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Research Report

New evidence of impaired expression recognition in developmental prosopagnosia

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ABSTRACT

Developmental prosopagnosia (DP) is a neurodevelopmental condition characterized by lifelong face recognition difficulties. To date, it remains unclear whether or not individuals with DP experience impaired recognition of facial expressions. It has been proposed that DPs may have sufficient perceptual ability to correctly interpret facial expressions when tasks are relatively easy (e.g., the stimuli are unambiguous and viewing conditions are optimal), but exhibit subtle impairments when tested under more challenging conditions. In the present study, we sought to take advantage of the COVID-19 pandemic to test this view.

It is well-established that the surgical-type masks worn during the pandemic hinder the recognition and interpretation of facial emotion in typical participants. Relative to typical participants, we hypothesized that DPs may be disproportionately impaired when asked to interpret the facial emotion of people wearing face masks. We compared the ability of 34 DPs and 60 age-matched typical controls to recognize facial emotions i) when the whole face is visible, and ii) when the lower portion of the face is covered with a surgical mask. When expression stimuli were viewed without a mask, the DPs and typical controls exhibited similar levels of performance. However, when expression stimuli were shown with a mask, the DPs showed signs of subtle expression recognition deficits. The DPs were particularly prone to mislabeling masked expressions of happiness as emotion neutral. These results add to a growing body of evidence that under some conditions, DPs *do* exhibit subtle deficits of expression recognition.

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1. Introduction

Developmental prosopagnosia (DP) is a neurodevelopmental condition characterized by lifelong face recognition difficulties that occur in the absence of brain damage, despite normal intelligence, and typical low-level vision (Behrmann & Avidan, 2005; Cook & Biotti, 2016; Duchaine & Nakayama, 2006b). The face recognition problems seen in DP hinder the identification of both same- and other-race faces (Cenac, Biotti, Gray, & Cook, 2019). In addition to their problems recognizing faces, some DPs also show deficits of body perception (Biotti, Gray, & Cook, 2017) and within-category object identification (Barton, Albonico, Susilo, Duchaine, & Corrow, 2019; Geskin & Behrmann, 2017; Gray, Biotti, & Cook, 2019). Despite their problems recognizing others from facial cues, DPs show typical recognition of others from voice cues (Liu, Corrow, Pancaroglu, Duchaine, & Barton, 2015; Tsantani & Cook, 2020). It has been suggested that around 2% of the population experience lifelong face recognition problems severe enough to disrupt their daily lives (Bowles et al., 2009; Kennerknecht et al., 2006; Kennerknecht, Ho, & Wong, 2008). It has been noted, however, that the proportion of people who meet the criteria for a diagnosis of DP is much lower than this estimate (Barton & Corrow, 2016; Bate & Tree, 2017).

Despite the growing interest in DP, the cause of the condition remains unclear. Evidence that DP runs in families suggests that it may have a genetic component (Duchaine, Germine, & Nakayama, 2007; Johnen et al., 2014; Lee, Duchaine, Wilson, & Nakayama, 2010; Schmalzl, Palermo, & Coltheart, 2008). This finding accords with the broader view that face recognition ability is a heritable trait (Shakeshaft & Plomin, 2015; Wilmer et al., 2010). Cognitive theories have suggested that holistic face processing, whereby local feature descriptions are integrated into a coherent whole (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Le Grand, & Mondloch, 2002; McKone & Yovel, 2009), may be impaired in cases of DP (DeGutis, Cohan, & Nakayama, 2014; Liu & Behrmann, 2014; Palermo et al., 2011), however this account has been challenged (Biotti, Wu, et al., 2017; Tsantani, Gray, & Cook, 2020). Neuroimaging has revealed differences in cortical structure (Behrmann, Avidan, Gao, & Black, 2007; Garrido et al., 2009), and structural (Song et al., 2015; Thomas et al., 2009) and functional connectivity (Avidan & Behrmann, 2009; Lohse et al., 2016; Rosenthal et al., 2017) in inferotemporal regions including the fusiform gyrus, thought to play a key role in face processing (Kanwisher & Yovel, 2006). Atypical responses have also been observed outside the core face-processing areas, including anterior temporal cortex (Avidan et al., 2014) and scene-selective regions, including parahippocampal place area (Jiahui, Yang, & Duchaine, 2018).

There has been considerable interest in whether people with DP show impaired recognition of facial expressions (Biotti & Cook, 2016; Djouab et al., 2020; Dobel, Bölte, Aicher, & Schweinberger, 2007; Duchaine, Parker, & Nakayama, 2003; Humphreys, Avidan, & Behrmann, 2007; Kress & Daum, 2003; Lee et al., 2010; Palermo et al., 2011). People with DP are known to experience embarrassment and social anxiety because of their face recognition difficulties (Dalrymple et al., 2014). Further difficulties recognizing the facial expressions of others would likely exacerbate these social interaction difficulties. Moreover, facial expressions are a key form of non-verbal communication that can be used to infer someone's emotional state and likely intentions (Adolphs, 2002; Frith, 2009). As such, the accurate recognition of expressions is important for the development of sophisticated mentalizing abilities and wider mechanisms of social cognition.

The question of expression recognition also has important theoretical implications for our understanding of DP. Early in the face processing stream, observers are thought to form a structural description of the target face that supports subsequent analysis of facial identity and expression (Bruce & Young, 1986; Duchaine & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000). Although, there may be some cross-talk (e.g., Kaufmann & Schweinberger, 2004; Schweinberger, Burton, & Kelly, 1999), the subsequent processing of identity and expression is thought to proceed with a large degree of independence, via parallel, dissociable routes (Bruce & Young, 1986; Duchaine & Yovel, 2015; Haxby et al., 2000). For example, findings from neuroimaging suggest that identity and expression processing may be mediated by fusiform and superior temporal cortex, respectively (e.g., Andrews & Ewbank, 2004; Hoffman & Haxby, 2000; Winston, Henson, Fine-Goulden, & Dolan, 2004). Where observed together, deficits of identity and expression recognition are suggestive of apperceptive prosopagnosia, whereby disruption early on in the face processing stream leaves individuals unable to form a precise structural representation (Bruce & Young, 1986; De Renzi, Faglioni, Grossi, & Nichelli, 1991). Alternatively, intact expression recognition despite impaired recognition of facial identity would suggest a locus of impairment later in the face processing stream, after the processing of facial expression and identity bifurcates (Bruce & Young, 1986; Duchaine et al., 2003).

Traditionally, expression recognition was thought to be intact in DP. Consistent with this view, several group studies (Dobel et al., 2007; Humphreys et al., 2007; Lee et al., 2010; Palermo et al., 2011) and a number of single case studies (Duchaine et al., 2003; Kress & Daum, 2003) have described typical expression recognition in this population. More recently, however, several group studies have observed group-level differences in expression recognition between DPs and matched controls (Biotti & Cook, 2016; Burns, Martin, Chan, & Xu, 2017; Djouab et al., 2020). Two of these studies employed sensitive psychophysical paradigms and analyses (Biotti & Cook, 2016; Burns et al., 2017). Biotti and Cook (2016) asked DPs and matched controls to classify ambiguous expression stimuli drawn from morph continua and used participants' decisions to model psychometric functions. The functions of the DPs, tended to be shallower than those of the controls suggestive of less precise categorization. A similar result was described by Burns et al. (2017) who found that DPs were less consistent than typical controls when classifying expression stimuli drawn from a morph continuum that blended expressions of happiness and sadness. A third study found that participants with DP took longer to find ‘oddball’ expression stimuli in a visual search task (Djouab et al., 2020).

