

Face-specific and domain-general visual processing deficits in children with developmental prosopagnosia

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ABSTRACT

Evidence suggests that face and object recognition depend on distinct neural circuitry within the visual system. Work with adults with developmental prosopagnosia (DP) demonstrates that some individuals have preserved object recognition despite severe face recognition deficits. This face selectivity in adults with DP indicates that face- and object-processing systems can develop independently, but it is unclear at what point in development these mechanisms are separable. Determining when individuals with DP first show dissociations between faces and objects is one means to address this question. In the current study, we investigated face and object processing in six children with DP (5–12-years-old). Each child was assessed with one face perception test, two different face memory tests, and two object memory tests that were matched to the face memory tests in format and difficulty. Scores from the DP children on the matched face and object tasks were compared to within-subject data from age-matched controls. Four of the six DP children, including the 5-year-old, showed evidence of face-specific deficits, while one child appeared to have more general visual-processing deficits. The remaining child had inconsistent results. The presence of face-specific deficits in children with DP suggests that face and object perception depend on dissociable processes in childhood.

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Faces are particularly salient and biologically relevant stimuli. They provide a wealth of information about a person's identity, sex, mood, and age, making them critical for navigating social interactions in daily life (Bruce & Young, 1986). Given the social importance and visual complexity of faces, it is not surprising that scientific studies using a variety of methodologies suggest that, in adulthood, face processing depends on dedicated and distinct neural circuitry within the occipito-temporal visual-processing stream (Duchaine & Yovel, 2015; Haxby & Gobbini, 2011; Kanwisher, 2000). Functional neuroimaging has identified areas that show a greater response to faces than objects (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, & Gore, 1997; Tsao, Moeller, & Freiwald, 2008). Similarly, face-selective activity has been detected over posterior temporal regions using event-related

potentials, with a larger response to faces than to objects approximately 140–200 ms post stimulus (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Botzel, Schulze, & Stodieck, 1995; Jeffreys, 1989). A double dissociation between face and object processing has been demonstrated using transcranial magnetic stimulation (TMS): TMS applied to the right occipital face area (rOFA) selectively disrupts certain aspects of face processing, but not object processing, while TMS applied to the right lateral occipital area (rLO) disrupts object processing, but not face processing (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009).

A similar double dissociation exists in neuropsychology: there are reports of individuals with severe object agnosia with preserved face recognition (McMullen, Fisk, Phillips, & Maloney, 2000; Moscovitch, Winocur, & Behrmann, 1997; Rumati, Humphreys,

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 Supplemental Table 1 is available via the "Supplemental" tab on the article's online page (<http://dx.doi.org/10.1080/17470218.2015.1122642>).

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Riddoch, & Bateman, 1994) and individuals with acquired prosopagnosia (severe face recognition deficits resulting from brain damage; Bodamer, 1947) with preserved object processing (e.g., Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; Farah, Levinson, & Klein, 1995; Farah, Wilson, Drain, & Tanaka, 1995; Henke, Schweinberger, Grigo, Klos, & Sommer, 1998; McNeil & Warrington, 1993; Rezsescu, Barton, Pitcher, & Duchaine, 2014; Rezsescu, Pitcher, & Duchaine, 2012; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008; Susilo, Yovel, Barton, & Duchaine, 2013). Face-specific deficits in acquired prosopagnosia are informative because they can elucidate structural and functional dissociations in the adult brain.

In contrast to deficits that arise from brain damage, developmental disorders can provide information about the developmental processes that enable efficient and effective face and object processing, and, like acquired agnosias, evidence for a double dissociation between faces and objects also exists for developmental agnosias. Germine, Cashdollar, Düzél, and Duchaine (2011) reported the only existing case of a 19-year-old woman with severe developmental object agnosia with preserved face perception. This case provides an interesting contrast to the more commonly reported cases of developmental prosopagnosia (DP), which are defined by severe face recognition deficits due to the failure to develop the visual mechanisms required for processing faces (Duchaine & Nakayama, 2006b). Several studies have reported face-specific deficits in adults with developmental prosopagnosia (Duchaine & Nakayama, 2005; Duchaine, Yovel, Butterworth, & Nakayama, 2006; Garrido et al., 2009; Lee, Duchaine, Nakayama, & Wilson, 2010; Susilo et al., 2010), while others have reported cases with comorbid object-processing deficits (Behrmann & Avidan, 2005; de Haan & Campbell, 1991; Duchaine, Germine, & Nakayama, 2007; Duchaine & Nakayama, 2005; Duchaine, Nieminen-von Wendt, New, & Kulomaki, 2003; Garrido et al., 2009; Lee et al., 2010; see Table 1). Face-specific cases of developmental prosopagnosia provide evidence that object processing can be preserved despite abnormal development of the mechanisms dedicated to face processing.

Although these adult cases provide evidence that face processing and object processing function at least partially independently, it is unclear at what point in ontogeny these mechanisms diverge or whether they are separate from birth. One possibility is that face and object processing are served by common mechanisms at birth, and that exposure to

faces leads to the construction of mechanisms dedicated to face processing. This view is consistent with the two process theory of face recognition (Morton & Johnson, 1991), which suggests that an innate mechanism ("CONSPEX") compels infants to preferentially orient to faces early in life, and that this orienting allows infants to gain the requisite experience needed to acquire specialized face-processing capacities distinguishable from general visual perception/recognition systems ("CONLERN"). An alternative possibility is that face- and object-processing mechanisms are separate at birth. Studies with non-human primates have found evidence of experience-independent face-processing mechanisms: monkeys denied exposure to faces for the first two years of life displayed the ability to make fine discriminations between individual faces when they were tested with them at the end of the deprivation period (Sugita, 2008). Similarly, in human infants, 6-month-olds can differentiate between individual human faces and between individual monkey faces, but the ability to individuate monkey faces is typically lost by 9 months. Interestingly, infants who are regularly exposed to monkey faces between 6- and 9-months-of-age retain their ability to individuate monkey faces, suggesting that exposure to a particular type of face maintains a pre-existing ability to process those faces effectively (Pascalis et al., 2005).

There has been a long-standing debate about the developmental trajectory of face processing in typically developing school-age children. One view is that face processing matures more slowly than the mechanisms used to process other objects over the first 10+ years of life. Early studies suggested a qualitative difference in face processing until the age of 10—specifically, that children process faces in parts, whereas adults process faces holistically (Carey & Diamond, 1977). More recent advocates of this late maturity view have noted only quantitative changes: for example, large improvements in upright (compared to inverted) face recognition from 6–12 years (de Heering, Rossion, & Maurer, 2012) and linear improvements in face processing from 6–10 years, followed by further improvement from 13–16 years (even when controlling for IQ) (Lawrence et al., 2008). Online testing of over 60,000 participants indicates that face memory may peak as late as 32 years of age (Germine, Duchaine, & Nakayama, 2011; Susilo, Germine, & Duchaine, 2013).

