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**What do we know about people with developmental prosopagnosia?**

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## **Abstract**

Developmental prosopagnosia (DP) is a severe deficit in recognising facial identity in the absence of known brain damage or other cognitive, socio-emotional, or low-level visual impairments. Although initially thought to be quite rare, DP has been estimated to affect between 1.0% and 2.5% of the population, with different estimates reflecting different tools and analytical approaches to categorising DP. Research over the last 25 years has identified several cognitive and neural mechanisms that appear to contribute to face recognition deficits in DP, and both structural and functional neural differences have been found between individuals with DP and neurotypical participants. Nevertheless, clear neurocognitive signatures of this condition remain elusive, likely due to a) the high degree of individual variability observed in the behavioural and cognitive profiles of individuals with DP and b) the focus on group-based analyses rather than on in-depth, individual-level investigations. We recommend that future studies emphasise the latter approach.

**Keywords:** Prosopagnosia; Face recognition; Face perception; Individual differences; Neuropsychology

## What do we know about people with developmental prosopagnosia?

The first cases of individuals with severe face identity recognition deficits were described in the mid-19th century. Wigan (1844) briefly reported the case of a man with an “utter inability to remember faces.” The man revealed he could engage in conversations with people for as long as an hour but still fail to recognise their faces the next day. Even personally familiar faces, like those of his friends, would be easily forgotten by him, and he would have to resort to other types of social clues to correctly recognise those individuals, such as the sound of their voices. About two decades later, Quaglino and Borelli presented the case of LL, a 54-year-old man who had recently started to experience extreme difficulty in remembering familiar faces, buildings from his town, and visual scenes in addition to having lost his ability to perceive and discriminate almost any colour (Della Sala & Young, 2003; Quaglino & Borelli, 1867). Interestingly, while LL’s visual impairments immediately followed the occurrence of a right-hemisphere stroke, there was no suggestion of brain damage in the case described by Wigan.

Acquired prosopagnosia (AP) and developmental prosopagnosia (DP) are both face-processing disorders defined by severe face identity recognition impairments. AP occurs following brain damage, often resulting from stroke, traumatic brain injury, or neurodegenerative diseases, and leads to a sudden loss of the ability to recognise people from their faces (Barton et al., 2019; Bodamer, 1947; Damasio et al., 1982; Ellis & Florence, 1990; Rossion et al., 2003). This is what occurred, for example, to Pierrette Sapey (PS), who is probably the most extensively investigated AP in the scientific literature (Mayer et al., 1999; Rossion et al., 2003; for a comprehensive review of over 30 studies assessing PS, see Rossion, 2022a, 2022b). In 1992, at age 41, PS suffered a closed head injury after being hit in the back of the head by the mirror of a London bus on Tower Bridge. The accident resulted in severe brain damage, including to her right inferior occipital gyrus and left middle fusiform gyrus (Rossion et al., 2003; Sorger et al., 2007). Despite the damage, after undergoing extensive neuropsychological rehabilitation, she was able to recover most of her sensory, motor, and cognitive abilities – for example, she had no problem recognising everyday objects by their forms, like animals, cars, or fruits. However, PS permanently lost her ability to identify individuals by their faces, including close family members and herself (Rossion, 2022a).

In contrast, developmental prosopagnosia (DP), also known as *congenital prosopagnosia*, is defined by a severe difficulty in recognising faces in the absence of known brain damage, cognitive or socio-emotional impairments, or low-level visual acuity limitations that could

account for the recognition deficits (Barton et al., 2021; Bate & Tree, 2017; Duchaine & Nakayama, 2006; McConachie, 1976; Susilo & Duchaine, 2013). Unlike AP, DP is believed to arise due to the atypical development of the neural circuitry underlying the face-processing system. This atypical development can, in principle, occur at different points in an individual's development, and as a result, we prefer to use the term *developmental* rather than *congenital*, as the latter implies the presence of impairments that are present at birth (Dalrymple et al., 2017; Susilo & Duchaine, 2013; for a different view, see Behrmann & Avidan, 2005). Examples of DP include AB, a 12-year-old girl (McConachie, 1976), and MJ, a seven-year-old boy (Duchaine, 2011), both of whom severely struggled to recognise the faces of familiar people from an early age. Both children consistently failed to identify friends at school, especially when their classmates wore similar clothes or uniforms. MJ could also not recognise the faces of neighbours he would frequently see and would often confuse the identity of beloved family members – for instance, he would mistake his mother for his aunt and vice-versa when the two women had similar hairstyles. Crucially, neither AB nor MJ were known to have suffered brain damage nor were they diagnosed with other neurodevelopmental disorders that could result in, but not be limited to, face recognition impairments (Duchaine, 2011; McConachie, 1976). Furthermore, consistent with self-reports from other individuals with DP, de Haan and Campbell (1991) found that AB's visual recognition deficits were stable: in a follow-up study of her case 15 years after the original report, she continued to show deficits with facial identity, facial expression, and within-class object recognition.

In this chapter, we focus on what we know about people with extreme difficulty recognising faces due to atypical development – i.e., individuals with DP. Even though cases of AP have been crucial to understanding prosopagnosia and, more broadly, some of the cognitive and neural mechanisms underlying the typical face-processing system in humans (Barton et al., 2019; Bruce & Young, 1986; Duchaine & Yovel, 2015; Rezlescu et al., 2014), it is the study of DP that provides us with the best opportunity to explore naturally occurring individual differences in facial recognition and relate these findings to the investigation of other populations of particular interest for face-processing research like super-recognizers (Geskin & Behrmann, 2018; Russell et al., 2009; Wilmer, 2017; see also Chapter 3). In addition, the impairments in recognising faces observed in developmental cases are often quite severe, with deficits that can match those of acquired cases (Behrmann & Avidan, 2005; Susilo & Duchaine, 2013; but see Barton et al., 2019). A final reason is that, although DP was initially believed to be quite rare, with its first report separated by almost a hundred years from the first published case

of AP (Bornstein, 1963), we now understand that developmental cases are more prevalent than initially supposed (Bate & Tree, 2017; Susilo & Duchaine, 2013), and some studies estimate that DP affects between 1.2% and 2.5% of the population (e.g., Kennerknecht et al., 2006; Zhao et al., 2018; but see the discussion below on new prevalence estimates).

### **How is developmental prosopagnosia identified?**

Given how ubiquitous faces are in our social experiences and how distressing it can be for individuals with DP to struggle to recognise them daily, one might assume that identifying DP should be straightforward. However, both researchers and practitioners have used several different methods to categorise individuals with DP, resulting in different proportions of detected cases (Barton & Corrow, 2016; Dalrymple & Palermo, 2016; DeGutis, Bahierathan, et al., 2023).

#### ***Questionnaires about face recognition***

The simplest tools used for assessing DP are self-report questionnaires. Fortunately, many individuals with DP have provided vivid descriptions of the face recognition challenges they experience in various contexts (Duchaine et al., 2006; McConachie, 1976; for an interesting collection of interviews with individuals with prosopagnosia, see 60 Minutes, 2012). These detailed descriptions have helped researchers develop several self-report questionnaires to measure the extent to which an individual's face recognition may be compromised by assessing the respondent's difficulties across different daily activities (Table 1) (Arizpe et al., 2019; Kennerknecht et al., 2006; Shah et al., 2015). Nevertheless, while subjective reports have helped researchers and practitioners to identify many cases of DP, self-assessments by themselves are insufficient. Several studies have shown that the relationship between self-perceived face recognition and objectively measured face recognition is weak to moderate (Arizpe et al., 2019; Bobak et al., 2019; Gray et al., 2017; Matsuyoshi & Watanabe, 2021; Palermo et al., 2017). In fact, although some individuals do appear to have good insight into their face recognition impairments, others may either overestimate their abilities – for example, by conflating their proficiency with familiar and unfamiliar faces (Bindemann et al., 2014; Bobak et al., 2019) or assuming that most people experience the same difficulties they do (Bowles et al., 2009; Dalrymple et al., 2012) – or underestimate them, a bias possibly subject to age and gender differences (DeGutis, Yosef, et al., 2023; Murray & Bate, 2019). Therefore, despite self-report questionnaires being an inexpensive, quick, and a useful tool for screening potential individuals with DP in large samples, they must be combined with objective measures to

achieve higher levels of discriminative validity (Arizpe et al., 2019; Barton et al., 2021; Dalrymple & Palermo, 2016; DeGutis, Bahierathan, et al., 2023; for a different view, see Burns et al., 2023).

