.*, 2000, 2002). The finding that face identity and facial expression processing may be mediated by different mechanisms raises the possibility that impaired face detection could lead to disproportionate or exclusive

deficits with face identity processing while leaving expression recognition intact. It is also possible that face identity processing is more sensitive to early experience with faces than facial expression processing.

To summarize, the present findings provide mixed support for the prediction that face recognition impairments in the context of DP originate in failures of face detection. These findings have implications for models of face processing, suggesting that face detection and face recognition are dissociable abilities. Face detection appears to be an important precursor to face recognition and it may be worthwhile including it in future neural and cognitive models of face processing. These findings also have implications for understanding abnormal development of face processing, suggesting that there may be different subtypes of DP, with impairments being linked to deficits at different stages of processing. Specifically, heterogeneity in face detection abilities indicates an early stage distinction that may be important in classification of DP.

Acknowledgements

KAD was supported by a Banting Postdoctoral Fellowship awarded by the Canadian Institutes of Health Research and an Economic and Social Research Council (ESRC) grant awarded to BD (grant number RES-062-23-2426).

References

- Barton, J. (2008). Structure and function in acquired prosopagnosia: lessons from a series of 10 patients with brain damage. *Journal of Neuropsychology*, *2*, 197–225.
- Barton, J., & Cherkasova, M. (2003). Face imagery and its relation to perception and covert recognition in prosopagnosia. *Neurology*, *61*, 220–225.
- Barton, J., Press, D., Keenan, J., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology*, *58*, 71–78.
- Behrmann, M., Avidan, G., Marotta, J., & Kimchi, R. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 1. Behavioral findings. *Journal of Cognitive Neuroscience*, *17* (7), 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* (6), 551–565.
- Bentin, S., Deouell, L., & Soroker, N. (1999). Selective visual streaming in face recognition: evidence from developmental prosopagnosia. *NeuroReport*, *10*, 823–827.
- Botzel, K., Schulze, S., & Stodieck, S. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research*, *104*, 135–143.
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, *77*, 305–327.
- Cauchoix, M., & Crouzet, S. (2013). How plausible is a subcortical account of rapid visual recognition? *Frontiers in Human Neuroscience*, *7*, 1–4.
- Crawford, J., & Garthwaite, P. (2002). Investigation of the single case in neuropsychology: confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia*, *40*, 1196–1208.
- Crawford, J., Garthwaite, P., & Howell, D. (2009). On comparing a single case with a control sample: an alternative perspective. *Neuropsychologia*, *47* (13), 2690–2695.
- Crawford, J., & Howell, D. (1998). Comparing an individual's test score against norms derived from small samples. *Clinical Neuropsychologist*, *12* (4), 482–486.
- Dalrymple, K., Corrow, S., Yonas, A., & Duchaine, B. (2012a). Developmental prosopagnosia in childhood. *Cognitive Neuropsychology*, *29* (5–6), 393–418.
- Dalrymple, K., Garrido, L., & Duchaine, B. (2014). Dissociation between face perception and face memory in adults, but not children, with developmental prosopagnosia. *Developmental Cognitive Neuroscience*, *10*, 10–20.
- Dalrymple, K., Gomez, J., & Duchaine, B. (2012b). CFMT-Kids: a new test of face memory for children. *Journal of Vision*, *12* (9), 492.
- Damasio, A., Tranel, D., & Damasio, H. (1990). Face agnosia and the neural substrates of memory. *Annual Review of Neuroscience*, *13*, 89–109.
- Davies-Thompson, J., Pancaroglu, R., & Barton, J. (2014). Acquired prosopagnosia: structural bias and processing impairments. *Frontiers in Bioscience*, *E6*, 159–174.
- de Gelder, B., Frissen, I., Barton, J.J., & Hadjikhani, N. (2003). A modulatory role for facial expressions in prosopagnosia. *Proceedings of the National Academy of Sciences, USA*, *100* (22), 13105–13110.
- de Gelder, B., & Rouw, R. (2000). Configural face processes in acquired and developmental prosopagnosia: evidence for two separate face systems? *NeuroReport*, *11* (14), 3145–3150.
- Dricot, L., Busigny, T., & Rossion, B. (2008). Behavioral and neural evidence for preserved holistic face detection in acquired prosopagnosia. *Journal of Vision*, *8*, 410a.
- Duchaine, B., Germine, L., & Nakayama, K. (2007). Family resemblance: ten family members with prosopagnosia and within-class object agnosia. *Cognitive Neuropsychology*, *24*, 419–430.
- Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience*, *17* (2), 249–261.
- Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: results from neurologically intact individuals and an investigation of its validity using inverted stimuli and prosopagnosic participants. *Neuropsychologia*, *44* (4), 576–585.
- Duchaine, B., Nieminen-von Wendt, T., New, J., & Kulomaki, T. (2003a). Dissociations of visual recognition in a develop-