In contrast to the late maturity view, the early maturity view suggests that face-processing skills are both qualitatively and quantitatively adult-like by 5–7 years, and possibly earlier (Crookes & McKone,

Table 1. Publications reporting object recognition scores in adults with developmental prosopagnosia

Publication	Case (AgeGender)	Face-specific deficits	Face- and object-processing deficits	Object used; Comments
Behrmann & Avidan (2005)	T.M. (27M) K.M. (60F) N.I. (40M) M.T. (41M) B.E. (29F)	0	5	Non-face discrimination tasks. Same/different judgment using common objects such as birds, chairs, etc. Objects either were identical or differed at the basic, subordinate, or exemplar level. DPs were slowed for objects. Not as severe as face-processing deficits.
de Haan and Campbell (1991)	A.B. (27F)	0	1	Mild object-processing deficits based on several object-processing batteries, e.g., Visual Naming and Description of Use subtests from Spreen–Benton Aphasia Battery (Spreen & Benton, 1969).
Duchaine, Nieminen-von Wendt, et al. (2003)	N.M. (40F)	0	1	Individual-item object recognition of natural landscapes, horses, and cars. Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993), Overlapping Figures test, Minimal Feature Match, Foreshortened Match, Object Decision, Drawing from Memory test, Snodgrass and Vanderwart (1980) line drawings.
Duchaine, Parker, and Nakayama (2003)	T.A. (24M)	0	1	Old/new object discrimination: impaired with faces, horses, cars; borderline impaired with guns and sunglasses; normal with tools and places.
Duchaine and Nakayama (2005)	4 female, 3 male, (21–44-years-old)	4	3	Tested with individual identification of cars, tools, guns, horses, scenes, and houses.
Duchaine et al. (2006)	Edward, 53M	1	0	Basic tests of low-level vision. Old/new discriminations of horses, cars, tools, sunglasses, guns, houses, and scenes.
Garrido et al. (2009); Dalrymple, Garrido, and Duchaine (2014)	11 female, 5 male, 20–46-years-old	8	9	Old/new discrimination for houses, cars, horses. Had difficulty with at least one of these tests.
Hasson, Avidan, Deouell, Bentin, and Malach (2003)	Y.T. (39M)	1	0	Object recognition assessed by, and reported in, Bentin, Deouell, and Soroker (1999): Car models, familiar locations, animals
Lee et al. (2010)	67M, 39F, 34F	2	1	Old/New discrimination for cars, guns, houses, sunglasses, tools, and scenes. 3 DPs from the same family. Two were normal on object tasks; one was impaired for houses and tools.
Todorov & Duchaine (2008)	J.K. (36F) T.U. (31M) J.P. (24F) J.L. 62(F)	2	2	Old/new discrimination of cars, guns, sunglasses, tools, and scenes. Were >2 SDs below the mean with cars.
Susilo et al. (2010)	S.P. (21F)	1	0	Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993), Cambridge Car Memory Test (Dennett et al., 2012).
Totals		19	23	

Note: F = female; M = male; DPs = developmental prosopagnosics.

2009; McKone, Crookes, Jeffery, & Dilks, 2012). This conclusion was drawn from an extensive review of the literature, which revealed that past tests used to support the late maturity view had limitations (e.g., restriction of range) that produced misleading data (Crookes & McKone, 2009; McKone et al., 2012), and through new tests of holistic processing, encoding of novel faces, and measures of face-space (Crookes & McKone, 2009). A more recent study (Weigelt et al., 2014) offered an explanation for the conflicting late versus early maturity findings by parsing face recognition into face perception, defined as the ability to

discriminate individual faces that are presented simultaneously (i.e., with little-to-no memory requirements), and face memory, defined as the ability to recognize faces after a delay. In their study of children 5–10 years and adults, Weigelt et al. (2014) found that face perception and non-face perception (i.e., perception of cars, bodies, scenes) appear to develop at the same rate, with similar slopes across ages for face and non-face categories. In contrast, face memory and object memory appear to develop at different rates, with steeper developmental slopes for faces than objects from 5-years-old to adulthood. Thus

these findings provide evidence for a separation between face- and object-processing mechanisms in children as young as 5, but only for face memory.

The mixed results from typically developing children suggest the need for alternative approaches to address the question of when in development face and object processing separate. One alternative is to study face specificity in children with DP; however, little research has been done with this population, and no cases have demonstrated convincing dissociations between face and object recognition (Table 2). One study reported face-specific deficits in a five-year-old child with prosopagnosia (Jones & Tranel, 2001), but only basic-level, and not individual-level, recognition was tested. Another study (Wilson, Palermo, Schmalzl, & Brock, 2010) reported normal object processing in an 8-year-old with DP, but only one object task was used, and the child scored in the normal range for the matched face task, suggesting that these tasks might have been too easy. This latter study and three others have reported face- and object-processing impairments in children with DP (a 5-year-old, 7-year-old, two 8-year-olds, and a 12-year-old; Ariel & Sadeh, 1996; Brunsdon, Coltheart, Nickels, & Joy, 2006; McConachie, 1976), though one of the 8-year-olds was later found to have deficits in early visual cortex (Gilaie-Dotan, Perry, Bonne, Malach, & Bentin, 2009).

In the current study, we investigated face and object processing in a sample of six children with DP between the ages of 5 to 12. Each child was assessed with one face perception test, two different face memory tests, and two object memory tests matched in format and difficulty to the face memory tests. Scores from the DP children on the matched face and object tasks were compared to within-subject paired test scores from typically developing children of the same age. If the results show normal object processing in some DP children, this will indicate that face and object perception depend on separate processes in childhood, and the youngest child showing the dissociation will provide an upper bound on when the two processes are separate. In contrast, if all of the DP children have impaired face and object processing, this pattern of results will tentatively suggest that these abilities depend on common processes in childhood. Given prior evidence that face-specific deficits exist in adulthood, if all DP children have comorbid object-processing deficits, this would additionally suggest that object recognition abilities might improve for some DPs as they become adults.

EXPERIMENTAL STUDY

Method

Participants

Controls. Control participants ($n = 158$, 74 = females, 147 = right-handed) aged 5–13 years ($M = 8.9$, $SD = 2.5$) were recruited by email or over the phone through the research participant registry at the Institute of Child Development at the University of Minnesota. Upon arrival, the experimenter explained that the purpose of the study was to assess face and object processing in typically developing children in order to generate data that can be compared to data from children who have difficulties recognizing faces. Children were motivated by the opportunity to help other children and were told that they would receive a \$10 gift card for their participation. After the study was explained in detail, parents signed permission forms, and children who were 8-years-old or older signed assent forms to confirm their willingness to volunteer in the study. Children completed the Cambridge Bicycle Memory Test, Cambridge Face Memory Test–Kids, Dartmouth Face Perception Test, Old/New Flowers, and Old/New Faces tasks, in that order. Breaks were given between tasks when requested. Testing took less than 1 hour.

Children with developmental prosopagnosia.

Potential participants were selected from a group of children whose parents reported that their child experienced 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 5-years-old, and parents reported that the child 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 and were asked whether they were interested in having their child participate in an in-home assessment of face recognition. A member of the research team (K.A.D.) travelled to the family homes. Parents and children first signed permission and assent forms to confirm their willingness to volunteer in the study. Assessment, which included additional tasks for other studies, took 4 to 6 hours, and children were compensated for their participation. This study was approved by the Committee for the Protection of

Table 2. Publications reporting object recognition scores in children with developmental prosopagnosia

Publication	Case (Age/Gender)	Face-specific deficits	Face- and object-processing deficits	Objects used; Comments
Ariel and Sadeh (1996)	L.G. (8M)	0	1	35/45 common real objects by sight, (could recognize all by touch). 17/30 colour photographs of common objects (e.g., phone, chair). 16/22 plastic toy animals. Later discovered to have deficits in early visual cortex.
Jones and Tranel (2001)	T.A. (5M)	1	0	Visual naming of common objects was above average.
Joy and Brunsdon (2002); Brunsdon et al. (2006)	A.L. (4M) (8M)	0	1	Common object naming task devised by authors, Picture Naming and Spoken Word Picture Matching from Psycholinguistic Assessment of Language Processing in Aphasia test (Kay, Coltheart, & Lesser, 1992). Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993)
McConachie (1976)	A.B. (12F)	1	0	Naming and Description of Use subtests of Spreen–Benton Aphasia test (Spreen & Benton, 1969). Normal for Naming, “poor” for Description of Use, but this was attributed to unfamiliarity with the objects.
Wilson et al. (2010)	A (8M) N (7M) P (5M)	1 (A)	2 (N and P)	Sequential shoe matching task. “A” performed normally on the object task, but also on the matched face task.
Present study	6 cases, 5 clear	4	1	Cambridge Bicycle Memory Test, Old/New Flowers. H.P.H.’s data were unclear because he showed differences between face and objects on Cambridge Memory tests, but not on Old/New tests.
Totals		7	5	

Human Subjects at Dartmouth College and the Institutional Review Board at the University of Minnesota.