In an attempt to explain these mixed findings, it has been proposed that DPs may have sufficient perceptual ability to correctly interpret facial expressions when tasks are relatively easy (e.g., the stimuli are unambiguous and the viewing conditions are optimal) but exhibit subtle impairments when tested under more challenging conditions; for example, when image morphing is used to render stimuli more ambiguous (Biotti & Cook, 2016; Burns et al., 2017), or when participants are put under time pressure (Djouab et al., 2020). In the present study, we sought to take advantage of the COVID-19 pandemic to further interrogate this possibility. During the pandemic, we have been required to interact with people wearing surgical-type masks that cover the lower portion of the face. Unsurprisingly, these masks have been shown to hinder the recognition and interpretation of facial emotion (Carbon, 2020; Noyes, Davis, Petrov, Gray, & Ritchie, 2021; Tsantani, Podgajecka, Gray, & Cook, 2022). Relative to typical individuals, we hypothesized that DPs may be disproportionately impaired when asked to interpret the facial emotion of people wearing face coverings like those used during the pandemic. To investigate this possibility, we compared the ability of 34 DPs and 60 age-matched typical controls to recognize facial emotions i) when the whole face is visible, and ii) when the lower portion of the face is covered with a surgical mask.

2. Research transparency and openness

Neither the study procedure nor the intended analyses were pre-registered prior to the start of the research. In the following sections we report how we determined our sample size, all data exclusions, all inclusion criteria, and whether inclusion/exclusion criteria were established prior to data analysis. All manipulations and all measures in the study are reported. The experimental task is available as Open Materials at gorilla.sc (https://app.gorilla.sc/openmaterials/276504). The Twenty-Item Prosopagnosia Index (PI20) is freely available (see: Shah, Gaule, Sowden, Bird, & Cook, 2015). Legal copyright restrictions prevent public archiving of the Cambridge Face Memory Tests (Duchaine & Nakayama, 2006a; McKone et al., 2011) and the Cambridge Car Memory Test (Dennett et al., 2012), which can be obtained from the authors and copyright holders. Study data and an R analysis script are available via the Open Science Framework (https://osf.io/cnmw5/).

Ethical clearance was granted by the Departmental Ethics Committee for Psychological Sciences, Birkbeck, University of London. The experiment was conducted in line with the ethical guidelines laid down in the 6th (2008) Declaration of Helsinki. All participants provided informed consent.

3. Participants

Thirty-four individuals with DP (21 female, 13 male, $M_{age} = 38.3$ years, $SD_{age} = 13.2$ years) and 60 typical controls (44 female, 15 males, 1 non-binary, $M_{age} = 41.9$ years, $SD_{age} = 10.0$ years) were included in the study. The groups did not differ significantly in terms of age [$t(54.637) = 1.367$, $p = .177$, $d = .304$] or the proportion of male participants [$\chi^2_{(1)} = 1.818$, $p = .178$]. Sample size was based on previous group studies of DP (Marsh, Biotti, Cook, & Gray, 2019; Tsantani & Cook, 2020; Tsantani et al., 2020). All participants completed the study remotely using their own desktop/laptop.

DP participants were recruited through www.troublewithfaces.org. Participants were informed that to be eligible for the study they must have no history of brain damage, autism spectrum disorder, or schizophrenia. Diagnostic decisions were based on participants' scores on two versions of the Cambridge Face Memory Test (CFMT), the CFMT-original (Duchaine & Nakayama, 2006a) and the CFMT-Australian (CFMT-A; McKone et al., 2011), and on the Twenty-Item Prosopagnosia Index (PI20; Gray, Bird, & Cook, 2017; Shah et al., 2015; Tsantani, Vestner, & Cook, 2021). The CFMT is a computer-based test of face identification that employs a match-to-sample format. Participants are asked to identify recently learned target faces from a line-up of three response options (a target plus two foils). In the latter stages, task difficulty is increased via changes in viewpoint and through the addition of visual noise to the test images. The CFMT-original and CFMT-Australian are identical in format and both present images of White male faces. The PI20 is a self-report measure of prosopagnosic traits.

All but one of the DP participants scored 65 or higher on the PI20 – the recommended cut-off for DP (Shah et al., 2015). The remaining DP scored 64. All participants included in the final sample scored at least 2 SDs from a given control sample mean on the CFMT and CFMT-A. DPs also completed the Cambridge Car Memory Test (CCMT; Dennett et al., 2012) to assess their within-class object recognition ability. The CCMT has the same format as the CFMT but presents images of cars instead of faces. Diagnostic information for each DP is provided in Table 1. Two DP participants were replaced, having experienced technical difficulties during the experimental task.

Typical participants were recruited through Prolific (www.prolific.co), and had a Prolific approval rate of at least 75%. Only those who reported no formal diagnosis of autism spectrum disorder via Prolific's prescreening were eligible to participate. Typical participants were screened for DP using the PI20. Three typical controls were replaced having scored more than 65. A further 3 typical controls were replaced, having experienced technical issues during the experimental task.

All participants (DPs and typical controls) were required to be between 18 and 60 years-old and to have normal or corrected-to-normal visual acuity. To ensure that all participants had similar experiences of the COVID-19 pandemic and the associated use of face masks as a protective measure, participants were required to be currently resident in the UK, and to have resided in the UK during the pandemic. These inclusion criteria were identified at the outset.

4. Experimental task

The study was conducted online using Gorilla Experiment Builder (Anwyl-Irvine, Massonnié, Flitton, Kirkham, & Evershed, 2020). Face stimuli were obtained from the Radboud Faces Database (Langner et al., 2010). Masked versions were created by superimposing surgical-type masks over the nose and mouth using Adobe Photoshop (Fig. 1a). Participants

Table 1 – Diagnostic information for the DP participants. *At least 1 SD from typical mean; **at least 2 SDs from typical mean; ***at least 3 SDs from typical mean.

	Age	Gender	PI20	CFMT (%)	CFMT-A (%)	CCMT (%)
1	56	M	90***	54.2***	52.8**	86.1
2	38	M	71***	55.6***	58.3**	65.3
3	27	M	76***	38.9***	58.3**	51.4*
4	41	F	74***	43.1***	38.9***	50.0*
5	56	F	82***	52.8***	56.9**	65.3
6	22	M	76***	58.3***	54.2**	75.0
7	49	F	96***	54.2***	56.9**	79.2
8	39	M	78***	58.3***	59.7**	88.9
9	47	F	69***	58.3***	50.0***	69.4
10	42	F	90***	50.0***	54.2**	55.6*
11	54	F	82***	50.0***	58.3**	58.3*
12	54	F	64***	47.2***	47.2***	58.3*
13	19	M	79***	62.5**	59.7**	81.9
14	19	F	73***	38.9***	48.6***	63.9
15	53	F	86***	40.3***	58.3**	75.0
16	27	F	80***	62.5**	52.8**	63.9
17	42	F	84***	44.4***	47.2***	75.0
18	54	M	83***	47.2***	54.2**	81.9
19	45	F	69***	50.0***	47.2***	59.7*
20	52	F	86***	63.9**	56.9**	62.5
21	23	F	86***	54.2***	58.3**	55.6*
22	34	F	80***	52.8***	59.7**	86.1
23	19	M	84***	45.8***	44.4***	61.1*
24	48	M	80***	50.0***	58.3**	86.1
25	36	M	70***	45.8***	48.6***	58.3*
26	29	F	77***	36.1***	23.6***	58.3*
27	28	F	82***	54.2***	56.9**	63.9
28	28	M	83***	55.6***	45.8***	94.4
29	19	F	76***	55.6***	58.3**	63.9
30	27	F	84***	59.7**	54.2**	63.9
31	46	F	90***	47.2***	51.4**	52.8*
32	50	M	84***	29.2***	33.3***	37.5**
33	20	M	90***	29.2***	31.9***	56.9*
34	59	F	79***	58.3***	51.4**	68.1
DP mean			80.4	50.1	51.4	66.9
DP SD			7.1	8.9	8.7	13.0
Comparison mean			38.0	85.0	80.2	73.5
Comparison SD			9.1	8.9	10.2	12.6