**Table 1**

*Example questions from the 20-Item Prosopagnosia Index (PI20) and mean scores for participants*

Question number	Statement	Controls	Suspected prosopagnosics
6	When people change their hairstyle, or wear hats, I have problems recognizing them.	1.86 (0.95)	4.33 (0.86)
10	Without hearing people's voice, I struggle to recognize them.	1.66 (0.87)	3.78 (1.03)
14	I sometimes find movies hard to follow because of difficulties recognizing characters.	1.73 (1.08)	4.52 (0.75)

*Note.* The PI20 is a self-report questionnaire that assesses the presence of prosopagnosia traits. Agreement with each statement is scored on a five-point scale (1 – strongly disagree to 5 – strongly agree). Mean scores for control and suspected prosopagnosic participants are shown for each item. Standard deviations are shown in parentheses. Adapted from Shah, P. et al. (2015). The 20-item prosopagnosia index (PI20): A self-report instrument for identifying developmental prosopagnosia. *Royal Society Open Science*. 2(6): 140343. <https://doi.org/10.1098/rsos.140343> under a Creative Commons Attribution 4.0 International (CC BY 4.0).

### ***Tests of face recognition***

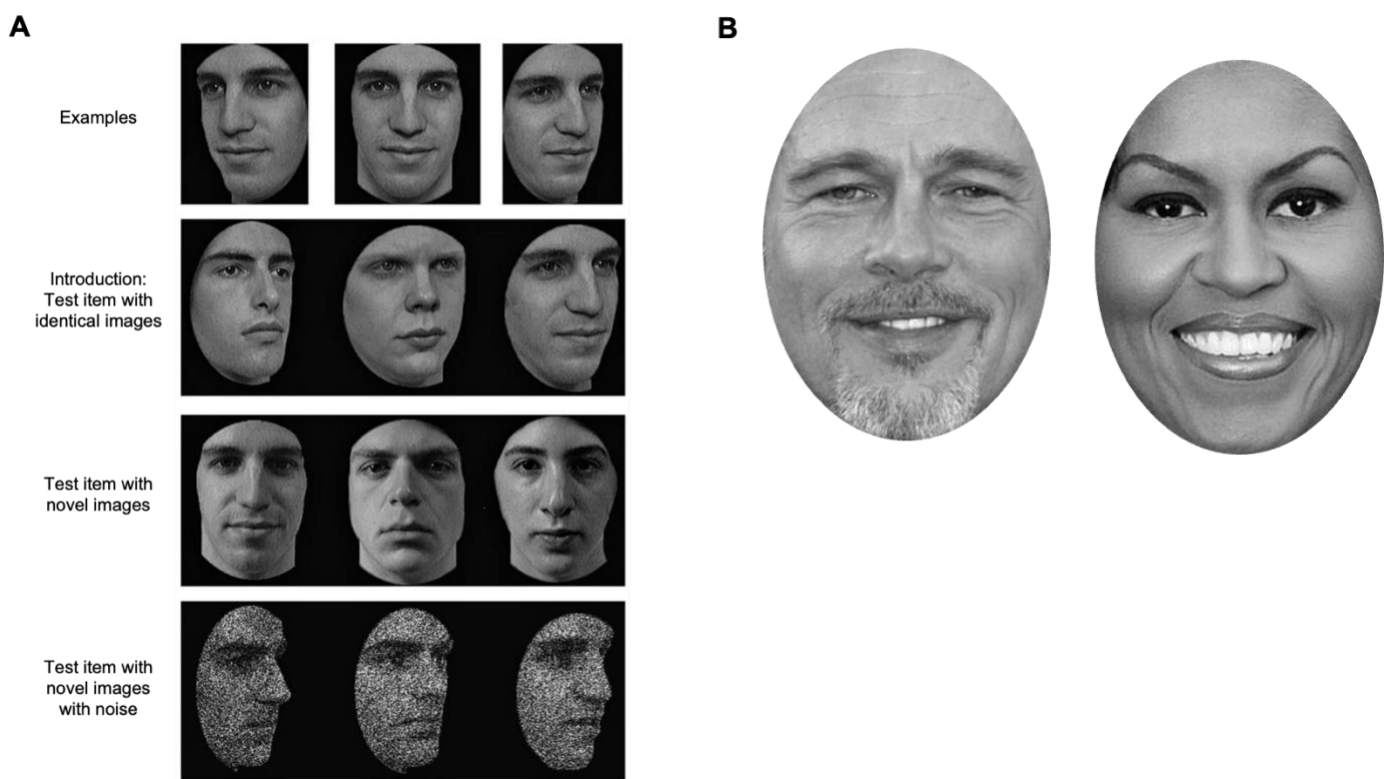
These objective measures are usually standardised tests of face identity recognition. One of the most commonly used tests is the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) (Figure 1A), a test of unfamiliar face identity recognition in which participants must memorise a set of six previously unseen faces and then recognise these identities among distractor faces and under new conditions, such as changes in viewing angles and lighting. Multiple studies have shown that the CFMT presents evidence of strong validity and reliability, both in laboratory and online participants (Cho et al., 2015; Germine et al., 2012; Wilmer et al., 2010, 2012). A key feature of this test is that all faces presented are comprised exclusively of internal facial clues, so external clues such as the hair or clothes of a target identity are not available for the subjects to memorise. This feature is fundamental for the identification of prosopagnosia because it is common for individuals with DP to use non-facial clues to compensate for their face recognition deficits, a pattern overlooked by other tests developed to assess face recognition abilities (Duchaine & Weidenfeld, 2003; Warrington, 1984). A common cutoff approach in studies using the CFMT is to consider accuracy scores around two standard deviations below the control mean to be suggestive of severe face identity deficits (Bate et al., 2019; Bowles et al., 2009; DeGutis, Bahierathan, et al., 2023; Duchaine & Nakayama, 2006; for an alternative diagnostic analysis that aims at minimizing trade-offs between accuracy and speed in the CFMT, see Lowes et al., 2024).

However, the stimuli used in the CFMT are unfamiliar faces, and the faces that prosopagnosics struggle with in daily life have been encountered many times. Therefore, many studies have also employed measures of familiar face identity recognition, such as variations of famous faces tests (Figure 1B), in which participants are presented with the faces of celebrities (e.g., actors and politicians) and asked to identify them (Bate et al., 2024; Behrmann et al., 2005; DeGutis, Bahierathan, et al., 2023; Duchaine & Nakayama, 2005; Mishra et al., 2019). Naturally, interpreting the results of such tests requires considering the degree of familiarity each participant has with the presented identities. For example, familiarity with the faces of many athletes and politicians can vary drastically between groups of participants of different nationalities and with sociodemographic characteristics or personal interests, so unrecognised faces should only be taken into account when a participant appears to have had enough exposure to a face. To assess this issue, researchers usually inquire whether participants have encountered each unrecognised individual in the test on multiple occasions prior to taking the test (Dalrymple & Palermo, 2016). This can be a challenging question for prosopagnosics

because, in essence, they are being asked if they have seen a celebrity often enough that they should have recognised them. However, many participants can often answer quite confidently (“Brad Pitt?! I watched a movie he starred in last week.”). Famous faces tests have proved to be a valuable resource for assessing face identity recognition abilities in individuals with DP, especially when combined with measures of unfamiliar face identity recognition (Barton & Corrow, 2016; Dalrymple & Palermo, 2016; Susilo & Duchaine, 2013).