Participating children with prosopagnosia ($n = 6$, 2 females) were right-handed and 5–12-years-old ($M = 9.2$, $SD = 2.5$). Two tests of face memory (Cambridge Face Memory Test–Kids, CFMT–K; Old/New Faces) and one test of face perception (Dartmouth Face Perception Test, DFPT) were used to confirm face identity deficits in the children. Children were considered prosopagnosic if their parents provided anecdotal evidence of the child’s difficulties with faces in daily life (Table 3), the child’s scores on the DFPT were greater than two standard deviations below the control mean, and they additionally demonstrated poor performance on one or both face memory tasks (i.e., $z < -1.50$). This less stringent criterion for the face memory tasks was adopted because of floor effects in the younger age groups. C.N. (5-years-old) was included because she experienced difficulties with face recognition in daily life and because her performance on the DFPT, CFMT–Kids, and Old/New Faces were all at or near chance. Floor effects in her control group made it difficult to conclusively demonstrate that her face recognition is significantly below normal, so her results are interpreted with caution. To determine the face selectivity of their deficits, children were tested with object memory tests that were matched in format and difficulty to the face memory tests. All tests are described below.

To determine whether impaired scores on face tests may have resulted from general factors (e.g., poor test-taking skills, lack of interest), we evaluated IQ (Wechsler Abbreviated Scale of Intelligence–II, WASI–II; Wechsler, 2011). We also assessed low-level vision using the length, size, orientation, and position of gap subscales of the Birmingham Object Recognition Battery (BORB; Riddoch & Humphreys, 1993). H.P.H. and S.W.J. did not complete the BORB. BORB performance for the remaining children was compared to the published norms from adults that are distributed with the test (Riddoch & Humphreys, 1993). All BORB scores were in the normal range except that C.N. was in the impaired range on the position of gap subscale. We believe this single impaired score is not sufficient to suggest low-level visual impairments because C.N.’s object memory score was above average. WASI–II and BORB scores can be found in Table 3, along with parent reports of the child’s daily difficulties with face recognition.

Tests

Below are descriptions of the test of face perception, the two tests of face memory, and the matched memory tasks that were used with the children with DP. Example stimuli from the tests are displayed in Figure 1.

Table 3. Supplementary assessments for children with developmental prosopagnosia

DP	WASI-II	BORB	BORB z- scores	Parent report
C.N. (5F)	VIQ 138 PIQ 120	Line length:24/30 Dot size: 23/30 Line orientation: 21/30 Gap position:25/ 40	-1.81 -1.79 -1.46 -2.53	She has been unable to recognize “classmates in hallway, friends out of context, people—even parents—in large groups of people, characters in kids books/movies that change appearance”.
A.O. (8M)	VIQ 132 PIQ 122	Line length:28/30 Dot size: 27/30 Line orientation: 29/30 Gap position: 35/ 40	0.69 -0.13 1.62 -0.03	“We have been attending this church for 5 years almost every week. And he still can’t tell me if he knows anyone.”
H.P.H. (9M)	VIQ 134 PIQ 102	Line length: n/a Dot size: n/a Line orientation: n/a Gap position: n/a	n/a n/a n/a n/a	“My son’s teacher has noted that he is unable to recognise his classmates or identify his learning partner at the end of the week. ... He can identify a small number of distinctive children (red hair, curly hair). He is unable to differentiate between his 2 girl cousins whom he sees regularly.”
N.L. (10M)	VIQ 120 PIQ 117	Line length: 29/30 Dot size: 27/30 Line orientation: 23/30 Gap position: 37/ 40	1.31 -0.13 -0.69 0.48	“We have run into friends he’s known for years in the grocery store and he’s unable to identify them. He identifies his friends and family based on hair, clothing, and skin tone.”
S.W.J. (11M)	VIQ 154 PIQ 126	Line length: n/a Dot size: n/a Line orientation: n/a Gap position: n/a	n/a n/a n/a n/a	“[He] cannot recognise me when we go to the swimming pool. This is because my hair is wet. ... Last Friday he failed to recognise one of his best friends even when he was looking out for him. My son says it was only when he spoke that he was shocked to realize that he was standing a short way from him and was one of only 3 in his school’s uniform.”
M.F. (12F)	VIQ 91 PIQ 86	Line length: 25/30 Dot size: 26/30 Line orientation: 25/30 Gap position: 30/ 40	-1.19 -0.54 0.08 -1.28	“... the school staff waits for me to come pick her up before they let her into the wrong car in error. As she matured, we tried to instill a healthy fear of strangers in her, but found that she would identify something familiar about total strangers and therefore think they were someone she already knew.”

Note: DP = developmental prosopagnosia; VIQ = verbal intelligence quotient; PIQ = performance intelligence quotient. Children are listed by their initials, with age and gender in parentheses. IQ (Wechsler Abbreviated Scale of Intelligence-II, WASI-II; Wechsler, 2011) and Birmingham Object Recognition Scores (BORB; Riddoch & Humphreys, 1993) are listed for each child, along with an excerpt from parent report of daily difficulties with face recognition (used with permission).

Face tests.

Dartmouth Face Perception Test (DFPT). This test begins with three practice trials. In these trials, a cartoon face is presented at the top of the screen facing 30° to the viewer’s left. Below the target face are three cartoon faces (frontal views), one of which is the same identity as the target face. The participant is asked to choose the face that looks the most like the target face. The target face and choice faces in the DFPT appear at different viewpoints to force reliance on typical face-processing procedures by lessening the effectiveness of abnormal strategies such as feature matching (Hay & Young, 1982).

The test phase of the DFPT is identical to the practice, except that the eight target faces are male and female faces with neutral expressions chosen from

the Dartmouth Database of Children’s Faces (Dalrymple, Gomez, & Duchaine, 2013). Faces were converted to greyscale and cropped closely to remove hair and ears. Choice faces were created by morphing targets with a distractor face of the same gender. Each morph continuum progressed from the target identity to the distractor identity by increments of 10% (10% target/90% distractor, 20% target/80% distractor, etc.).