Nb. Comparison data ($N = 54$, $M_{age} = 39.2$; $SD_{age} = 13.4$; range: 20–69 years) for the PI20, and CFMT were taken from Biotti et al. (2019), *Neuropsychologia*. Comparison data ($N = 75$, $M_{age} = 21.67$; $SD_{age} = 2.96$; range: 18–32 years) for the CFMT-A were taken from McKone et al. (2011), *Cognitive Neuropsychology*. Comparison data ($N = 61$, $M_{age} = 37.0$; $SD_{age} = 9.8$; range: 27–60 years) for the CCMT were taken from Gray et al. (2019), *Cognitive Neuropsychology*.

viewed ten identities (five women, five men), each posing seven facial expressions: neutral, happy, sad, angry, fearful, disgusted, and surprised. Each expression stimulus was presented twice: once wearing a face mask, and once without a mask. In total, participants completed 140 trials (10 identities × 7 expressions × 2 mask conditions) in a random order. Images appeared 4.8 cm × 7 cm on participants' displays. Trials began with a fixation cross (1000 msec) followed by a face image presented for 500 msec (Fig. 1b). The stimulus image was replaced by a mask constructed of high-contrast greyscale ovals (500 msec), followed by a response screen on which participants selected one of seven response options (neutral, happy, sad, angry, fearful, disgusted, surprised). There was no time limit on participants' responses.

5. Results

Accuracy (% correct) was calculated separately for each of the 14 Emotion × Mask conditions (Table 2, Fig. 2). Pairwise contrasts were calculated using Welch's *t*-test. Correction for multiple comparisons was performed using the False Discovery Rate (FDR) with $q < .05$. Cohen's *d* effect sizes were calculated using the rstatix package (v0.7.0; function 'cohens_d') in R (v4.0.4). All reported *p*-values are two-tailed.

5.1. *Categorization accuracy*

Participants' accuracy scores were subjected to ANOVA with Expression (neutral, happy, sad, angry, fearful, disgusted, surprised) and Mask (unmasked, masked) as within-subject factors and Group (DP, control) as a between-subject factor. Results for the within-subject factors were consistent with previous findings (Carbon, 2020; Noyes et al., 2021): we observed main effects of Mask [$F(1, 92) = 765.028$, $p < .001$, $\eta_p^2 = .893$] and Expression [$F(4.41, 405.63) = 150.628$, $p < .001$, $\eta_p^2 = .621$], as well as a Mask × Expression interaction [$F(4.76, 437.75) = 135.380$, $p < .001$, $\eta_p^2 = .595$]. Planned pairwise contrasts showed that accuracy was significantly higher for unmasked faces compared with masked faces for expressions of happiness, sadness, fear, disgust, and surprise, for both DPs (all *t*s > 2.94, all *p*s < .006, *d* range = .505–2.623) and controls (all *t*s > 3.98, all *p*s < .001, *d* range = .514–2.813). There was no difference in accuracy across mask conditions for neutral faces for DPs [$t(33) = .865$, $p = .393$, $d = .148$] or controls [$t(59) = .913$, $p = .365$, $d = .118$]. Accuracy for angry faces was higher for masked faces than unmasked faces for DPs [$t(33) = 2.729$, $p = .010$, $d = .468$] and controls [$t(59) = 2.394$, $p = .020$, $d = .309$].

Crucially, there was a main effect of Group [$F(1, 92) = 6.374$, $p = .013$, $\eta_p^2 = .065$], with DPs being less accurate overall, compared to controls. We also observed a significant Mask × Group interaction [$F(1, 92) = 4.423$, $p = .038$, $\eta_p^2 = .046$], as well a significant Mask × Group × Expression interaction [$F(4.76, 437.75) = 2.357$, $p = .042$, $\eta_p^2 = .025$]. Planned pairwise contrasts revealed that DPs were significantly less accurate than controls when evaluating masked happy faces [$t(41.726) = 3.697$, $p < .001$, $d = .860$]. DPs also tended to be less accurate with masked sad faces [$t(68.408) = 2.095$, $p = .040$, $d = .450$], and unmasked angry faces [$t(56.561) = 2.256$, $p = .028$, $d = .500$], but these simple effects did not survive correction for multiple comparisons. No other significant differences were found for masked faces or unmasked faces (all *t*s < 1.92, all *p*s > .06). The Group × Expression interaction was not significant [$F(4.41, 405.63) = 1.644$, $p = .156$, $\eta_p^2 = .018$].

To confirm that face masks had a greater impact on the DPs' recognition of happiness than that of the typical controls, for each participant we computed the difference in accuracy scores between unmasked faces and masked faces, separately for each expression (Table 2). Pairwise contrasts revealed that differences in accuracy between unmasked and masked faces were significantly larger in DPs than controls for happy faces

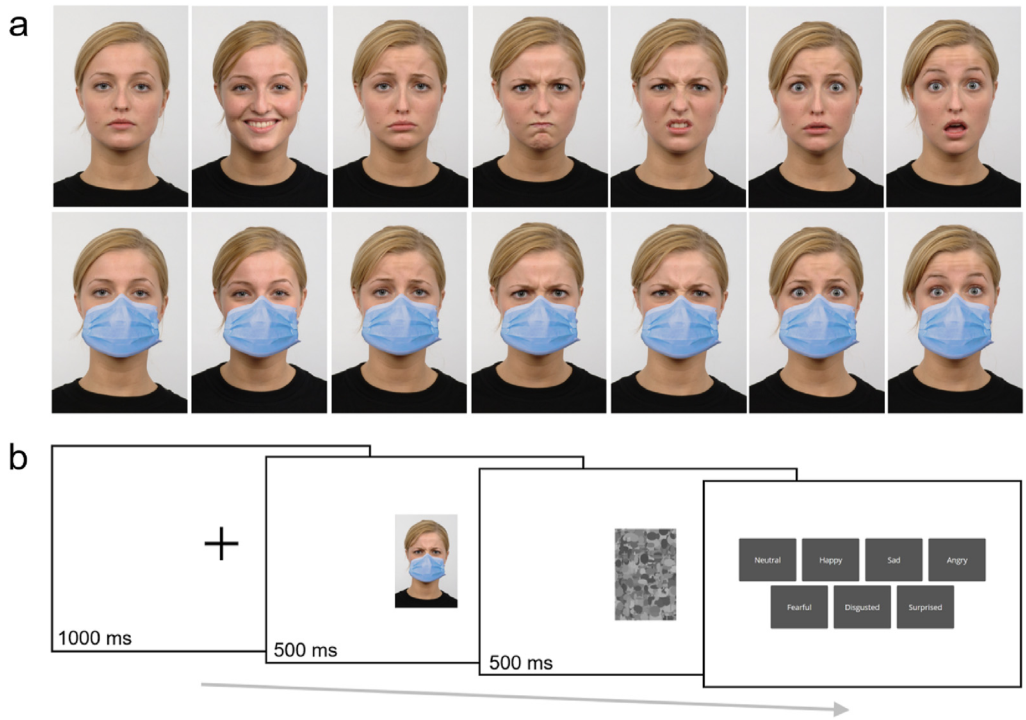

Fig. 1 – (a) Example stimulus images. Participants viewed ten identities (five women, five men), each posing seven facial expressions: neutral, happy, sad, angry, fearful, disgusted, and surprised. Original images were sourced from the Radboud Faces Database (Langner et al., 2010). (b) Illustration of a trial sequence.

Table 2 – Mean accuracy (% correct) for unmasked and masked faces, and mean differences in accuracy (unmasked – masked) for DPs and controls, with standard deviations in brackets.