## Figure 1

*Face recognition tests used to identify developmental prosopagnosia*



*Note.* (A) Example items from the Cambridge Face Memory Test. (B) Two example items from a version of the famous faces test. Images in (A) are reproduced with permission from Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia*, 44(4): 576–585.

<https://doi.org/10.1016/j.neuropsychologia.2005.07.001>. Images in (B): [Brad Pitt's](#) image (left) is licensed under a Creative Commons Attribution 4.0 International ([CC BY-SA 4.0](#)); [Michelle Obama's](#) image (right) is in the public domain.



Self-report questionnaires and standardised face memory tests are the most frequently employed tools to detect individuals with DP, but they are not the only ones used to assess their face processing. As we discuss below, DP can affect other face-processing abilities, extending beyond the domain of face identity memory (DeGutis et al., 2012; Duchaine, Yovel, et al., 2007; Fisher et al., 2016; Peterson et al., 2019; Tardif et al., 2019). Thus, supplementary measures – i.e., measures that help inform decision-making in DP research but are not critical for diagnosis – of other abilities such as face detection and face identity discrimination are often used in combination with face identity recognition tests (DeGutis, Bahierathan, et al., 2023; White et al., 2022).

### ***Prevalence estimates of developmental prosopagnosia***

We noted before that studies have estimated the prevalence of DP to lie between 1.2% and 2.5% (Bowles et al., 2009; Kennerknecht et al., 2006; Zhao et al., 2018). However, we have also pointed out that a wide variety of measures are available to assess face-processing abilities, each with its set of norms and recommended diagnostic cutoffs. Therefore, it is not surprising that there is no consensus on prevalence estimates. In a recent, long-due examination of different criteria used by researchers to identify individuals with DP and estimate population prevalence rates, DeGutis and colleagues (2023) suggested that the 2% prevalence rate, a number widely reported in scientific publications on DP and in the media, is higher than the rate researchers would find if they adhered to the most common diagnostic criteria observed in the field. The authors reviewed the diagnostic criteria adopted by 104 DP studies from 2008 to 2021 and then selected the studies that used any combination (i.e., one or more tests) of self-report questionnaires, the CFMT, and a famous faces test to assess participants (68 out of 104 studies). They then used the diagnostic cutoffs for DP in a large web-based sample of 3116 participants (18-55 years,  $M = 30.99$ ,  $SD = 10.54$ ). The sample was assessed using the Cambridge Face Memory Questionnaire (a self-report questionnaire), the CFMT-3 (identical to the CFMT, except that the CFMT-3 uses computer-generated faces; see Arizpe et al., 2019), and a famous faces test. The main question DeGutis and colleagues aimed to answer was: instead of assuming that 2% of the population has DP, what prevalence rates do we find if the tests and diagnostic cutoffs used in previous studies are applied to the results from a large sample of participants?

Unsurprisingly, the prevalence rates in their sample varied considerably, ranging from .13 to 5.42% depending on the tools and cutoffs used (DeGutis, Bahierathan, et al., 2023). For

example, when using the diagnostic criteria of studies involving only a single test, the observed DP prevalence rate in their sample reached up to 3.11% with cutoffs based on z-scores and 2.09% with cutoffs based on percentiles. In contrast, when three diagnostic tests were used, the prevalence rate in the same sample dropped to as low as .64% with z-scores and .13% with percentiles. This inconsistency underscores the need for a unified diagnostic approach in the field and illustrates that the same individuals may or may not meet the criteria for DP depending on more liberal or strict diagnostic approaches (DeGutis, Bahierathan, et al., 2023).

Despite the considerable variation, DeGutis and colleagues found that nearly half of the selected studies (46%, 31 out of 68) administered three tests – a self-report measure, the CFMT, and a famous faces test – and adopted the criteria of two standard deviations below the control mean in both objective tests (i.e., the CFMT and the famous faces test), as well as subjective reporting of face recognition impairments, to determine whether a participant had DP or not. When the researchers specifically replicated this approach with the large web-based sample, they found a prevalence rate of .93%. For the authors, this number, which is representative of the diagnostic standards employed by almost half of the recent studies in the field, is likely to be a better estimate of the population prevalence rate of DP than the widely reported rate of about 2%. Moreover, it stems from combining evidence from two objective tests and subjective reporting of face identity recognition impairments, an approach endorsed by others in the DP literature (Barton & Corrow, 2016; Bate & Tree, 2017; Dalrymple & Palermo, 2016; Mishra et al., 2021; Stumps et al., 2020) and recommended by the Diagnostic and Statistical Manual of Mental Disorders (DSM-5) for diagnosing mild and major neurocognitive disorders through standardised neuropsychological testing (American Psychiatric Association, 2013; Sachdev et al., 2014).

Diagnosing DP also demands ruling out other visual, neurological, cognitive, and socio-emotional factors that could account for the observed face identity recognition deficits (Barton et al., 2021; Bate & Tree, 2017; Dalrymple et al., 2014). For example, face-processing impairments have been reported in the context of macular degeneration (Mazzoli et al., 2019), dementia syndromes (Kumfor et al., 2015), autism spectrum disorder (ASD, Dwyer et al., 2019), and schizophrenia (Megreya, 2016). Although someone affected by one of these conditions may experience, among other symptoms, a severe impairment in their capacity to recognise people by their faces, the etiology of their face-processing difficulties is different from participants without these conditions (Barton et al., 2021; Dalrymple et al., 2017; Susilo & Duchaine, 2013). Still, it is possible for an individual to be affected by both DP and a different disorder (e.g., ASD;

Bell et al., 2023), a scenario that often introduces substantial challenges for the assessment and diagnostic decision-making processes (Dalrymple & Palermo, 2016).

Another potential source of confusion in diagnosing DP is the co-occurrence of face recognition impairments in the context of other face-processing disorders, for example, prosopometamorphopsia (PMO), a striking condition in which faces can appear distorted in shape, texture, position, and colour, often in the absence of distortions to non-facial visual categories (Blom et al., 2021; Herald et al., 2023). Despite nearly all PMO reports to date having described cases that emerged in the context of brain damage or other neurological disorders (Herald et al., 2023; but see Blom et al., 2014), PMO can manifest as a result of atypical development. Our lab has recently carried out in-depth assessments of two cases of PMO with likely lifelong histories of perceiving face distortions (Ezri, a 32-year-old female, and Zed, a 15-year-old male). Both individuals experienced distortions that alter the shape, texture, configuration, and colour of faces, including those presented in the CFMT and the famous faces test. While Ezri presented no signs of face recognition deficits, Zed performed poorly in both tests. However, it is unclear if his performance is a consequence of limitations in accurately representing faces due to the interference of perceptual distortions (PMO) or results from problems similar to those in typical DP. These results highlight the diagnostic challenges of confirming or excluding DP when considering the potential comorbidity with other developmental disorders that impact face processing.