On each trial, a target face is presented at the top of the screen facing 30° to the viewer’s left. Below the target are frontal views of three faces from a morph continuum involving the target. The task is to choose the face that most resembles the target face. Each choice face contained 10–90% of the target face. The greater the percentage difference between the choice faces, the easier the trial, and the exact

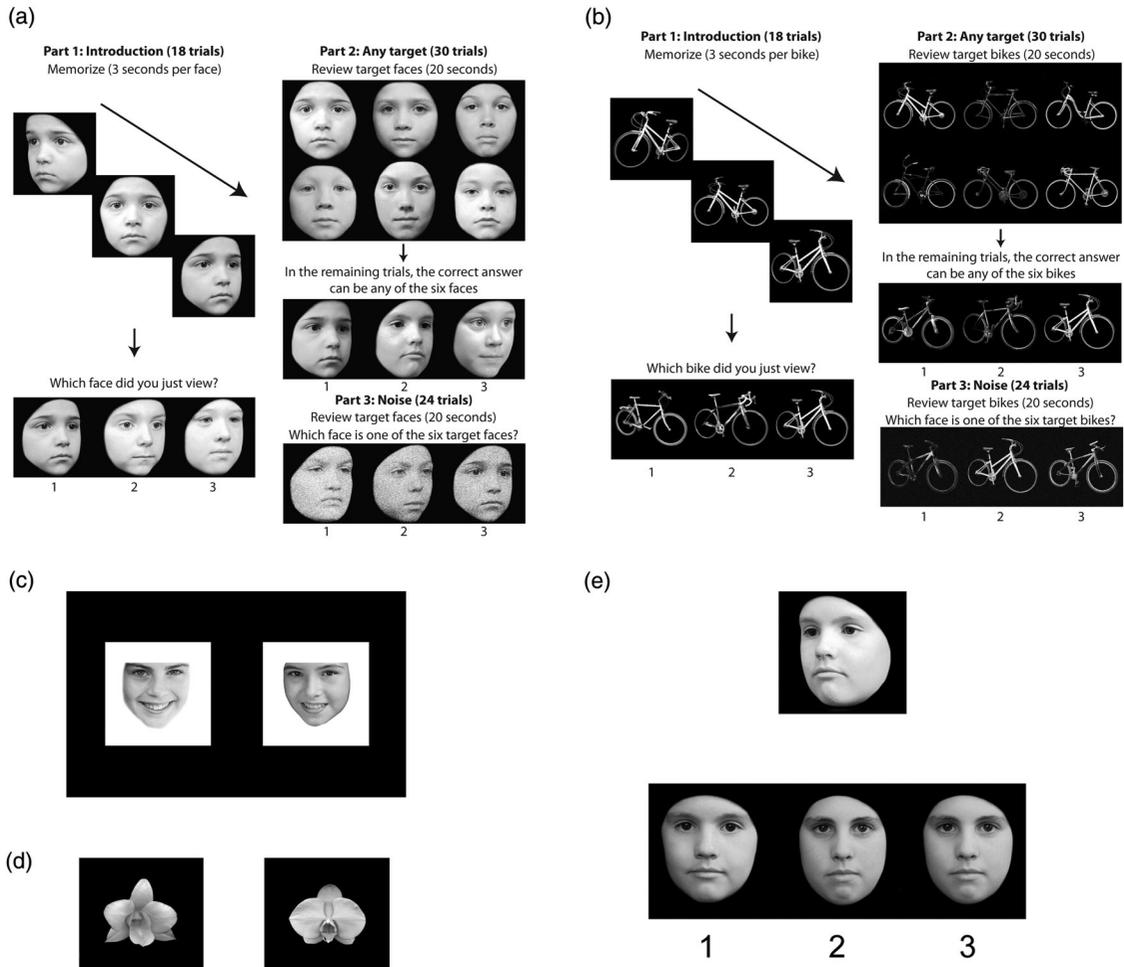


Figure 1. Examples from children's tasks: (a) Six-target version of the Cambridge Face Memory Test-Kids (CFMT-K); (b) six-target version of the Cambridge Bicycle Memory Test (CBMT); (c) Old/New Faces; (d) Old/New Flowers; (e) the Dartmouth Face Perception Test (DFPT).

combination of choice faces was determined through piloting. Each target appears five times with different combinations of choice faces from the target's morph continuum, for a total of 40 trials. Participants respond by key press, and there is no time limit. Because the 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%.

Cambridge Face Memory Test-Kids (CFMT-K). The Cambridge Face Memory Test-Kids is based on the adult version of the task (CFMT; Duchaine & Nakayama, 2006a). Unlike the original CFMT, the CFMT-K uses faces of children instead of adults. Targets and distractors are male faces with neutral

expressions chosen from the Dartmouth Database of Children's Faces (Dalrymple et al., 2013) and cropped so that hair and ears are not visible.

This task begins with a practice session. A cartoon face is presented three times from three different angles (30° left, front, 30° right) for 3 s each. The participant is asked to try to remember the face and then to pick it out from a choice of three cartoon faces. Choice faces are presented at the same angles as the target faces in the memorization phase: 30° left, front, 30° right, on three separate trials. The practice session is designed to familiarize the participant with the format of the test.

In the first part of the test the participant is introduced to the target faces using a procedure identical to that in the practice session, except that real faces

are used instead of cartoons. Children 10-years-of-age and older learn six target faces (18 trials in Part 1), and children 9-years-of-age and younger learn four targets (12 trials in Part 1).¹ In the second part of the test, the participant is asked to review frontal views of the target faces, which are presented together on the screen for 20 s. At the end of the review period, test trials again consist of three choice faces. The participant is told that one of the choice faces is one of the targets, but is not informed which target will appear on any given trial. Each target appears five times in the second part of the test (6 targets: 30 trials; 4 targets: 20 trials). All choice faces on a given trial were presented from the same viewpoint, (30° left, frontal, or 30° right). In the final part of the task, the participant is again asked to review frontal images of the target faces for 20 s and then to choose the targets from a choice of three faces (which again appear at 30° left, frontal, or 30° right). This final part of the task differs from the second part because visual noise is added to the choice faces. Each target appears four times (6 targets: 24 trials; 4 targets: 16 trials). In total, the children 10-years-of-age and older children complete 72 trials, while children 9-years-of-age and younger complete 48 trials. Testing takes 10 to 15 minutes. Chance-level performance on these tasks is 33.3%.

Old/New Task. Ten target and 30 distractor faces were chosen from the Internet. All faces were female children and were matched for age, facial orientation, and facial expression. Faces were frontal view, greyscale, with hair, ears, and any identifiable moles or freckles not visible.

For the encoding portion of this task, target faces are presented one at a time for 3 s each in the centre of the screen. Targets are immediately shown again for 3 s each, and in the same order (i.e., each target was presented twice). The participant is instructed to look at the faces and try to remember them. For the test phase, one target and a similar-looking distractor appear simultaneously on the screen for 1 s. The target is the same image from the encoding phase, while the distractor is a face that they have not seen before. The participant is asked to press a key to indicate which face is one of the target faces (i.e., which is the “old” face). If the participant does not respond within the 1-s window, a blank screen with text, “Please respond now”

appears, which remains until a response is provided. Targets appear three times each, for a total of 30 trials. The order of appearance of the targets is random, but fixed across participants so that they are all taking the exact same test. There are 30 unique distractors that are never repeated. Chance-level performance for this test is 50%.

Object tests.

Cambridge Bicycle Memory Test (CBMT). The CBMT is identical to the CFMT–K, except it uses bicycles instead of faces. Fifty-two adults’ bicycles were photographed from three different angles (30° left, 0°, 30° right) such that 0° was a view of the bicycle from the side. Photographs were taken against a plain background, and care was taken to ensure that all bicycles were in the same position (e.g., pedals were positioned vertically, at 6 and 12 o’clock). Images were converted to greyscale, and identifying text and logos were removed using Adobe Photoshop. Bicycles were then removed from the background and pasted onto a plain black background. Wheel spokes were removed in this process.