		Neutral	Happy	Sad	Angry	Fearful	Disgusted	Surprised
Unmasked	Controls	87.83 (16.17)	99.17 (2.79)	87.67 (13.82)	76.67 (19.97)	59.50 (27.58)	84.33 (16.91)	93.17 (8.73)
	DPs	89.71 (10.87)	97.35 (5.11)	85.00 (18.13)	65.29 (25.25)	57.94 (26.94)	82.94 (21.40)	89.71 (14.46)
Masked	Controls	89.33 (11.77)	87.67 (12.12)	50.67 (21.70)	82.17 (20.09)	30.83 (24.52)	22.50 (17.91)	85.00 (17.52)
	DPs	91.76 (11.93)	70.59 (25.34)	40.88 (21.79)	76.76 (25.07)	26.18 (20.89)	17.35 (16.75)	81.18 (22.12)
Unmasked-Masked	Controls	−1.50 (12.73)	11.50 (11.91)	37.00 (20.94)	−5.50 (17.80)	28.67 (27.83)	61.83 (21.98)	8.17 (15.89)
	DPs	−2.06 (13.88)	26.76 (26.02)	44.12 (18.77)	−11.47 (24.51)	31.76 (24.05)	65.59 (25.01)	8.53 (16.90)

[$t(40.973) = 3.234$, $p = .002$, $d = .754$]. No other significant group differences were found for the remaining expressions (all $ts < 1.70$, all $ps > .09$).

To test whether DPs were impaired in the recognition of masked happy faces at the single-subject level, we conducted Crawford–Howell *t*-tests (Crawford & Howell, 1998) to compare individual DP accuracy scores with the typical controls. These tests showed that 12 DPs were significantly impaired when viewing masked happy faces (Fig. 3). We also tested whether individual DPs showed a greater effect of face masks on the recognition of happy faces compared to the controls using one-sided revised standardized difference tests (RSDT; Crawford & Garthwaite, 2005). These tests revealed that 9 DPs showed a greater difference in accuracy between masked and unmasked faces compared to the distribution of differences in the control group. These 9 DPs overlap with the 12 DPs who were impaired in the recognition of masked happy faces (all except participants 18, 32, and 33 in Fig. 3).

To determine whether individual differences in the degree to which masks affected emotion recognition were associated with face recognition ability, we compared the mask-induced differences in accuracy (unmasked accuracy – masked accuracy) with scores on the CFMT, the CFMT-A, and the PI20, using Spearman rank correlation (Table 3). None of the correlations with CFMT or PI20 survived correction for multiple comparisons. There was a significant negative correlation between differences in accuracy for angry faces and scores on the CFMT-A ($r_s = -.56$, $p < .001$). In contrast to the other expressions, the presence of a mask tended to increase categorization accuracy for angry faces for the majority of typical participants. DPs who scored higher on the CFMT-A tended to show this pattern. However, those DPs who scored lower on the CFMT-A tended to show little effect of mask versus unmasked or a slight advantage for the whole face condition.

5.2. *Categorization errors*

The distributions of categorization errors across the different expression labels for each facial expression are shown in

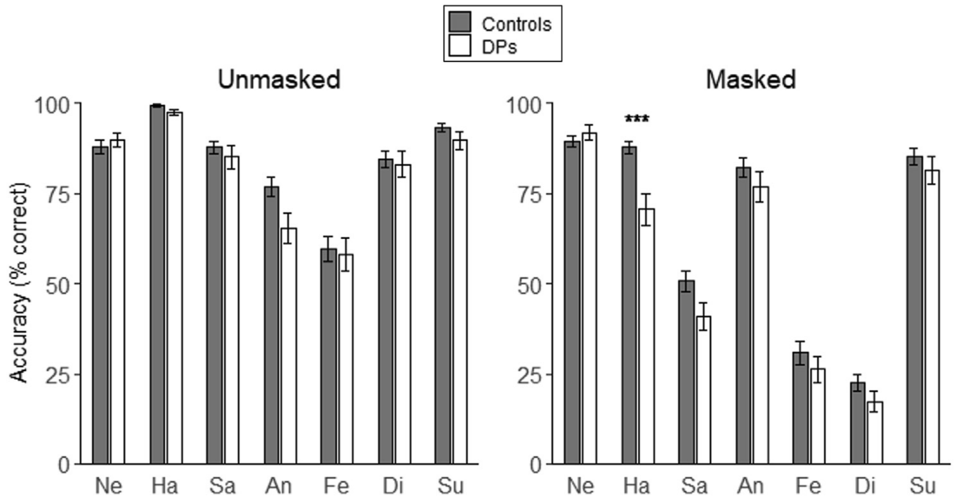

Fig. 2 – Mean accuracy scores for unmasked faces and masked faces for individuals with developmental prosopagnosia (DP; N = 34) and neurotypical controls (N = 60), showing the proportion of stimuli that were correctly labeled for each emotion. Asterisks indicate statistically significant *t*-tests after FDR correction for 7 comparisons. Ne: neutral, Ha: happiness, Sa: sadness, An: anger, Fe: fear, Di: disgust, Su: surprise. ****p* < .001.

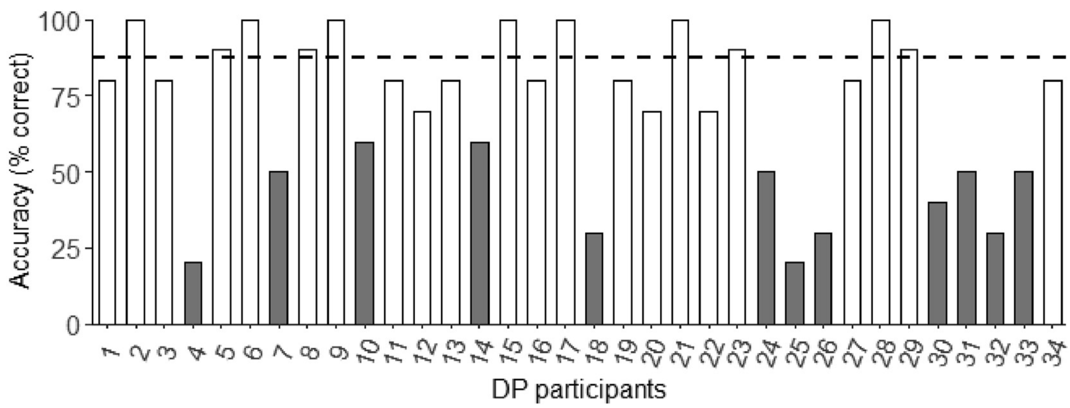

Fig. 3 – Accuracy scores for masked happy faces in individuals with developmental prosopagnosia, showing the proportion of stimuli that were correctly labeled as "happy". The dashed line indicates the control mean, and gray bars indicate accuracy scores that were significantly lower than the control mean based on Crawford–Howell *t*-tests.

Fig. 4. To compare these error patterns across DPs and controls, we conducted separate ANOVAs for each expression with Mask (masked, unmasked) and Non-target Expression (e.g., for happiness, the six levels of Non-target Expression were neutral, sadness, anger, fear, disgust, surprise) as within-subjects factors, and Group (DPs, controls) as a between-subjects factor. These analyses are described in full in the Supplementary information. With the exception of neutral faces [$F(1, 92) = 1.588$, $p = .211$, $\eta_p^2 = .017$], all facial expressions showed a main effect of Mask (all *F*s > 14.93, *p*s < .001). All facial expressions showed a main effect of Non-target Expression (all *F*s > 11.09, all *p*s < .001) and an interaction between Mask and Non-target Expression (all *F*s > 5.71, all *p*s < .001). For the sake of brevity, however, we focus below on the effects of Group.