### **What are the cognitive bases of developmental prosopagnosia?**

Researchers have investigated a variety of cognitive mechanisms that may underlie face identity recognition deficits in DP (Dalrymple & Palermo, 2016; Duchaine, 2011). One possibility is that such deficits result from the atypical development of domain-specific mechanisms specialised in face processing, an account known as the “face-specificity hypothesis” (Duchaine et al., 2006). In contrast, alternative accounts posit that the mechanisms disrupted in DP are not face-specific and produce visual recognition deficits affecting other categories, including non-biological objects (e.g., cars and human-made tools). The work investigating these dueling accounts of DP has contributed to the longstanding debate in the literature about the nature of the mechanisms supporting face processing (Behrmann & Plaut, 2013; Diamond & Carey, 1986; Duchaine et al., 2006; Yin, 1969). Interestingly, the relationship between face and object recognition in DP was already discussed in the first formal report of the condition (McConachie, 1976).

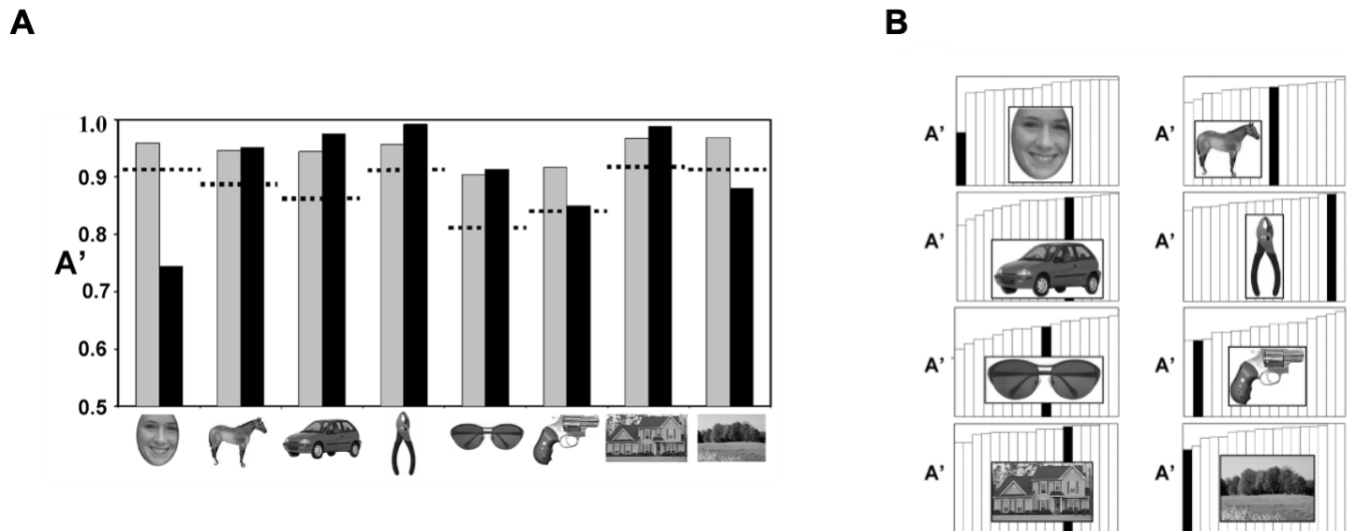
A large number of studies have presented evidence of co-occurring face and object recognition deficits among DP cases (e.g., Behrmann et al., 2005; Duchaine & Nakayama, 2005; Garrido et al., 2008; Lee et al., 2010). More recently, a review of over 700 cases of DP reported between 1976 and 2016 found that, in the cases whose object recognition was tested, nearly 80% (191 out of 238) showed evidence of both face and object recognition impairments (Geskin & Behrmann, 2018). We recommend considering these numbers with caution, as the criteria adopted by the authors to classify an individual's object recognition ability as impaired were overly liberal and produced a significant number of false positives (see Garrido et al., 2018). Still, the review does clearly support the observation that object recognition deficits are common, and probably even more likely to co-occur than not, among individuals with DP (Barton et al., 2019; Biotti, Gray, et al., 2017; Dalrymple et al., 2017; Duchaine & Nakayama, 2005; Gray & Cook, 2018). The co-occurrence of object recognition impairments has been reported for both non-biological (e.g., cars and guns; Biotti, Gray, et al., 2017; Duchaine, Germine, et al., 2007) and biological (e.g., human bodies and non-human animals; Biotti, Gray, et al., 2017; Epihova et al., 2023) object categories. These co-occurrent deficits may reflect either the comorbidity of independent neurodevelopmental disorders (for example, DP and developmental object agnosia) affected by the atypical development of shared structures in the occipital-temporal cortex (Gray & Cook, 2018), the existence of anatomically widespread functional deficits in category-selective areas of the visual-processing system (Jiahui et al., 2018), or the atypical development of domain-general mechanisms that contribute to both face and object recognition (Geskin & Behrmann, 2018).

More revealing to this debate about the basis for face recognition, however, is the evidence of face recognition deficits without object recognition impairments in numerous cases of DP. Even if we assumed that no more than around 20% of the cases reviewed by Geskin and Behrmann (2018) have face-specific deficits (an estimate likely to be imprecise), the inferential value of this substantial number of cases showing a dissociation should be clear (Crawford et al., 2003; Garrido et al., 2018; Nickels et al., 2022; Shallice, 1988). One notable case of dissociation is Edward, a 53-year-old man with severe DP who was extensively tested for face and non-face recognition abilities by Duchaine et al. (2006). The researchers explored five alternative explanations to the face-specific hypothesis that might account for Edward's dissociation results, including hypotheses proposing prosopagnosia results from deficits with within-class discrimination (Damasio et al., 1982) and the development of expertise (Diamond & Carey, 1986; Gauthier et al., 1998). Despite his broad face-processing deficits, Edward performed

normally on tasks requiring him to recognise individual items within the same non-face object category (e.g., cars, houses, or “greebles”; Gauthier et al., 1998), use second-order configural information (i.e., spacing between features) to discriminate changes in houses, and match the identity of upright human bodies or inverted faces (Figure 2). Duchaine and colleagues concluded that Edward’s dissociation between face and object recognition could not be explained by the alternative hypotheses and instead provided strong evidence that his impairments resulted from deficits in face-specific mechanisms (Duchaine et al., 2006). More recently, Barton et al. (2019) tested 12 individuals with DP and found that at least two cases presented intact object recognition even when stringent criteria for determining the absence of impairments – for example, both normal expertise-adjusted accuracy and reaction time (RT) across several object recognition tests (Geskin & Behrmann, 2018) – were applied. In addition, Gerlach and Starrfelt (2016), who had previously reported evidence of an association between face and object recognition deficits in a sample of 10 individuals with DP, did not replicate these findings in a larger sample of 21 individuals using the same paradigm (Gerlach & Starrfelt, 2024). The researchers found that the larger group performed poorly on face but not object recognition and met the criteria for a classical dissociation (Gerlach & Starrfelt, 2024). Interestingly, while Gerlach and Starrfelt (2024) observed deficits in face recognition but not in face-matching abilities in the larger DP group, Bate and colleagues found evidence of classical dissociation beyond face-memory paradigms (Bate, Bennetts, Tree, et al., 2019). The researchers reported that at least six out of 15 tested individuals with DP showed impaired face-matching but intact object-matching abilities (Bate, Bennetts, Tree, et al., 2019). Importantly, there is also evidence for an opposite dissociation between face and object recognition in a developmental case. Germine et al. (2011) reported the case of AW, a 19-year-old female without neurological or psychiatric history who presented a severe visual recognition deficit across several object categories (e.g., tools, horses, and scenes) but preserved memory for faces and complex visual shapes. AW’s developmental case adds another layer of support for a double dissociation between face-processing and object-processing abilities, a phenomenon already observed in several cases with acquired brain damage (e.g., Busigny et al., 2010; Feinberg et al., 1994; Moscovitch et al., 1997). Taken together, these results support the conclusion that, although associations between face and object recognition impairments are common in DP, the mechanisms underlying such impairments are dissociable, and that in some cases, face identity recognition deficits characteristic of DP can be accounted for by disruption of face-specific mechanisms alone (Duchaine, 2011; Susilo & Duchaine, 2013).