Old/New Task. The Old/New Task is identical to the Old/New Task described above with faces, except it uses photographs of flowers instead of faces. Photographs were taken from the Internet, converted to greyscale, and pasted onto a black background. Targets were paired with similar-looking distractors.

Analyses

Data handling. Children serving as controls were carefully observed while they performed the tasks, and data from any child who did not pay adequate attention to the task, pressed keys randomly, or did not appear to understand the tasks were not analysed ($n = 6$, all 5-years-old). Using the remaining data, we created different control groups for DPs of different ages. For each test, the data from each child with DP were compared to data from between 26–45 typically developing children who were the same age, ± 1 year (e.g., data from A.O., who was 8, were compared to data from 7-, 8-, and 9-year-olds). Because 4-year-olds were deemed too young for the tasks, data from C.N., who was 5, were compared to data from 5- and 6-year-olds. Scores from the 9-year-old DP (H. P.H.) were compared to data from 8-, 9- and 10-year-

¹Extensive piloting of the six-target version of the task with children ages 7-12 years indicated floor effects with children 9 and younger, hence a four-target version of the task was created for children under 10 years.

olds who performed the four-target versions of the CFMT-style tasks, and scores from the 10-year-old DP (N.L.) were compared to data from 9-, 10-, and 11-year-olds who performed the six-target versions of the CFMT-style tests (i.e., we had two groups of 9-year-olds and two groups of 10-year-olds to accommodate the different task versions).

For the Dartmouth Face Perception Task, several steps were taken to remove control scores that were likely to reflect inadequate attention to the task. First, the data from controls of the appropriate ages were combined to calculate a mean and standard deviation for each task. Any score more than two standard deviations below the mean was considered an outlier. These scores were removed, and new means and standard deviations were calculated. We then computed *z*-scores for each child and ran Crawford and colleagues' modified *t*-tests using SINGLIMS software (Crawford & Garthwaite, 2002; Crawford & Howell, 1998) to compare each child to their age-matched control group. This modified *t*-test is a relatively 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 $\alpha = .05$. The number of children tested and final sample sizes for each age on this test are included in Table 4.

Similar steps were taken for the paired face and object memory tasks. First, the data from controls of the appropriate ages were combined to calculate a mean and standard deviation for each task. Any score that was more than two standard deviations below the mean was considered an outlier. These scores were removed, and new means and standard deviations were calculated. Next, because the critical analyses are within-subjects comparisons of scores on paired face and object tasks, data from any child who was missing one test score from a pair were removed for that test pair (e.g., if a child was missing the CFMT, we would remove the CFMT and CBMT, but not the Old/New Faces and Old/New Flowers). To determine the standard difference between face and object test pairs, difference scores were calculated (CFMT – CBMT, and Old/New Faces – Old/New Flowers). Because positive and negative difference scores can average out, producing a misleading representation of the difference between test difficulties, the absolute value of the difference between scores was calculated for each child. The absolute values were used to compute a mean and standard deviation of the difference scores. The data from any child whose difference score was greater than two standard

deviations above the mean (i.e., a very large difference) were considered outliers and were removed for that test pair. Control data from the matched face and object tasks are summarized in Table 5.

Using the filtered data, we first compared the scores from each DP child to data from their control group to identify scores that were two standard deviations or more below the control mean. Next, we used Crawford et al. (2009) modified *t*-statistics to identify scores that were significantly below the control mean, $\alpha = .05$, Supplemental Table 1. Finally, we used Bayesian inferential methods to determine whether there was a significant difference between face and object memory scores for each child with DP (DiffBayes_ES_CP.EXE software; Crawford & Garthwaite, 2007; Crawford, Garthwaite, & Porter, 2010; Crawford, Garthwaite, & Ryan, 2011). This method takes into account control means and standard deviations from two tests and the correlation between the scores on those tests to determine the probability that the difference between an individual's scores is consistent with the expected difference between scores from the control group. If an individual's difference score is outside the normal range, it is unlikely that the individual is part of the normative group.

Results

Dartmouth Face Perception Test

Dartmouth Face Perception Test scores for DPs and age-matched controls are in Table 4 and plotted in Figure 2. All children were more than two standard deviations below the control mean on the DFPT, except for C.N., who was -1.55 standard deviations below the mean. These results were in line with results from the modified *t*-tests (Crawford et al., 2009; Sokal & Rohlf, 1995), which identified five of the six children as scoring significantly below the control mean (all but C.N., $p = .138$). Given the floor effects seen with typically developing 5- and 6-year-olds, we chose to retain C.N.'s data, but to interpret it with caution.

Cambridge memory tests

Test scores for each DP are in Table 6, and difference scores (faces–bicycles) for DPs and age-matched controls are plotted in Figure 3. Four of the six DPs were more than two standard deviations below controls on the Cambridge Face Memory Test–Kids. C.N. was -1.28 , and H.P.H. was -1.77 standard deviations below the mean. In contrast, none of the DPs was more than two standard deviations below the

Table 4. Percentage accuracy and z-scores from children with developmental prosopagnosia on Dartmouth Face Perception Test

DP	Control ages (years)	Tested <i>n</i>	Final <i>n</i>	Control mean (<i>SD</i>)	Accuracy (%)	z-score	<i>p</i>
C.N. (5F)	5, 6	37	29	56.7 (13.9)	35.0	-1.55	.138
A.O. (8M)	7, 8, 9	39	36	72.3 (12.5)	40.0	-2.58	.015**
H.P.H. (9M)	8, 9, 10	39	38	74.3 (12.8)	42.5	-2.49	.019**
N.L. (10M)	9, 10, 11	39	36	78.5 (10.6)	30.0	-4.59	<.001**
S.W.J. (11M)	10, 11, 12	46	45	81.2 (11.4)	35.0	-4.04	<.001**
M.F. (12F)	11, 12, 13	43	40	83.9 (10.8)	47.5	-3.28	.002**

Note: DP = developmental prosopagnosia. The *p*-values from Crawford, Garthwaite, and Howell (2009) modified *t* tests indicate whether scores are significantly lower than the control mean. Bold = z-scores > 2 standard deviations below the control mean.

***p* < .050.

Table 5. Percentage accuracy from control participants on matched face and object tasks

Control group used for	Tests	Control ages (years)	Tested <i>n</i>	Final <i>n</i>	Faces % (<i>SD</i>)	Objects % (<i>SD</i>)	Difference (absolute value) (%)	Correlation
C.N. (5F)	CMT	5, 6	37	26	54.3 (13.2)	57.5 (12.9)	3.2	.46
	Old/New			24	68.5 (13.2)	65.7 (14.4)	2.8	.63
A.O. (8M)	CMT	7, 8, 9	39	35	75.9 (15.8)	80.0 (16.5)	4.1	.44
	Old/New			35	80.1 (12.6)	83.2 (11.2)	3.1	.39
H.P.H. (9M)	CMT	8, 9, 10	39	35	78.5 (14.9)	79.3 (16.3)	0.8	.34
	Old/New			31	80.2 (11.0)	83.9 (11.7)	3.7	.35
N.L. (10M)	CMT	9, 10, 11	39	35	69.8 (10.0)	73.3 (13.2)	3.5	.28
	Old/New			31	86.1 (10.5)	85.3 (13.4)	0.8	.64
S.W.J. (11M)	CMT	10, 11, 12	46	42	78.0 (12.2)	71.1 (11.1)	6.9	.43
	Old/New			39	87.6 (10.6)	86.7 (9.1)	0.9	.56
M.F. (12F)	CMT	11, 12, 13	43	38	78.4 (12.8)	73.7 (12.0)	4.7	.46
	Old/New			34	88.2 (8.8)	86.5 (9.7)	1.7	.67

Note: Cambridge Memory Tests (CMT) are Cambridge Face Memory Test–Kids and Cambridge Bicycle Memory Test. Old/New tests are Old/New Faces and Old/New Flowers.

control mean for the Cambridge Bicycle Memory Test. Three of the DPs (C.N., A.O., N.L.) had significantly lower scores on the face test than the object test. The difference between face and object scores for H.P.H. and M.F. approached significance (H.P.H., *p* = .083; M.F., *p* = .073).