In line with our results for categorization accuracy, a main effect of Group on categorization errors was found for happy faces [$F(1, 92) = 22.512$, $p < .001$, $\eta_p^2 = .197$], with more errors made by DPs than controls (Fig. 4). For happy faces, we observed a Group × Mask interaction [$F(1, 92) = 15.150$, $p < .001$, $\eta_p^2 = .141$], a Group × Non-target Expression interaction [$F(1.42, 130.47) = 16.808$, $p < .001$, $\eta_p^2 = .154$], as well as a Group × Mask × Non-target Expression interaction [$F(1.42, 130.47) = 18.568$, $p < .001$, $\eta_p^2 = .168$]. Pairwise tests revealed that DPs made more neutral responses to masked happy faces compared to controls [$t(39.231) = 3.825$, $p < .001$, $d = .899$]. No significant effects of Group were found in errors involving other Non-target Expressions (all *t*s < 1.71, all *p*s > .09), and no differences were found for unmasked happy faces (all *t*s < 1.79, all *p*s > .08).

There was also a main effect of Group on categorization errors for angry faces [$F(1, 92) = 4.019$, $p = .048$, $\eta_p^2 = .042$], with more errors made by DPs than controls. For angry faces, however, Group did not interact with any other factor (all *F*s < 2.46, all *p*s > .06). Pairwise tests showed no significant group differences in errors involving any of the Non-target Expressions for masked angry faces (all *t*s < 1.63, all *p*s > .10), or unmasked angry faces (all *t*s < 1.97, all *p*s > .05).

Table 3 – Spearman rank correlations seen between the mask-induced differences (unmasked accuracy – masked accuracy) and scores on the CFMT, CFMT-A, and PI20. Asterisks indicate statistically significant *p*-values prior to FDR correction for multiple comparisons. Only the correlation for CFMT-A and anger (in bold) survived FDR correction for 7 comparisons, at an FDR threshold of $p \leq .001$. Ne: neutral, Ha: happiness, Sa: sadness, An: anger, Fe: fear, Di: disgust, Su: surprise. *$p < .05$; **$p < .01$; ***$p < .001$.

	Expression						
	Ne	Ha	Sa	An	Fe	Di	Su
CFMT (N = 34)	.05	−.39*	−.32	−.45**	.25	.37*	−.30
CFMT-A (N = 34)	.04	−.32	−.31	**−.56*****	.01	.28	−.27
PI20 (N = 94)	−.03	.24*	.15	−.13	.07	.20	.07

Nb. Higher CFMT and CFMT-A scores indicate better face memory, and higher scores on the PI20 indicate worse self-reported face recognition ability. While all participants completed the PI20, only the participants with DP completed the CFMT and CFMT-A.

Inspection of Fig. 4 suggests a tendency for DPs mislabel masked expressions as 'neutral' more often than controls. In an exploratory post-hoc analysis, we tested whether, in addition to happiness, other masked expressions were also be mislabeled as 'neutral' more often by DPs than controls. DPs made significantly more 'neutral' responses to masked sad faces [$t(58.902) = 2.323$, $p = .024$, $d = .551$] and masked disgusted faces [$t(42.156) = 2.625$, $p = .012$, $d = .609$], compared to controls. DPs also tended to make more 'neutral' responses to masked surprised faces, but this result did not survive correction for multiple comparisons [$t(51.188) = 2.144$, $p = .037$, $d = .482$]. There were no significant group differences for masked fearful and masked angry faces (both *ts* < 1.56, both *ps* > .12), or for unmasked sad, angry, fearful, disgusted, and surprised faces (all *ts* < 1.14, all *ps* > .26).

6. General discussion

The present study sought to compare the expression recognition ability of DPs and typical controls when the to-be-judged facial images were shown uncovered or wearing a face mask. When expression stimuli were viewed without a mask, the DPs and typical controls exhibited similar levels of performance. However, when expression stimuli were shown with a mask, the DPs showed signs of subtle expression recognition deficits. In particular, the DP group tended to mislabel expressions of happiness as emotion neutral more frequently than controls. This suggests that the DPs were less able to detect subtle cues of happiness from the eye region alone. For a long time, it was thought that expression recognition was unimpaired in DP and a number of early group studies found no significant differences between the performance of DPs and matched controls (Dobel et al., 2007; Humphreys et al., 2007; Lee et al., 2010; Palermo et al., 2011).

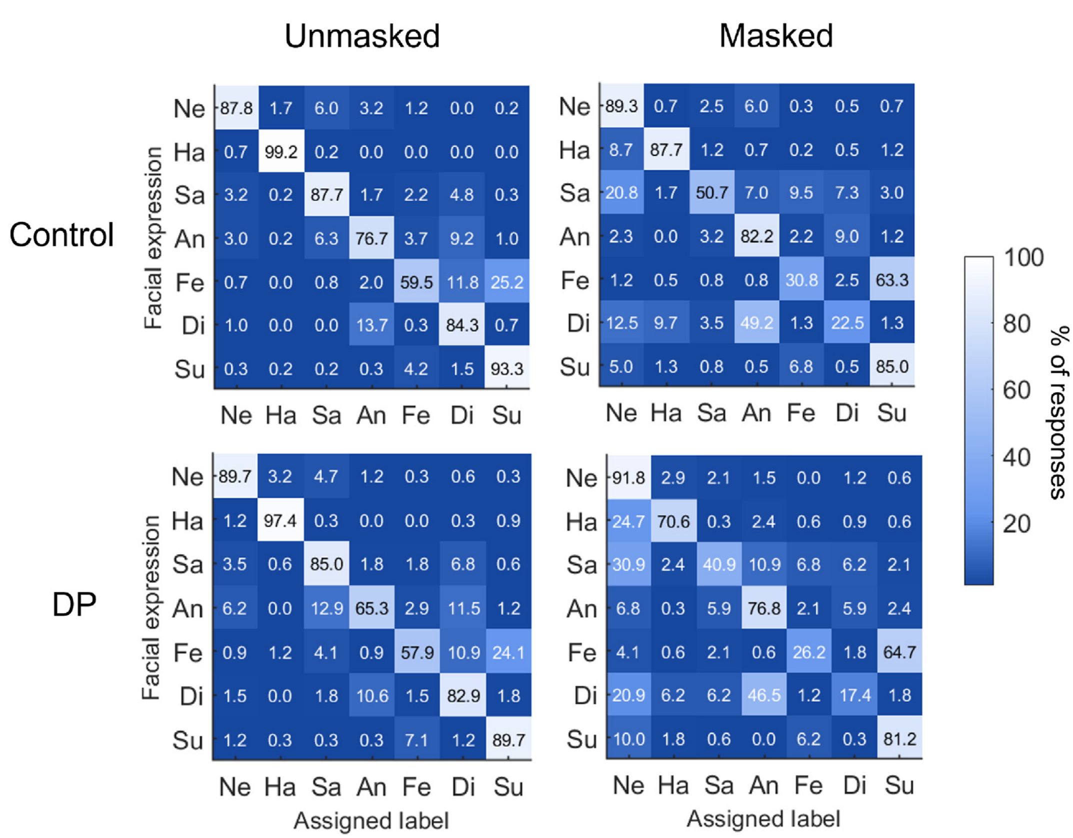

Fig. 4 – Confusion matrices illustrating how the mean response likelihood varied as a function of target expression, mask and group. Cells on the diagonal show accuracy scores, and cells off the diagonal categorization errors. Ne: neutral, Ha: happiness, Sa: sadness, An: anger, Fe: fear, Di: disgust, Su: surprise.

However, the present results add to a growing body of evidence that under some conditions, DPs *do* exhibit subtle deficits of expression recognition (Biotti & Cook, 2016; Burns et al., 2017; Djouab et al., 2020).