**Figure 2**

*Edward's performance on old-new discrimination tests of face and non-face objects*



*Note.*  $A'$  is a bias-free measure of discrimination that varies between 0.5 and 1.0, with higher scores indicating better discrimination. (A) Average  $A'$  scores for the control participants (gray bars) and Edward (black bars), with dashed lines indicating a score two standard deviations below the control mean. (B) Individual  $A'$  scores for each control participant (white bars) and Edward (black bars) in each old-new discrimination test. Images are reproduced with permission from Duchaine, B. et al. (2006). Prosopagnosia as an impairment to face-specific mechanisms: Elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology*, 23(5): 714–747. <https://doi.org/10.1080/02643290500441296>.

Deficits with configural processing – representing the relationships between features of a stimulus (e.g., the spacing between face parts or the perceptual “whole” they form) rather than just the individual features themselves (Maurer et al., 2002) – have also been suggested to underlie face recognition impairments in DP (Avidan et al., 2011; Behrmann et al., 2005). The representation of configural information has been considered critical in numerous theories of face perception (Maurer et al., 2002), and this view draws support from classic behavioural results such as the composite effect (Young et al., 1987), the inversion effect (Yin, 1969), and the part-whole effect (Tanaka & Farah, 1993). One might predict that, if the configural processing of faces is significantly reduced in some individuals, they would experience severe difficulties in representing facial information, resulting in prosopagnosia. Indeed, many

individuals with DP have shown configural deficits, for example, in discriminating second-order relationships among internal features of faces but not of other objects (Duchaine et al., 2006; Le Grand et al., 2006; Yovel & Duchaine, 2006), as well as reduced or even abolished face composite, inversion, and part-whole effects, especially when group-level analyses are used to compare the performance of DP and control samples (Avidan et al., 2011; Behrmann et al., 2005; Bennetts et al., 2022; DeGutis et al., 2012; Klargaard et al., 2018). These findings, however, are also subject to considerable individual differences, and when individual-level (i.e., case-by-case) analyses are performed within DP samples, the evidence supporting reduced configural processing of faces in DP is often mixed. For example, Yovel and Duchaine (2006) found that the average performance of the DP group (N = 8) in discriminating spacing between internal features of inverted faces was significantly lower than that of the control group, but two DP cases in their sample (LA and DD, 25%) performed almost identically to control participants in the same task while still presenting reduced performance in discriminating face parts. Similarly, only seven out of the 14 individuals with DP tested by Avidan et al. (2011) presented reduced face composite effects, as indexed by accuracy or RT rates, that deviated more than 1 SD from the control mean (see also Susilo et al., 2010). More recently, Bennetts et al. (2022) also found two different clusters (i.e., subgroups) of cases in a large DP sample (N = 37) that illustrate the heterogeneity of cognitive profiles in DP: one that showed reduced inversion effects (n = 16) and another that showed typical inversion effects (n = 21) across several face perception tasks when compared to control participants (Biotti et al., 2019; Biotti, Wu, et al., 2017; Klargaard et al., 2018). Collectively, the results suggest that, while disruption of the configural processing of faces can contribute to and even underpin observed face-processing deficits in numerous DP cases, it may not always be necessary for the emergence of DP. However, an alternative interpretation of these results is that, given the fundamental role that configural processing plays in human face recognition (Maurer et al., 2002; Young et al., 1987), its disruption may indeed underlie face-processing deficits in DP in general, but different behavioral paradigms that have been employed to infer typical or atypical configural processing (e.g., measures of composite, inversion, and part-whole effects) actually target distinct mechanisms (i.e., not always configural processing), as suggested by the small to non-existent correlations between these measures (Rezlescu et al., 2017).

In a more analytical direction, other studies have investigated the role that extracting (or failing to extract) information from facial features essential for identifying faces may have in DP. For example, as we mentioned above, impairments in both discriminating spacing between face

parts (suggestive of configural processing) and discriminating face parts themselves (suggestive of part-based processing) were found to be present in DP cases (Yovel & Duchaine, 2006). More recently, Tardif et al. (2019) used the “bubbles” method – selectively uncovering small regions of a face at random and assessing how each region impacts one’s performance in face identification (Gosselin & Schyns, 2001) – and replicated previous findings showing that the eyes, eyebrows, and mouth are the most diagnostic facial features for this process (Abudarham & Yovel, 2016; Butler et al., 2010; Gosselin & Schyns, 2001). Central to their study’s question, the researchers also found that reliance on these features for face identification varied systematically across individuals with different proficiency in face recognition, with super-recognizers (SRs; Russell et al., 2009) making the most usage of those diagnostic features, individuals with DP making the least, and participants with intermediate face recognition abilities in between those, in a continuum (Tardif et al., 2019). This result suggests that perceptual mechanisms underlying DP differ quantitatively, not qualitatively, when compared to the typical population and even SRs. Providing further support to this hypothesis, Abudarham et al. (2021) investigated whether, like typical individuals, individuals with DP and SRs rely more on *critical features* than non-critical ones for face identification. Critical features are specific dimensions of face parts (e.g., eyebrow thickness and eye shape) to which individuals show higher perceptual sensitivity (i.e., better discriminability) and which, when altered, are more likely to result in the perception of a different facial identity than non-critical features (e.g., eye distance and mouth size; Abudarham & Yovel, 2016). Interestingly, Abudarham et al. (2021) found that both individuals with DP and SRs are affected by changes to the same critical features as control participants. Taken together, these results suggest that mechanistic accounts of face-processing deficits in DP may benefit from considering i) potential part-based-processing abnormalities affecting this population in addition to potential disruption to configural processing, and ii) quantitative rather than just qualitative differences in cognitive mechanisms as a potential source of variation between the DP and typical population (DeGutis, Bahierathan, et al., 2023; Russell et al., 2009; Tardif et al., 2019).