Old/New tests

Test scores for each DP are in Table 6, and difference scores (faces–flowers) for DPs and age-matched controls are plotted in Figure 4. Results from the Old/New tests were largely in line with results from the CMT-style tests. The oldest children, N.L., S.W.J., and M.F., were more than two standard deviations below the mean on the Old/New Faces test. C.N. was -1.41, and A.O. was -1.85, whereas H.P.H.'s score was just below average: -0.32. None of the children was more than two standard deviations below the control mean for the Old/New Flowers test. A.O., N.L., and M.F. performed significantly worse on the face test than on the object test, and the difference between face and object scores for C.N. approached

significance (*p* = .061). The differences between face and object scores for H.P.H. and S.W.J. were not significant.

Summary

As can be seen in Table 6, C.N., A.O., N.L., and M.F. scored worse on the face tasks than on the matched object tasks, showing evidence of face-specific deficits. The differences between S.W.J.'s face and object scores were not significant, indicating more general visual-processing deficits. H.P.H.'s scores were inconsistent, with a difference score that approached significance for the CMT-style tests, but similar scores on the Old/New Faces and Old/New Flowers tasks. Thus H.P.H.'s scores are difficult to interpret.

DISCUSSION

We tested six children with developmental prosopagnosia on matched tests of face and object memory to assess whether their visual-processing deficits were face-specific, or whether they extended to other

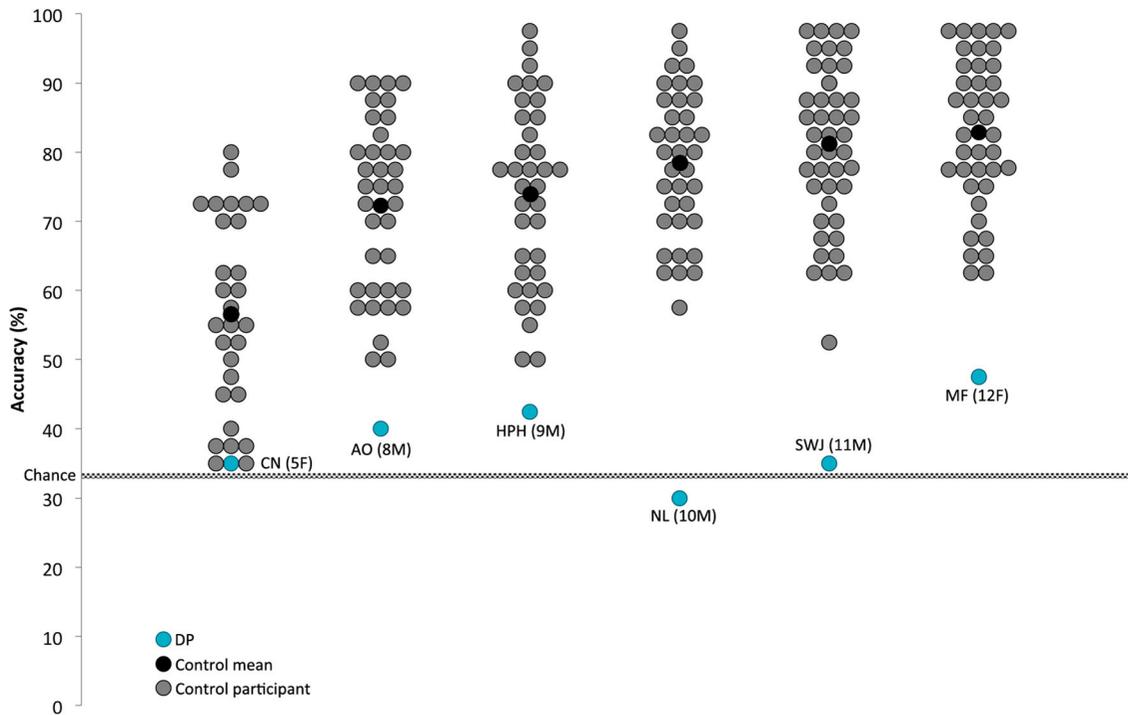


Figure 2. Dartmouth Face Perception Test (DFPT) scores for developmental prosopagnosics (DPs) and age-matched controls. Children with DP denoted by initials (AgeGender), F = female, M = male. To view this figure in colour, please visit the online version of this Journal.

classes of objects. Five of the six children had consistent results across tests, with four showing evidence of face-specific deficits, and one demonstrating more general face and object memory deficits. The remaining child showed evidence of face-specific deficits on one pair of tests, and more general object-processing deficits on the other pair of tests, making it difficult to interpret

his results. Taken together, this study provides behavioural evidence of a separation between face- and object-processing mechanisms in children as young as 8-years-old and may extend to children as young as 5-years-old. This study also documents another element of phenotypic heterogeneity in developmental prosopagnosia in childhood.

Table 6. Percentage accuracy and z-scores from children with developmental prosopagnosia on matched face and object tasks

DP (AgeGender)	Tests	Control ages (years)	Tested <i>n</i>	Final <i>n</i>	Faces (%)	Objects (%)	Faces (z)	Objects (z)	<i>p</i>
C.N. (5F)	CMT	5, 6	37	26	37.5	77.1	-1.28	1.52	.012**
	Old/New			24	50.0	70.0	-1.40	0.30	.061*
A.O. (8M)	CMT	7, 8, 9	39	35	37.5	79.2	-2.43	-0.05	.034**
	Old/New			35	56.7	90.0	-1.85	0.61	.033**
H.P.H. (9M)	CMT	8, 9, 10	39	35	52.0	84.7	-1.77	0.33	.083*
	Old/New			31	76.7	66.7	-0.32	-1.47	.339
N.L. (10M)	CMT	9, 10, 11	39	35	34.7	84.7	-2.91	1.49	.001**
	Old/New			31	33.3	90.0	-3.89	0.37	<.001**
S.W.J. (11M)	CMT	10, 11, 12	46	42	44.4	59.7	-2.75	-1.03	.131
	Old/New			39	60.0	73.3	-2.61	-1.35	.212
M.F. (12F)	CMT	11, 12, 13	43	38	51.4	72.2	-2.11	-0.13	.073*
	Old/New			34	56.7	86.7	-3.58	0.02	<.001**

Note: DP = developmental prosopagnosia; Cambridge Memory Tests (CMT) are Cambridge Face Memory Test-Kids and Cambridge Bicycle Memory Test. Old/New tests are Old/New Faces and Old/New Flowers. DiffBayes_ES_CP software (Crawford & Garthwaite, 2007; Crawford et al., 2010; Crawford et al., 2011) was used to compute *p*-values indicating whether a child's score on a face task is significantly different from their score on the matched object task. Bold = z-scores > 2 standard deviations below the control mean.

p* < .100. *p* < .050.