It is noteworthy that DPs exhibited largely typical performance when the whole face was visible, but were impaired relative to controls when the mouth region of each target face was occluded by a mask. This finding accords with the view that DPs have sufficient perceptual ability to respond correctly on relatively easy tasks (e.g., where stimuli are unambiguous and the viewing conditions are optimal), but are outperformed by controls on more challenging tasks. Here, expression recognition was rendered more challenging through the addition of a mask that occluded the expression signals conveyed by the mouth region. Previous findings suggest that DPs are also less able to detect and encode expression cues made weaker through image morphing (Biotti & Cook, 2016; Burns et al., 2017). Subtle differences may also emerge between DPs and typical individuals when participants are put under time pressure (Djouab et al., 2020).

Evidence of impaired expression recognition is important because it suggests that DP has a locus of origin early in the face processing stream, before the processing of identity and expression bifurcates (Biotti & Cook, 2016; Biotti, Gray, & Cook, 2019; Marsh et al., 2019). This conclusion is consistent with reports that DPs exhibit imprecise categorization of facial sex (Esins, Schultz, Stemper, Kennerknecht, & Bulthoff, 2016; Marsh et al., 2019) and evidence that DPs struggle to sort simultaneously presented faces on the basis of resemblance (Biotti et al., 2019; Duchaine et al., 2007). It also accords well with evidence that the N170 ERP component – a negative potential evoked by faces 170 msec after stimulus onset, implicated in structural encoding (Eimer, 2000; Eimer & McCarthy, 1999) – is aberrant in DP (Fisher, Towler, & Eimer, 2016; Towler, Gosling, Duchaine, & Eimer, 2012). All of these findings point towards a problem early in the face processing stream that hinders the encoding of face structure. Noisy perceptual descriptions of the eye region may explain why participants in the present study were more likely than controls to mislabel happy expressions as emotion neutral. Evidently, typical participants were able to detect expression cues around the eyes, that the DPs were not.

Limbic structures are thought to exert a top-down influence that helps observers interpret the emotional content of facial expressions (Calder & Young, 2005; Haxby et al., 2000). Poor expression recognition seen in other developmental conditions – notably developmental alexithymia (Cook, Brewer, Shah, & Bird, 2013; Grynberg et al., 2012) – has been attributed to differences in this top-down contribution (Bird & Cook, 2013). We do not believe this kind of deficit is likely to explain poor expression identification in DP. While deficient face encoding potentially explains many features of DP (e.g., poor face matching and identification, imprecise categorization of expressions and facial sex), an aberrant top-down contribution from the limbic system would appear to explain expression recognition deficits only. Moreover, the kind of top-down deficit seen in alexithymia appears to impact perception and cognition beyond the visual processing of facial expressions; for example, people with developmental alexithymia also find it hard to interpret the emotional content of vocal stimuli (e.g., Heaton et al., 2012). In contrast, deficits of affective processing in DP appear to be limited to the perception and recognition of facial expressions; for example, DPs exhibit normal identification of vocal affect (Biotti & Cook, 2016).

The present findings indicate that DPs exhibit perceptual impairment when only a portion of the to-be-judged face is visible. It has been suggested that DP may be caused by a deficit of whole-face or "holistic" processing; relative to typical individuals, DPs may be less able to integrate information derived from different facial regions into a coherent, unified percept (DeGutis et al., 2014; T. T. Liu & Behrmann, 2014; Palermo et al., 2011). Our findings speak against this account. It is clear that deficits are seen in this population when judging isolated facial regions in the absence of the wider face context – the condition does not selectively impair the perception of "whole-faces" (see also: Biotti & Cook, 2016; Tsantani et al., 2020). Instead, our results are more consistent with the view that individuals form imprecise descriptions of local regions (Tsantani et al., 2020), notably the eyes (Biotti & Cook, 2016; Duchaine, Yovel, Butterworth, & Nakayama, 2006; Fisher et al., 2016). In principle, problems encoding local regions could be accompanied by co-occurring deficits of holistic processing. There is, however, growing evidence that DPs exhibit behavioral hallmarks of typical holistic processing (Biotti, Wu, et al., 2017; Le Grand et al., 2006; Tsantani et al., 2020).

Our analysis of categorization accuracy revealed a main effect of group and a group × mask interaction, whereby the expression categorization of DPs was less accurate overall, and in the mask condition in particular. However, these findings were qualified by group × mask × expression interaction, and the only simple effect of group to survive correction for multiple comparisons was seen for masked displays of happiness. We consider it unlikely that DPs have particular problems processing facial happiness. Although the simple contrasts did not reach significance/survive correction for multiple comparisons, we observed a similar trend for masked displays of sadness, anger, fear, disgust, and surprise, whereby DPs were less accurate than typical controls. Moreover, previous findings suggest that DPs have problems with other expressions; for example, relative to typical controls, DPs were less able to distinguish subtle morphs of fear and surprise (Biotti & Cook, 2016).

It is unclear why expression recognition deficits in DP were revealed most clearly in the masked happiness condition. For some of the emotions, the effect of the mask manipulation was quite striking: For example, typical controls' recognition of fear dropped from 59.5% to 30.8%, while their recognition of disgust dropped from 84.3% to 22.5%. For these emotions, it is possible that floor effects in the control distributions made it harder to detect deficits of masked expression recognition in DP. For other emotions (e.g., anger and surprise), the presence of the mask had relatively little effect on recognition accuracy. When confronted with the similarity between anger and disgust in the mask condition, participants may have been more likely to guess "anger". Similarly, participants may have been more likely to guess "surprise" when confronted with the similarity between fear and surprise. These biases may reflect the greater likelihood of encountering anger and surprise in our day-to-day interactions, compared to disgust and fear

(Tsantani et al., 2022). However, it is possible that high guessing base rates impacted our ability to detect significant group differences in the masked anger and surprise conditions.

6.1. *Limitations & recommendations for future research*

The present study was conducted online, an approach that is increasingly common. Carefully-designed online tests of cognitive and perceptual processing can yield high-quality data, indistinguishable from that collected in the lab (Crump, McDonnell, & Gureckis, 2013; Germine et al., 2012; Woods, Velasco, Levitan, Wan, & Spence, 2015). To give recent examples from our own research, we have found that online testing has produced clear, replicable results in visual search and attention cueing experiments (Vestner, Gray & Cook, 2021, 2022; Vestner, Over, Gray, & Cook, 2021), and studies of visual illusions (Bunce, Gray, & Cook, 2021; Gray et al., 2020). However, this approach also has some well-known limitations. For example, it is not easy to control the testing environment, participants' viewing distance, or their monitor settings. In future research, it would be interesting to examine the ability of DPs to identify dynamic expression stimuli. At present, however, this question is not easily addressed using online testing (e.g., the different computers used by participants in their homes are likely to vary widely in their graphics capabilities).

Consistent with the methods employed in previous studies (Carbon, 2020; Noyes et al., 2021), face masks were superimposed over images of facial expressions. This treatment maximizes the likelihood that any recognition decrement is attributable to the presence of the mask, rather than differences in the underlying expression. It is possible, however, that mask wearers may alter their expressions to compensate for presence of the mask. Responses to a UK survey on the impact of face coverings on communication revealed conscious attempts to convey emotion using the eyes, such as "smiling with the eyes", and attempts to exaggerate facial expressions when wearing a mask (Saunders, Jackson, & Visram, 2021). It remains unclear whether attempts to augment visible expression cues help or hinder non-verbal communication – people have surprisingly little insight into the appearance of their facial gestures and expressions (Cook, Johnston, & Heyes, 2013). Nevertheless, we acknowledge that findings obtained with artificially-masked faces may underestimate the ability of people to interpret the expressions of mask wearers in everyday life.

6.2. *Conclusion*

When expression stimuli were viewed without a mask, the DPs and typical controls exhibited similar levels of performance. However, when expression stimuli were shown with a mask, the DPs showed signs of subtle expression recognition deficits. In particular, DPs were prone to mislabeling masked expressions of happiness as emotion neutral. These results provide important new evidence of expression recognition impairment in DP. The fact that DPs show impaired recognition of both facial identity and facial expression, suggests a locus of impairment early in the face processing stream, before the processing of facial expression and identity bifurcates.