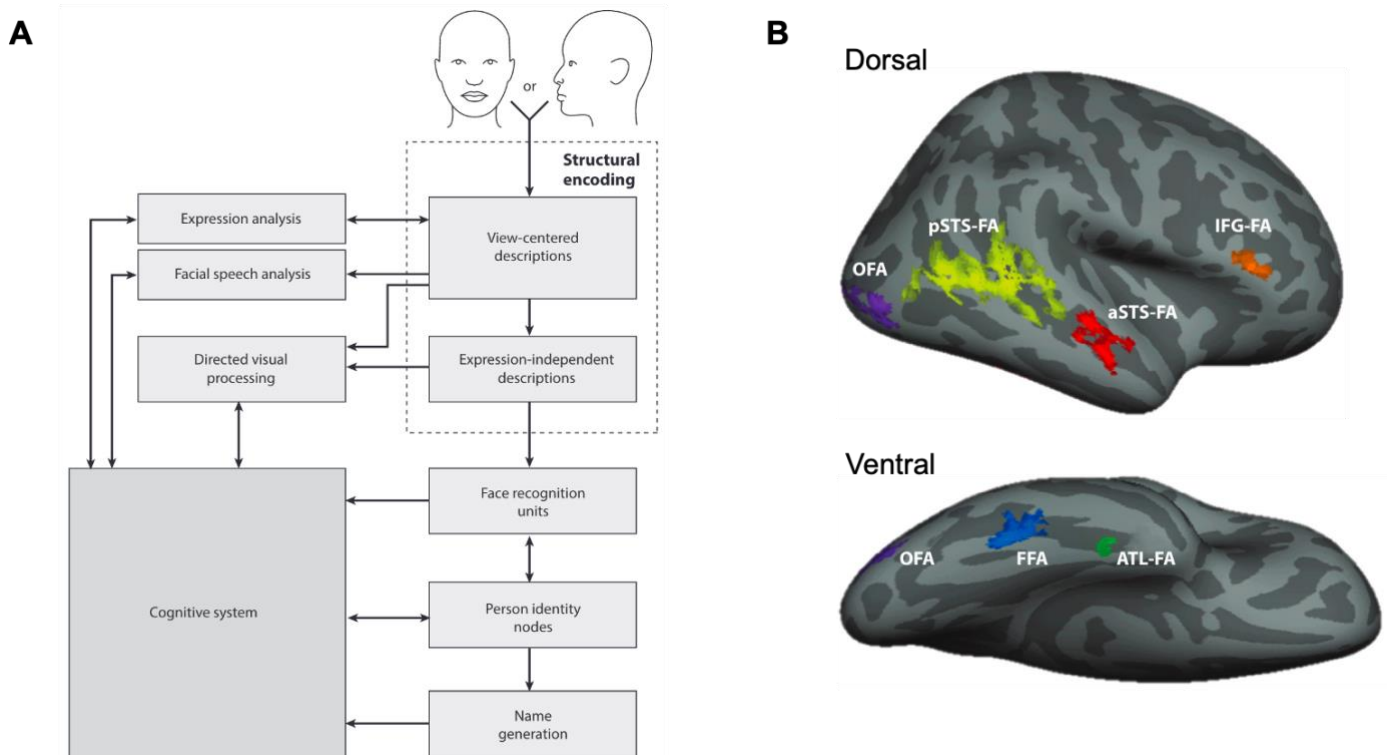
Individuals with DP can also present impairments that affect aspects of face processing beyond identity recognition. Cognitive and neural models of face processing have proposed hierarchically organized mechanisms specialised for carrying out computations about different aspects of faces (e.g., Bruce & Young, 1986; Duchaine & Yovel, 2015; Haxby et al., 2000). For example, Bruce and Young (1986) suggested faces are represented differently by perceptual and memory mechanisms, and Haxby et al. (2000) proposed that distinct brain areas are



responsible for carrying out analyses of invariant (e.g., identity and sex) and changeable (e.g., expression and eye-gaze) aspects of faces (Figure 3A) (for a review, Duchaine & Yovel, 2015). Therefore, given that the processing of facial identity and the processing of other aspects of face perception are hypothesised to depend on the same mechanisms, it is not surprising that deficits with faces in DP often extend beyond impairments in facial identity recognition (Barton et al., 2021; Susilo & Duchaine, 2013). For example, Garrido et al. (2008) presented evidence of face detection – i.e., spotting a face in a visual scene, one of the first computations involved in face processing – impairments on two tasks demanding fast detection of facial stimuli in at least ten out of 14 individuals in a DP sample. While the normal performance of the remaining cases may suggest face recognition impairments associated with higher-level mechanisms, the results of Garrido et al. (2008) indicate that deficits in a large proportion of DP cases are present early in the face processing stream. Other studies have shown that some individuals with DP have impaired performance in other tasks that also recruit early face-processing mechanisms, such as face-matching of simultaneously presented identities and sorting of faces by identity resemblance (Bate, Bennetts, Tree, et al., 2019; Biotti et al., 2019; White et al., 2017). In addition, some adults with DP score normally on tasks of facial identity perception, but one study suggested that this dissociation between normal perception and impaired memory is not present in children with DP so it may emerge only later in life (Dalrymple et al., 2014). Evidence for other face-processing deficits beyond face identity recognition in DP is mixed. For example, returning to Edward's case, he also presented an impaired performance in recognising facial expressions, differentiating male and female faces, and making attractiveness judgments for faces when compared to control participants (Duchaine et al., 2006; Sadr et al., 2004). On the other hand, several studies have reported cases of DP with normal facial expression recognition (Bell et al., 2023; Duchaine et al., 2003; Garrido et al., 2009; Humphreys et al., 2007; Tsantani et al., 2022), gender perception (Behrmann et al., 2005; Nunn et al., 2001), and judgment of social attributes from faces (Sadr et al., 2004; Todorov & Duchaine, 2008). It is important to note that many of these studies found evidence for *both* normal and impaired processes among DP samples, so while dissociations between face identity recognition and other face-processing abilities exist, rates of non-face identity deficits are elevated in DP (Susilo & Duchaine, 2013). Overall, these findings emphasize the heterogeneity of cognitive profiles in DP and illustrate that, as predicted by several models of face processing, deficits involving the face-processing network are unlikely to affect single, isolated cognitive mechanisms (Duchaine & Yovel, 2015; Jiahui et al., 2018).

### Figure 3

The Bruce & Young (1986) model of face processing and face-selective areas in the human brain



Note. (A) The cognitive model proposed by Bruce & Young (1986) for face processing. (B) Two views of the right hemisphere of a neurotypical individual show six face-selective areas distributed in dorsal and ventral streams throughout the ventral occipitotemporal cortex. Images are reproduced with permission from Duchaine, B., & Yovel, G. (2015). A revised neural framework for face processing. *Annual Review of Vision Science*, 1(1): 393–416. <https://doi.org/10.1146/annurev-vision-082114-035518>. Copyright 2015 Annual Reviews, <https://www.annualreviews.org>.

In sum, even after 25 years of research on DP, we do not have a compelling account of the cognitive mechanisms underlying this condition. We suspect the limited progress on this issue arises in part from the fact that DP in different individuals results from deficits to different cognitive processes. In addition, most of the findings discussed above come from studies in which a group of individuals with DP was tested on a small number of tests, but we believe

more emphasis on in-depth single-case studies may help DP researchers make more rapid progress on these challenging issues (Nickels et al., 2022; Ramon & Striem-Amit, 2022).

### **What are the neural correlates of developmental prosopagnosia?**

Neuroimaging and neurophysiological techniques have been used to investigate potential structural and functional neural abnormalities underlying DP within the face-processing network and adjacent structures (Duchaine, 2011; Towler et al., 2017). This network relies on the coordinated activity of interconnected brain areas that respond selectively to faces, in particular, the occipital (OFA), fusiform (FFA), anterior temporal lobe (ATL-FA), superior temporal sulcus (STS-FA), and inferior frontal gyrus (IFG-FA) face areas (Duchaine & Yovel, 2015; Haxby et al., 2000). After reaching the early visual cortex, facial information is processed hierarchically from more posterior to more anterior face areas and along two separate but interacting streams, one running ventrally (OFA, FFA, and ATL-FA) and another running dorsally (STS-FA and IFG-FA) along the cortex (Figure 3B) (for a review, Duchaine & Yovel, 2015). Leveraging this knowledge, researchers have explored the possible neural correlates of DP using structural magnetic resonance imaging (MRI), functional MRI (fMRI), and electroencephalography (EEG).