- mental agnosia: evidence for separate developmental processes. *Neurocase*, **9**, 380–389.
- Duchaine, B., Parker, H., & Nakayama, K. (2003b). Normal recognition of emotion in a prosopagnosic. *Perception*, **32**, 827–838.
- Duchaine, B., Yovel, G., Butterworth, E., & Nakayama, K. (2006). Prosopagnosia as an impairment to face-specific mechanisms: elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology*, **23** (5), 714–747.
- Eimer, M., Gosling, A., & Duchaine, B. (2012). Electrophysiological markers of covert face recognition in developmental prosopagnosia. *Brain*, **135**, 542–554.
- Foldiak, P., Xiao, D., Keyser, C., Edwards, R., & Perrett, D. (2004). Rapid serial visual presentation for the determination of neural selectivity in area STSa. *Progress in Brain Research*, **144**, 107–116.
- Galaburda, A., & Kemper, T. (1979). Cytoarchitectonic abnormalities in developmental dyslexia: a case study. *Annals of Neurology*, **6**, 94–100.
- Galaburda, A., Sherman, G., Rosen, G., Aboitiz, F., & Geschwind, N. (1985). Developmental dyslexia: four consecutive patients with cortical anomalies. *Annals of Neurology*, **18** (2), 222–233.
- Garrido, L., Duchaine, B., & Nakayama, K. (2008). Face detection in normal and prosopagnosic individuals. *Journal of Neuropsychology*, **47**, 123–131.
- Gauthier, I., Tarr, M., Moylan, J., Skudlarski, P., Gore, J., & Anderson, A. (2000). The fusiform “face area” is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, **12** (3), 495–504.
- Giraud, A.-L., & Ramus, F. (2013). Neurogenetics and auditory processing in developmental dyslexia. *Current Opinion in Neurobiology*, **23**, 37–42.
- Goren, C., Sarty, M., & Wu, P. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, **56**, 545–549.
- Harris, A., Duchaine, B., & Nakayama, K. (2005). Normal and abnormal face selectivity of the M170 response in developmental prosopagnosics. *Neuropsychologia*, **43**, 2125–2136.
- Haxby, J., Hoffman, E., & Gobbini, M. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, **4** (6), 223–233.
- Haxby, J., Hoffman, E., & Gobbini, M. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, **51** (1), 59–67.
- Humphreys, K., Avidan, G., & Behrmann, M. (2007). A detailed investigation of facial expression processing in congenital prosopagnosia as compared to acquired prosopagnosia. *Experimental Brain Research*, **176** (2), 356–373.
- Jeffreys, D.A. (1989). A face-responsive potential recorded from the human scalp. *Experimental Brain Research*, **78** (1), 193–202.
- Johnson, M. (2005). Sub-cortical face processing. *Nature Reviews Neuroscience*, **7**, 766–774.
- Johnson, M.H., with de Haan, M. (2011). *Developmental cognitive neuroscience* (3rd edn.). Chichester: Wiley-Blackwell.
- Johnson, M., Senju, A., & Tomalski, P. (in press). The two-process theory of face processing: modifications based on two decades of data from infants and adults. *Neuroscience and Biobehavioral Reviews*.
- Kanwisher, N., McDermott, J., & Chun, M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, **17** (11), 4302–4311.
- Le Grand, R., Cooper, P., Mondloch, C., Lewis, T., Sagiv, N., deGelder, B., & Maurer, D. (2006). What aspects of face processing are impaired in developmental prosopagnosia? *Brain and Cognition*, **61**, 139–158.
- Le Grand, R., Mondloch, C., Maurer, D., & Brent, H. (2001). Early visual experience and face processing. *Nature*, **410**, 890.
- Lewis, M., & Ellis, H. (2003). How we detect a face: a survey of psychological evidence. *International Journal of Imaging Systems and Technology*, **13**, 3–7.
- Liu, J., Harris, A., & Kanwisher, N. (2002). States of processing in face perception: an MEG study. *Nature Neuroscience*, **5** (9), 910–916.
- McCarthy, G., Puce, A., & Gore, J. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, **9** (5), 2188–2199.
- Morton, J., & Johnson, M. (1991). CONSPEC and CONLERN: a two-process theory of infant face recognition. *Psychological Review*, **98**, 164–181.
- 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.
- Nestor, A., Vettel, J., & Tarr, M. (2008). Task-specific codes for face recognition: how they shape the neural representation of features for detection and individuation. *PLoS ONE*, **3** (12), e3978.
- Pascalis, O., Scott, L., Kelly, D., Shannon, R., Nicholson, E., Coleman, M., & Nelson, C. (2005). Plasticity of face processing in infancy. *Proceedings of the National Academy of Sciences*, **102** (14), 5297–5300.
- Pitcher, D., Charles, L., Devlin, J., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Current Biology*, **19**, 319–324.
- Ramus, F. (2004). Neurobiology of dyslexia: a reinterpretation of the data. *Trends in Neuroscience*, **27** (12), 720–726.
- Ramus, F. (2006). Genes, brain, and cognition: a roadmap for the cognitive scientist. *Cognition*, **101**, 247–269.
- Schmalzl, L., Palermo, R., Green, M., Brunsdon, R., & Coltheart, M. (2008). Training of familiar face recognition and visual scan paths for faces in a child with congenital prosopagnosia. *Cognitive Neuropsychology*, **25** (5), 704–729.
- Schultz, R. (2005). Developmental deficits in social perception in autism: the role of the amygdala and fusiform face area. *International Journal of Developmental Neuroscience*, **23**, 125–141.
- Sokal, R., & Rohlf, J. (1995). *Biometry*. San Francisco, CA: W.H. Freeman.

- Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. *Proceedings of the National Academy of Sciences, USA*, **105** (1), 394–398.
- Susilo, T., & Duchaine, B. (2013). Advances in developmental prosopagnosia research. *Current Opinion in Neurobiology*, **23** (3), 423–429.
- Tsao, D., & Livingstone, M.S. (2008). Mechanisms of face perception. *Annual Review of Neuroscience*, **31**, 411–437.

Tsao, D., Moeller, S., & Freiwald, W. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences, USA*, **105**, 19514–19519.

Received: 30 July 2014

Accepted: 4 March 2015