Author contributions

M.T., K.L.H.G., and R.C. designed the research. M.T. collected and analyzed the data. M.T. and R.C. wrote the manuscript.

Open practices

The study in this article earned an Open Data – Protected Access badge for transparent practices. Materials and data for the study are available at https://osf.io/cnmw5/ (p. 4).

Declaration of competing interest

The authors declare no competing interest.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2022.05.008.

REFERENCES

Adolphs, R. (2002). Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews, 1*(1), 21–62.

Andrews, T. J., & Ewbank, M. P. (2004). Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *NeuroImage, 23*(3), 905–913.

Anwyl-Irvine, A. L., Massonnié, J., Flitton, A., Kirkham, N., & Evershed, J. K. (2020). Gorilla in our midst: An online behavioral experiment builder. *Behavior Research Methods, 52*, 388–407.

Avidan, G., & Behrmann, M. (2009). Functional MRI reveals compromised neural integrity of the face processing network in congenital prosopagnosia. *Current Biology, 19*(13), 1146–1150.

Avidan, G., Tanzer, M., Hadj-Bouziane, F., Liu, N., Ungerleider, L. G., & Behrmann, M. (2014). Selective dissociation between core and extended regions of the face processing network in congenital prosopagnosia. *Cerebral Cortex, 24*, 1565–1578.

Barton, J. J., Albonico, A., Susilo, T., Duchaine, B., & Corrow, S. L. (2019). Object recognition in acquired and developmental prosopagnosia. *Cognitive Neuropsychology, 36*(1–2), 54–84.

Barton, J. J., & Corrow, S. L. (2016). The problem of being bad at faces. *Neuropsychologia, 89*, 119–124.

Bate, S., & Tree, J. J. (2017). The definition and diagnosis of developmental prosopagnosia. *Quarterly Journal of Experimental Psychology, 70*(2), 193–200.

Behrmann, M., & Avidan, G. (2005). Congenital prosopagnosia: Face-blind from birth. *Trends in Cognitive Sciences, 9*(4), 180–187.
Behrmann, M., Avidan, G., Gao, F., & Black, S. (2007). Structural imaging reveals anatomical alterations in inferotemporal cortex in congenital prosopagnosia. *Cerebral Cortex, 17*(10), 2354–2363.
Biotti, F., & Cook, R. (2016). Impaired perception of facial emotion in developmental prosopagnosia. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 81*, 126–136.
Biotti, F., Gray, K. L. H., & Cook, R. (2017). Impaired body perception in developmental prosopagnosia. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 93*, 41–49.
Biotti, F., Gray, K. L. H., & Cook, R. (2019). Is developmental prosopagnosia best characterised as an apperceptive or mnemonic condition? *Neuropsychologia, 124*, 285–298.
Biotti, F., Wu, E., Yang, H., Jiahui, G., Duchaine, B., & Cook, R. (2017). Normal composite face effects in developmental prosopagnosia. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 95*, 63–76.
Bird, G., & Cook, R. (2013). Mixed emotions: The contribution of alexithymia to the emotional symptoms of autism. *Translational Psychiatry, 3*(7), e285.
Bowles, D. C., McKone, E., Dawel, A., Duchaine, B., Palermo, R., Schmalzl, L., et al. (2009). Diagnosing prosopagnosia: Effects of ageing, sex, and participant-stimulus ethnic match on the cambridge face memory test and cambridge face perception test. *Cognitive Neuropsychology, 26*, 423–455.
Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology, 77*(3), 305–327.
Bunce, C., Gray, K. L. H., & Cook, R. (2021). The perception of interpersonal distance is distorted by the Muller-Lyer illusion. *Scientific Reports, 11*(1), 494.
Burns, E. J., Martin, J., Chan, A. H. D., & Xu, H. (2017). Impaired processing of facial happiness, with or without awareness, in developmental prosopagnosia. *Neuropsychologia, 102*, 217–228.
Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience, 6*(8), 641–651.
Carbon, C. C. (2020). Wearing face masks strongly confuses counterparts in reading emotions. *Frontiers in Psychology, 11*, 2526.
Cenac, Z., Biotti, F., Gray, K. L. H., & Cook, R. (2019). Does developmental prosopagnosia impair identification of other-ethnicity faces? *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 119*, 12–19.
Cook, R., & Biotti, F. (2016). Developmental prosopagnosia. *Current Biology, 26*, R312–R313.
Cook, R., Brewer, R., Shah, P., & Bird, G. (2013). Alexithymia, not autism, predicts poor recognition of emotional facial expressions. *Psychological Science, 24*(5), 723–732.
Cook, R., Johnston, A., & Heyes, C. (2013). Facial self-imitation: Objective measurement reveals no improvement without visual feedback. *Psychological Science, 24*(1), 93–98.
Crawford, J. R., & Garthwaite, P. H. (2005). Testing for suspected impairments and dissociations in single-case studies in neuropsychology: Evaluation of alternatives using Monte Carlo simulations and revised tests for dissociations. *Neuropsychology, 19*(3), 318–331.
Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *The Clinical Neuropsychologist, 12*(4), 482–486.
Crump, M. J., McDonnell, J. V., & Gureckis, T. M. (2013). Evaluating Amazon's mechanical Turk as a tool for experimental behavioral research. *PLoS One, 8*(3), Article e57410.
Dalrymple, K. A., Fletcher, K., Corrow, S. L., das Nair, R., Barton, J. J., Yonas, A., et al. (2014). "A room full of strangers every day": The psychosocial impact of developmental prosopagnosia on children and their families. *Journal of Psychosomatic Research, 77*(2), 144–150.
De Renzi, E., Faglioni, P., Grossi, D., & Nichelli, P. (1991). Apperceptive and associative forms of prosopagnosia. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 27*(2), 213–221.
DeGutis, J., Cohan, S., & Nakayama, K. (2014). Holistic face training enhances face processing in developmental prosopagnosia. *Brain: A Journal of Neurology, 137*(Pt 6), 1781–1798.
Dennett, H. W., McKone, E., Tavashmi, R., Hall, A., Pidcock, M., Edwards, M., et al. (2012). The Cambridge car memory test: A task matched in format to the Cambridge face memory test, with norms, reliability, sex differences, dissociations from face memory, and expertise effects. *Behavior Research Methods, 44*, 587–605.
Djouab, S., Albonico, A., Yeung, S. C., Malaspina, M., Mogard, A., Wahlberg, R., et al. (2020). Search for face identity or expression: Set size effects in developmental prosopagnosia. *Journal of Cognitive Neuroscience, 32*(5), 889–905.
Dobel, C., Bölte, J., Aicher, M., & Schweinberger, S. R. (2007). Prosopagnosia without apparent cause: Overview and diagnosis of six cases. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 43*(6), 718–733.
Duchaine, B., Germine, L., & Nakayama, K. (2007). Family resemblance: Ten family members with prosopagnosia and within-class object agnosia. *Cognitive Neuropsychology, 24*(4), 419–430.
Duchaine, B., & Nakayama, K. (2006a). 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*, 576–585.
Duchaine, B., & Nakayama, K. (2006b). Developmental prosopagnosia: A window to content-specific face processing. *Current Opinion in Neurobiology, 16*, 166–173.
Duchaine, B., Parker, H., & Nakayama, K. (2003). Normal recognition of emotion in a prosopagnosic. *Perception, 32*(7), 827–838.
Duchaine, B., & Yovel, G. (2015). A revised neural framework for face processing. *Annual Review of Vision Science, 1*, 393–416.
Duchaine, B., Yovel, G., Butterworth, E., & Nakayama, K. (2006). Prosopagnosia as an impairment to face-specific mechanisms: Elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology, 23*(5), 714–747.
Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport, 11*(10), 2319–2324.
Eimer, M., & McCarthy, R. A. (1999). Prosopagnosia and structural encoding of faces: Evidence from event-related potentials. *NeuroReport, 10*(2), 255–259.
Esins, J., Schultz, J., Stemper, C., Kennerknecht, I., & Bulthoff, I. (2016). Face perception and test reliabilities in congenital prosopagnosia in seven tests. *i-Perception, 7*(1), 1–37.
Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is "special" about face perception? *Psychological Review, 105*(3), 482–498.
Fisher, K., Towler, J., & Eimer, M. (2016). Reduced sensitivity to contrast signals from the eye region in developmental prosopagnosia. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 81*, 64–78.
Frith, C. (2009). Role of facial expressions in social interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1535), 3453–3458.
Garrido, L., Furl, N., Draganski, B., Weiskopf, N., Stevens, J., Tan, G. C. Y., et al. (2009). Voxel-based morphometry reveals reduced grey matter volume in the temporal cortex of developmental prosopagnosics. *Brain: A Journal of Neurology, 132*(12), 3443–3455.