Neuroimaging research has detected structural differences between individuals with DP and neurotypical controls (NTs). Both early and more recent studies reporting morphometric and volumetric MRI analyses found that some individuals with DP present smaller temporal lobes than controls (Behrmann et al., 2007; Bentin et al., 1999). For example, using voxel-based morphometry (VBM), researchers showed that 17 individuals with DP had less gray matter volume than controls in several regions associated with face-selective neural activity, such as the right middle fusiform gyrus, right inferior temporal gyrus, right and left middle superior temporal sulci and middle temporal gyri, and right anterior inferior temporal lobe (Garrido et al., 2009). Importantly, their results also suggested an association between regional gray matter volume and behavioural performance in face identity recognition (Garrido et al., 2009). In addition to volumetric analyses, investigations on structural connectivity between different regions within and in the vicinity of the face-processing network have also reported neuroanatomical differences in DP. For example, a study using diffusion tensor imaging (DTI) detected disruptions in white matter fibers that connect the ventral-occipital temporal cortex (VOTC) and more anterior cortical regions in individuals with DP (Thomas et al., 2009). Specifically, structural integrity deficits were observed in the inferior longitudinal fasciculus (ILF) and the inferior fronto-occipital fasciculus (IFOF), the two major long-range pathways extending

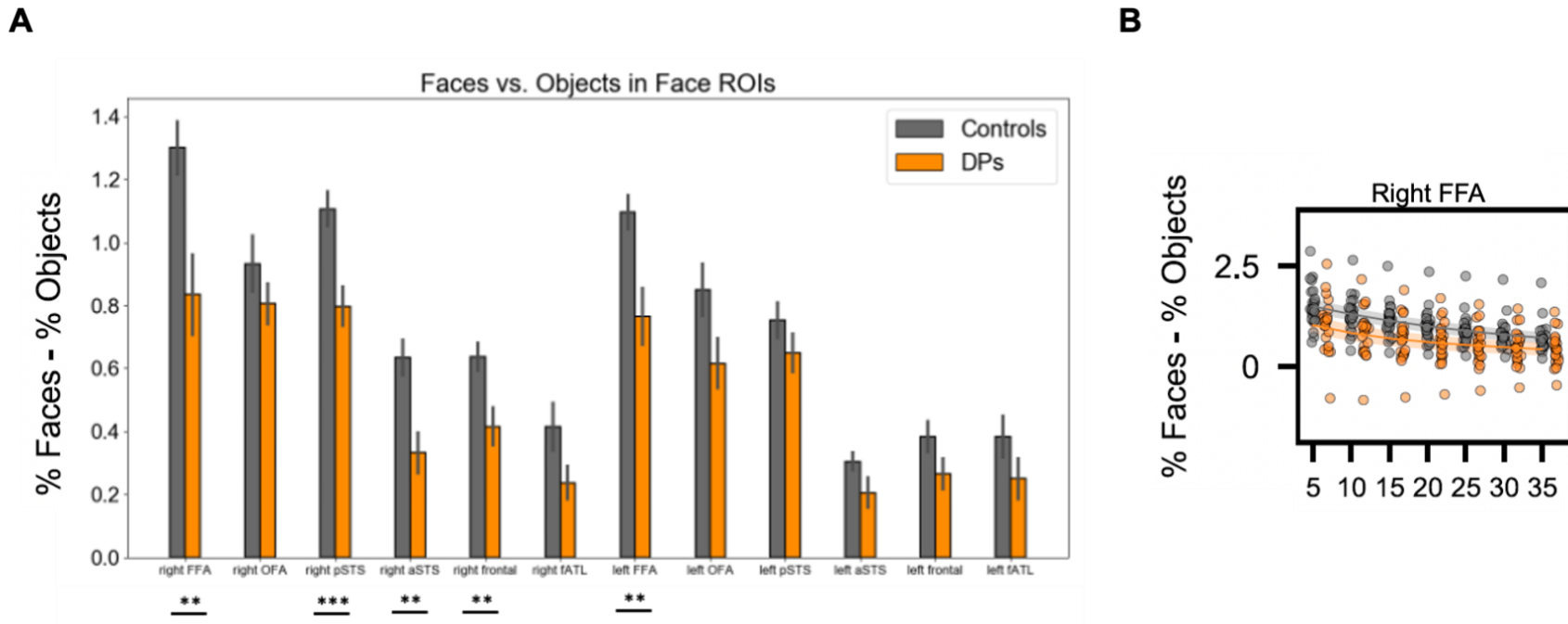
through the core fusiform region towards the anterior temporal and frontal cortices, respectively. The authors interpreted this finding as evidence that face-processing deficits in DP might derive from a disconnection between intact posterior occipitotemporal regions and more anterior parts of the brain – the “posterior-anterior disconnection syndrome” hypothesis (Behrmann & Plaut, 2013; Thomas et al., 2009). However, more recently, two studies using DTI with larger samples found no abnormalities in the IFL or IFOF of individuals with DP, but they did report differences specifically to fibers in face-selective regions of the fusiform gyrus or its vicinity, providing evidence contrary to the disconnection syndrome hypothesis (Gomez et al., 2015; Song et al., 2015). Lastly, building upon the existing evidence of structural differences in the fusiform gyrus of individuals with DP, a recent study investigated the role of mid-fusiform sulcus (MFS), a hominoid-specific structure within the fusiform gyrus, in face recognition. Parker et al. (2023) demonstrated that the MFS is shorter in individuals with DP compared to NTs and found a significant correlation between the MFS length in the right hemisphere and individual differences in face perception performance. Overall, these findings provide evidence that morphological, volumetric, and connectivity differences are associated with the behavioral impairments observed in DP, but that these differences are subject to substantial heterogeneity and a clear neuroanatomical signature of DP has not been identified (Duchaine, 2011; Manippa et al., 2023).

In parallel to structural differences, functional differences between individuals with DP and NTs controls have also been extensively investigated (Duchaine, 2011; Towler et al., 2017). The great majority of individuals with DP exhibit face-selective areas in the occipitotemporal cortex (OTC) and the locations of their face areas match those present in NTs (Avidan et al., 2005; Furl et al., 2011; Jiahui et al., 2018). However, a few DP cases have shown no face-selective voxels across the OTC (e.g., Duchaine et al., 2006), and even among DP cases that present face-selective areas, group-based analyses of DP samples have often revealed that these areas respond abnormally when compared to NT samples (Bentin et al., 2007; Furl et al., 2011; Jiahui et al., 2018; von Kriegstein et al., 2006). Variability has also been observed in studies that employed repetition-suppression (i.e., adaptation) paradigms, with some reporting that individuals with DP showed a typical reduction in functional response to repeated faces in face-responsive regions (e.g., Avidan et al., 2005; Furl et al., 2011), and others presenting evidence of atypical adaptation to recently learned faces despite a typical increase in FFA activation for faces relative to other visual stimuli (e.g., Williams et al., 2007). It is likely that one of the factors influencing these mixed fMRI results is the assessment of small, often single-case samples

(Barton et al., 2021; Manippa et al., 2023). To address this limitation, Jiahui et al. (2018) scanned a relatively large sample of 22 individuals with DP and provided evidence that atypical functional response patterns in DP can extend beyond core face-selective areas, manifesting in other category-selective regions across the OTC as well. The researchers found that, compared to NTs, individuals with DP showed a significant or marginally significant reduction in selectivity for faces in both posterior and anterior face-selective areas (Figure 4), for scenes in several scene-selective areas, and for bodies in at least two body-selective areas. These results argue against the above-mentioned posterior-anterior disconnection syndrome hypothesis (Behrmann & Plaut, 2013; Thomas et al., 2009), as reductions in face selectivity were also observed in posterior face-selective areas and the reductions in face selectivity in anterior and posterior face areas were comparable (Jiahui et al., 2018). These results suggest that individual differences reported in the DP literature, including regarding the co-occurrences of other deficits (e.g., comorbid visual navigation problems), may result from abnormalities in neighboring category-selective areas (Jiahui et al., 2018).