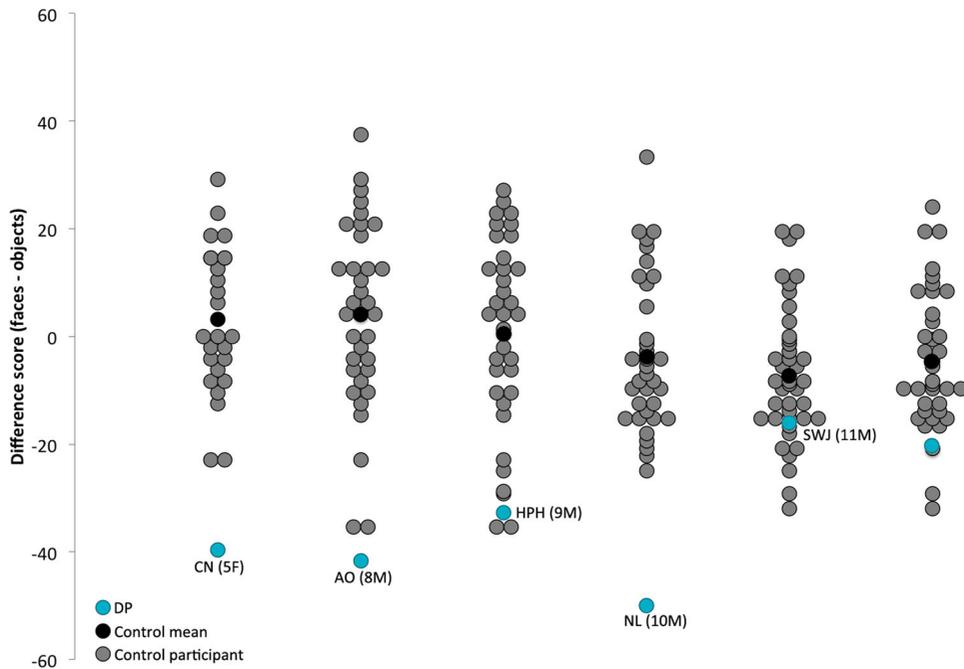


Figure 3. Difference scores for developmental prosopagnosics (DPs) and age-matched controls for Cambridge Memory Tests: Cambridge Face Memory Test–Kids and Cambridge Bicycle Memory Test. Difference scores were calculated for each individual by subtracting CBMT scores from CFMT–Kids scores (i.e., faces – bikes). A negative score indicates poorer performance on the face task than on the bicycle task. Children with DP denoted by their initials (AgeGender), F = female, M = male. To view this figure in colour, please visit the online version of this Journal.

Although our results suggest that face and object mechanisms are separate fairly early in childhood, they do not elucidate whether face- and object-processing mechanisms are separate at birth or become separate later in development. Figure 5 illustrates three possible accounts for our findings. (a) If face- and object-processing mechanisms are fully separate at birth, face-specific deficits could result from developmental abnormalities restricted to the face-processing stream, while general visual-processing deficits would result from developmental abnormalities affecting both streams (Figure 5a). (b) If face- and object-processing mechanisms separate later in development, face-specific deficits could result from abnormal development of face-processing mechanisms after face- and object-processing mechanisms have separated, while more general visual-processing deficits could result from abnormal development prior to this separation or abnormal development of both types of mechanisms after separation (Figure 5b). Finally, (c) face-specific deficits could result from a failure of face- and object-processing mechanisms to separate, resulting in a lack of specialization for faces. If this common system develops abnormally,

general object-processing deficits would occur (Figure 5c). Future research is needed to differentiate between these possibilities.

Our findings from children with DP are consistent with other studies that have demonstrated face-specific deficits in some children (Jones & Tranel, 2001; Wilson et al., 2010) and more general visual deficits in others (Ariel & Sadeh, 1996; Brunsdon et al., 2006; McConachie, 1976; Wilson et al., 2010). In adults, findings across studies show a similar distribution of face-specific versus general visual deficits. Table 1 provides an estimate of this distribution, indicating a relatively even split between adults with face-specific and those with more general object-processing deficits. Although tests of face and object processing vary across studies, this approximate proportion of face-specific and general visual deficits in adults is informative here because it provides a comparison for studies on DP in children. Little is known about the commonalities between DP in adulthood and childhood, but given that many adults with DP recall having face recognition deficits in childhood (Duchaine, Murray, Turner, White, & Garrido, 2009; Duchaine & Nakayama, 2006b; Duchaine et al., 2006;

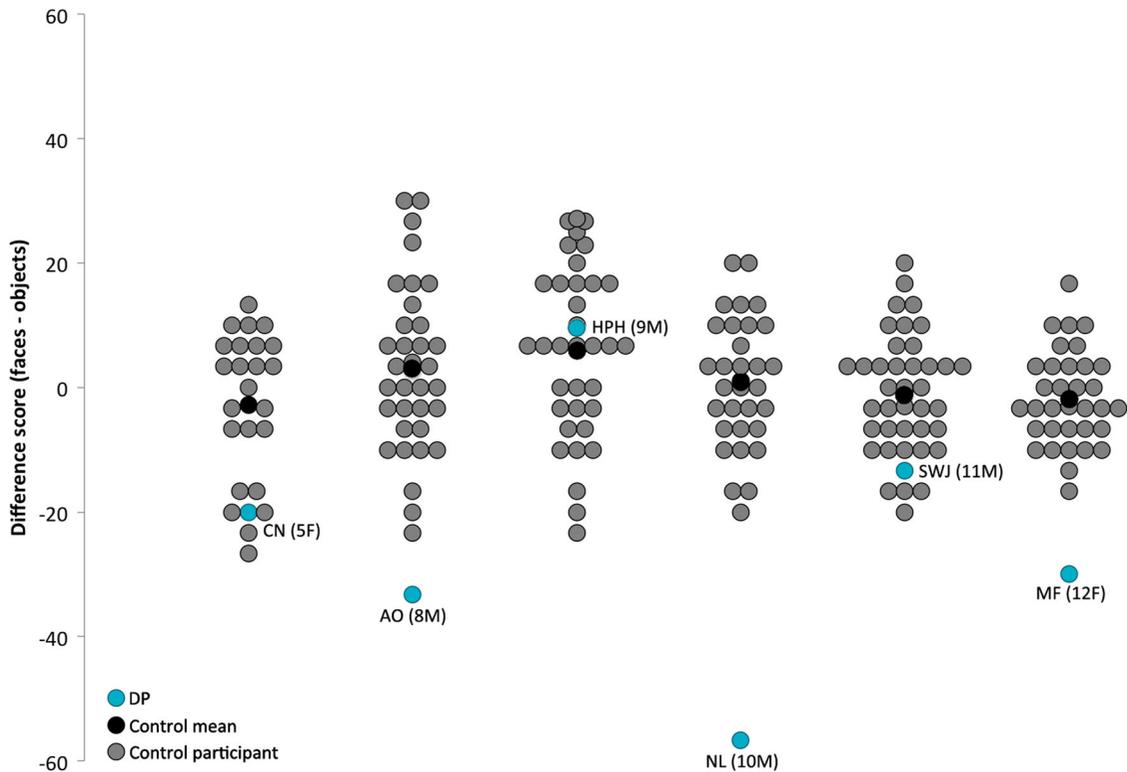


Figure 4. Difference scores for developmental prosopagnosics (DPs) and age-matched controls for Old/New tests: Old/New Faces and Old/New Flowers. Difference scores were calculated for each individual by subtracting Old/New Flowers scores from Old/New Faces scores (i.e., faces – flowers). A negative score indicates poorer performance on the face task than on the flower task. Children with DP denoted by their initials (AgeGender), F = female, M = male. To view this figure in colour, please visit the online version of this Journal.