**Figure 4**

Percent signal change to faces and objects in face-selective areas of control and prosopagnosic participants



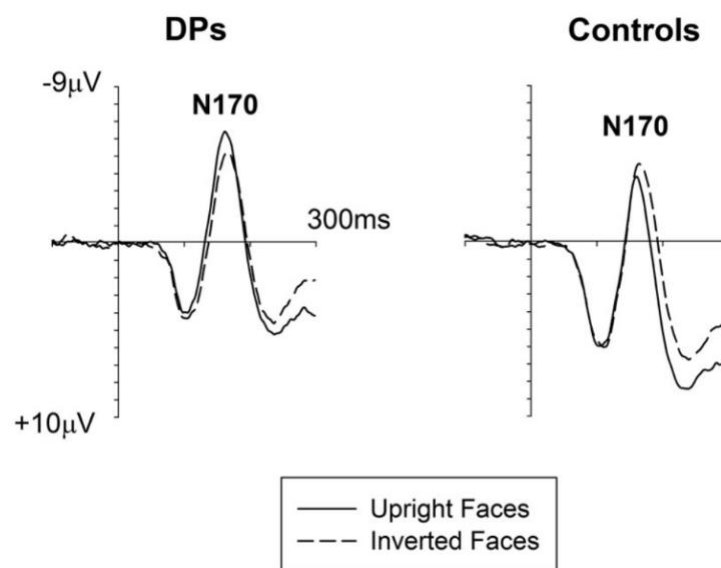
*Note.* (A) Grouped data for percent signal change to faces and objects in 12 face-selective areas in control and DP participants. Error bars represent  $\pm 1$  standard error for each group. \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ . (B) Individual data points for percent signal change to faces and objects at regions of interest (ROI) sizes from the top 5% more face-selective voxels to the top 35% most face-selective voxels in the right FFA of control and DP participants. Lines represent the mean for each group, and shaded areas above and below the line represent  $\pm 1$  standard error for each group. Images are adapted with permission from Jiahui, G. et al. (2018). Developmental prosopagnosics have widespread selectivity reductions across category-selective visual cortex. *Proceedings of the National Academy of Sciences*, 115(28): E6418–E6427. <https://doi.org/10.1073/pnas.1802246115>.

Differences in the temporal dynamics of brain activity between individuals with DP and NTs have been investigated through event-related potentials (ERPs). ERP research uses EEG time-locked to stimulus presentations to assess neural responses that, compared to fMRI, have far superior temporal resolution despite substantially inferior spatial resolution. ERP components that are stronger to faces than control categories are called face-selective, and these components often span the regions of the scalp above the OTC (Towler et al., 2017). One of the most investigated ERP components in DP is the N170, a component that typically exhibits a stronger response to faces than other objects in NTs and is generated by early face perception processes (Bentin et al., 1996; Eimer, 2011; Rossion & Jacques, 2011). Some individuals with DP have shown N170 responses with reduced or even absent face selectivity when compared to control participants (Bentin et al., 1999; DeGutis et al., 2007; Kress & Daum, 2003), but N170s in most individuals with DP exhibit typical face selectivity (Towler et al., 2012). In NTs, N170 responses to inverted faces, faces with scrambled features, and faces with contrast-reversed eyes are delayed and larger in amplitude relative to normal faces. However, N170s in individuals with DP at the group level were comparable (or even in the opposite direction) for normal faces and each of these face manipulations (Figure 5) (Fisher et al., 2016; Towler et al., 2012, 2017). Given their location and timing, these EEG differences likely reflect abnormalities in posterior face areas (Towler et al., 2017). However, it is important to note that no abnormalities in the N170 have been found in some DPs, which suggests the existence of deficits at later stages of face processing (Harris et al., 2005; Minnebusch et al., 2007; Towler et al., 2017). One ERP component associated with later stages is the N250, which shows a stronger response to familiar faces than to unfamiliar faces (Gosling & Eimer, 2011; Schweinberger et al., 1995; Tanaka et al., 2006). Eimer et al. (2012) found that, despite presenting impairments in face identity recognition, individuals with DP display an N250 response comparable to that of controls on trials in which a face is successfully recognized. Interestingly though, among the 12 individuals with DP tested, six exhibited a typical N250 response to familiar faces even when they failed to explicitly recognize them, a pattern absent in control participants. This dissociation suggests that individuals with DP sometimes match incoming percepts to stored face memories but fail to become aware that they recognized a face, a phenomenon known as covert recognition (Eimer et al., 2012; Towler et al., 2017). In contrast, the P600f, another ERP component indicative of later-stage face processing but thought to be a neural marker of conscious face recognition (Gosling & Eimer, 2011), did not differ for unrecognised famous faces and unrecognised non-famous faces in those individuals with DP whose N250 responses suggested covert recognition. Thus, their results indicated that

their deficit with face processing results from problems with face processing somewhere between 250 and 600 ms after stimulus presentation (Eimer et al., 2012; Towler et al., 2017). Taken together, ERP studies in DP suggest that impairments in many individuals with DP are caused by deficits in the early face processes in posterior face-selective areas, but much work remains to be done to understand the different temporal profiles in DP that EEG studies have revealed (Manippa et al., 2023; Towler et al., 2017).

### Figure 5

*N170 responses to upright and inverted faces in control and DP participants*



*Note.* Grand-averaged ERPs elicited by upright and inverted faces at the right occipital-temporal electrode P8 in the 300-ms interval after stimulus onset for a group of individuals with DP (left) and an age-matched control group (right). Control participants showed larger N170 amplitudes to inverted faces, while individuals with DP did not show this effect. Image is reproduced with permission from Towler, J. et al. (2017). The cognitive and neural basis of developmental prosopagnosia. *The Quarterly Journal of Experimental Psychology*, 70(2): 316–344. <https://doi.org/10.1080/17470218.2016.1165263>.

Overall, neuroimaging and neurophysiological studies have revealed a variety of differences between individuals with DP and the NT population. These differences range from morphological and volumetric alterations in or near the face-processing network to disruptions in



functional activity and connectivity in widespread regions of the visual cortex, highlighting DP's complex neurobiological foundation. These results underscore the high degree of heterogeneity found in the neural correlates of DP; an observation like the one we made when addressing possible cognitive mechanisms of poor face recognition.

### **Final remarks**

Individuals with a lifelong history of poor face identity recognition encounter a variety of challenges navigating a world where faces are a ubiquitous part of social interactions. These challenges can lead to several psychosocial consequences, such as the development of chronic anxiety, restriction of social circles, and loss of opportunities in many realms (Adams et al., 2020; Yardley et al., 2008). Several studies have investigated the effects of behavioral interventions to improve face identity recognition in DP and found some encouraging results (Bate, Adams, et al., 2019; Bate et al., 2022; DeGutis et al., 2014), but no effective and persisting treatments for DP have been developed so far (see Chapter 7 for an in-depth discussion).

From a theoretical perspective, investigating DP has also proved to be a useful model for understanding the cognitive and neural bases of face processing more generally. Research on DP has provided evidence for the existence of face-specific mechanisms, supported face-processing models that propose mechanisms specialized for representing different aspects of faces, and emphasized the relevance of intact occipital and temporal areas for typical face perception and recognition. Nevertheless, the heterogeneity of DP has repeatedly shown to be a challenge for advancing the field and impact issues from estimating prevalence rates of DP to defining clear neurocognitive signatures of this condition. We strongly recommend that future studies put more emphasis on in-depth, individual-level investigations of developmental prosopagnosia.

### **Key Information Box**

- It is fundamental to rely on both self-report assessments and several standardised neuropsychological tests to detect DP and estimate prevalence rates.
- Many individuals with DP also present deficits in recognising non-face objects. However, recognition deficits are limited to faces in some DP participants, which provides support for the existence of face-specific processes.
- Neuroimaging and neurophysiological methods have found structural and functional brain differences between groups of individuals with DP and neurotypical participants. However, far more research is necessary to understand the neural basis of DP.
- Future research on DP can greatly benefit from individual-level investigations that explore in depth the behavioural, cognitive, and neural profiles of individuals with DP, which would highlight both the similarities and differences across multiple cases.

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*\* Key recommended readings are highlighted in bold*

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