Garrido, Duchaine, & Nakayama, 2008), one plausible assumption is that DP remains stable throughout development. The current data show similarities between children and previously reported adult cases in terms of the face specificity of their deficits. While this supports the possibility that DP is a stable, life-long disorder, this finding may not be true for all aspects of DP: we recently found that at least half of a sample of 16 adult DPs had normal face perception despite deficits of face memory, but that all eight children with DP in our sample had impaired face perception and face memory (Dalrymple et al., 2014). This indicates that certain characteristics of DP may change with development. In the case of face perception and face memory, it is possible that for some, face perception improves later in life, whereas face memory remains impaired. In contrast, the face-specificity of an individual's DP may be relatively stable. Continued comparisons between DP in childhood and adulthood with larger samples and longitudinal studies of DP will be critical

for generating a more complete understanding of the developmental trajectory of this disorder.

Several neurophysiological studies have indicated that face and object processing may be separate early in development. Functional magnetic resonance imaging (fMRI) studies have detected face-selective responses in the fusiform face area of children as young as 4-years-old (Cantlon, Pinel, Dehaene, & Pelphey, 2011). However face-selective areas in the ventral stream are not adult-like in size by 12–16-years-old (Golarai et al., 2007; Golarai, Liberman, Yoon, & Grill-Spector, 2010). Fast periodic visual stimulation (FPVS, high temporal resolution electroencephalography, EEG) has detected face-selective activation in the right hemisphere of infants as young as 4–6-months-old (deHeering & Rossion, 2015), suggesting that face-processing mechanisms are distinct in infancy. Similarly, face-selective processing has been detected in the right hemisphere of 5–8-month-old infants using near-infrared spectroscopy (NIRS): infants showed increased activation to

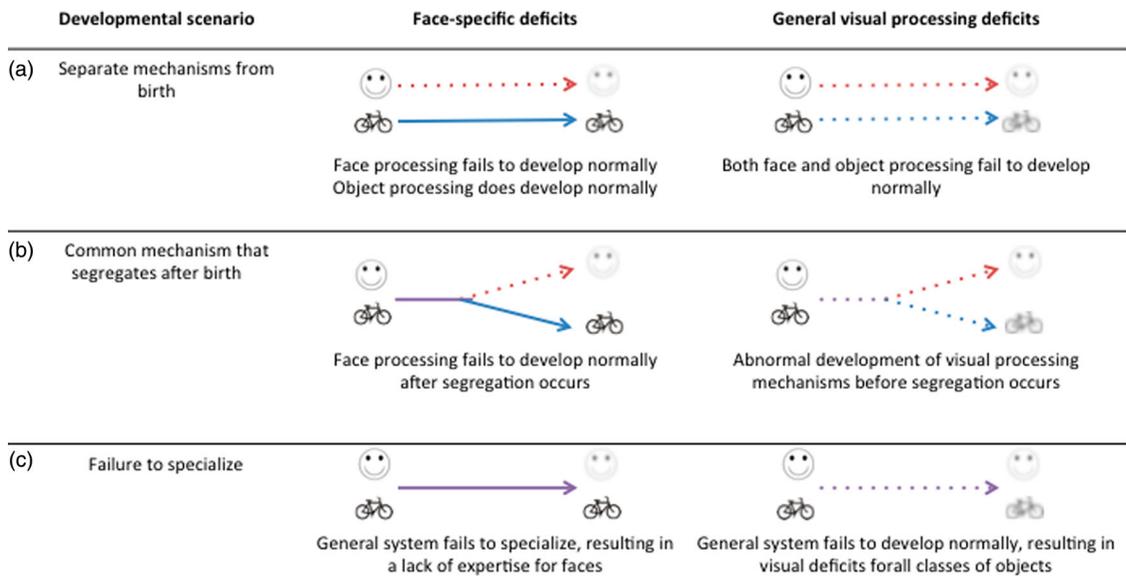


Figure 5. Different developmental scenarios that could explain the finding that some individuals with developmental prosopagnosia have face-specific deficits, while others have more general visual-processing deficits. (a) The processing mechanisms for faces and objects are separate from birth; (b) a common visual-processing mechanism separates after birth; (c) a common visual-processing mechanism fails to specialize. To view this figure in colour, please visit the online version of this Journal.

upright faces than to inverted faces and objects (Nakato et al., 2009; Otsuka et al., 2007). These imaging and EEG findings provide evidence for neural specialization, and the present study complements them by providing neuropsychological evidence that face- and object-processing abilities are dissociable in children as young as 5-years-old.

Little is known about what underlies abnormal development in DP, but one possibility is that face-specific deficits result from focal developmental abnormalities restricted to neural mechanisms specific to faces. In contrast, general visual-processing deficits that include both face- and object-processing impairments may result from more widespread neural abnormalities (i.e., that encompass both face- and object-processing regions). Ramus (2004) suggested that ectopias, abnormal cellular layering resulting from neural migration errors, could lead to particular behavioural deficits related to the function of the affected brain area. Ramus's general hypothesis about selective developmental deficits was motivated by evidence of abnormal cellular migration in the perisylvian cortex of dyslexics (Galaburda & Kemper, 1979; Galaburda, Sherman, Rosen, Aboitiz, & Geschwind, 1985; Humphreys, Kaufmann, & Galaburda, 1990), but similar cellular migration issues could underlie face- and object-processing deficits in DP. That is, specific

cortical abnormalities that affect face-processing areas alone could lead to the face-specific deficits that were found in four of the DP children in this study, while more extensive cortical abnormalities that affect face- and object-processing regions could lead to the generalized deficits that were found in the other DP children.

In addition to demonstrating a behavioural separation between face and object processing in children as young as 8, and possibly 5, the current study provides further evidence that DP is a heterogeneous disorder. Within the realm of face processing, impairments can extend beyond impaired identity recognition to problems with face detection (Dalrymple et al., 2014; Garrido et al., 2008), expression recognition (Duchaine et al., 2006), and gender discrimination (Duchaine et al., 2006), though these abilities are normal in a substantial proportion of people with DP (Duchaine, Parker, & Nakayama, 2003; Garrido et al., 2008; Garrido et al., 2009). Also, as mentioned above, some adults with DP have normal face perception despite their face memory deficits (Chatterjee & Nakayama, 2012; Dalrymple et al., 2014; Humphreys, Avidan, & Behrmann, 2007; McKone et al., 2011; Palermo et al., 2011), though in children it is possible that face memory and face perception deficits more often coexist (Dalrymple et al., 2014). The present findings confirm that, beyond

face processing itself, some children with DP have face-specific deficits, while others have more general visual-processing deficits that affect both face and object processing. We should note that one limitation of the current study is that the face memory tests that were paired with object memory tests to establish face-specificity were also used as part of our diagnostic criteria. This design creates a selection bias, but the limited number of tests of face memory that exist for children and the long development time for such tests forced us to rely on the same tests for both purposes. More tests of face memory for children must be developed to make future conclusions more robust.

In summary, we found face-specific deficits in some but not all individuals in a sample of children with DP. Past neuropsychological evidence from converging methodologies has provided evidence for a separation between face-processing and object-processing mechanisms, and work with adults with DP has demonstrated that object processing can develop normally even when face-processing mechanisms do not. The present finding that face-specific deficits can exist in young children provides an upper bound on when in development this separation occurs.

Disclosure statement

The authors have no conflict of interest to disclose.

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