Germine, L., Nakayama, K., Duchaine, B. C., Chabris, C. F., Chatterjee, G., & Wilmer, J. B. (2012). Is the web as good as the lab? Comparable performance from web and lab in cognitive/perceptual experiments. *Psychonomic Bulletin & Review, 19*(5), 847–857.

Geskin, J., & Behrmann, M. (2017). Congenital prosopagnosia without object agnosia? A literature review. *Cognitive Neuropsychology, 35*(1–2), 4–54.

Gray, K. L. H., Biotti, F., & Cook, R. (2019). Evaluating object recognition ability in developmental prosopagnosia using the Cambridge Car Memory Test. *Cognitive Neuropsychology, 36*(1–2), 89–96.

Gray, K. L. H., Bird, G., & Cook, R. (2017). Robust associations between the 20-item prosopagnosia index and the Cambridge Face Memory Test in the general population. *Royal Society Open Science, 4*(3), Article 160923.

Gray, K. L. H., Guillemin, Y., Cenac, Z., Gibbons, S., Vestner, T., & Cook, R. (2020). Are the facial gender and facial age variants of the composite face illusion products of a common mechanism? *Psychonomic Bulletin & Review, 27*(1), 62–69.

Grynberg, D., Chang, B., Corneille, O., Maurage, P., Vermeulen, N., Berthoz, S., et al. (2012). Alexithymia and the processing of emotional facial expressions (EFEs): Systematic review, unanswered questions and further perspectives. *PLoS One, 7*(8), Article e42429.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*, 223–233.

Heaton, P., Reichenbacher, L., Sauter, D., Allen, R., Scott, S., & Hill, E. (2012). Measuring the effects of alexithymia on perception of emotional vocalizations in autistic spectrum disorder and typical development. *Psychological Medicine, 42*(11), 2453–2459.

Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience, 3*(1), 80–84.

Humphreys, K., Avidan, G., & Behrmann, M. (2007). A detailed investigation of facial expression processing in congenital prosopagnosia as compared to acquired prosopagnosia. *Experimental Brain Research, 176*(2), 356–373.

Jiahui, G., Yang, H., & Duchaine, B. (2018). Developmental prosopagnosics have widespread selectivity reductions across category-selective visual cortex. *Proceedings of the National Academy of Sciences of the United States of America, 115*, E6418–E6427.

Johnen, A., Schmukle, S. C., Hüttenbrink, J., Kischka, C., Kennerknecht, I., & Dobel, C. (2014). A family at risk: Congenital prosopagnosia, poor face recognition and visuoperceptual deficits within one family. *Neuropsychologia, 58*, 52–63.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1476), 2109–2128.

Kaufmann, J. M., & Schweinberger, S. R. (2004). Expression influences the recognition of familiar faces. *Perception, 33*(4), 399–408.

Kennerknecht, I., Grueter, T., Welling, B., Wentzek, S., Horst, J., Edwards, S., et al. (2006). First report of prevalence of non-syndromic hereditary prosopagnosia (HPA). *American Journal of Medical Genetics Part A, 140*, 1617–1622.

Kennerknecht, I., Ho, N. Y., & Wong, V. C. (2008). Prevalence of hereditary prosopagnosia (HPA) in Hong Kong Chinese population. *American Journal of Medical Genetics Part A, 146*, 2863–2870.

Kress, T., & Daum, I. (2003). Event-related potentials reflect impaired face recognition in patients with congenital prosopagnosia. *Neuroscience Letters, 352*(2), 133–136.

Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D. H. J., Hawk, S. T., & van Knippenberg, A. (2010). Presentation and validation of the Radboud faces database. *Cognition & Emotion, 24*(8), 1377–1388.

Le Grand, R., Cooper, P. A., Mondloch, C. J., Lewis, T. L., Sagiv, N., de Gelder, B., et al. (2006). What aspects of face processing are impaired in developmental prosopagnosia? *Brain and Cognition, 61*(2), 139–158.

Lee, Y., Duchaine, B., Wilson, H. R., & Nakayama, K. (2010). Three cases of developmental prosopagnosia from one family: Detailed neuropsychological and psychophysical investigation of face processing. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 46*, 949–964.

Liu, T. T., & Behrmann, M. (2014). Impaired holistic processing of left-right composite faces in congenital prosopagnosia. *Frontiers in Human Neuroscience, 8*, 750.

Liu, R. R., Corrow, S. L., Pancaroglu, R., Duchaine, B., & Barton, J. J. (2015). The processing of voice identity in developmental prosopagnosia. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 71*, 390–397.

Lohse, M., Garrido, L., Driver, J., Dolan, R. J., Duchaine, B. C., & Furl, N. (2016). Effective connectivity from early visual cortex to posterior occipitotemporal face areas supports face selectivity and predicts developmental prosopagnosia. *Journal of Neuroscience, 36*(13), 3821–3828.

Marsh, J. E., Biotti, F., Cook, R., & Gray, K. L. H. (2019). The discrimination of facial sex in developmental prosopagnosia. *Scientific Reports, 9*, Article 19079.

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences, 6*(6), 255–260.

McKone, E., Hall, A., Pidcock, M., Palermo, R., Wilkinson, R. B., Rivolta, D., et al. (2011). Face ethnicity and measurement reliability affect face recognition performance in developmental prosopagnosia: Evidence from the Cambridge face memory test-Australian. *Cognitive Neuropsychology, 28*, 109–146.

McKone, E., & Yovel, G. (2009). Why does picture-plane inversion sometimes dissociate the perception of features and spacing in faces, and sometimes not? Toward a new theory of holistic processing. *Psychonomic Bulletin & Review, 16*(5), 778–797.

Noyes, E., Davis, J. P., Petrov, N., Gray, K. L. H., & Ritchie, K. L. (2021). The effect of face masks and sunglasses on identity and expression recognition with super-recognizers and typical observers. *Royal Society Open Science, 8*(3), Article 201169.

Palermo, R., Willis, M. L., Rivolta, D., McKone, E., Wilson, C. E., & Calder, A. J. (2011). Impaired holistic coding of facial expression and facial identity in congenital prosopagnosia. *Neuropsychologia, 49*(5), 1226–1235.

Rosenthal, G., Tanzer, M., Simony, E., Hasson, U., Behrmann, M., & Avidan, G. (2017). Altered topology of neural circuits in congenital prosopagnosia. *Elife, 6*, Article e25069.

Saunders, G. H., Jackson, I. R., & Visram, A. S. (2021). Impacts of face coverings on communication: An indirect impact of COVID-19. *International Journal of Audiology, 60*(7), 495–506.

Schmalzl, L., Palermo, R., & Coltheart, M. (2008). Cognitive heterogeneity in genetically based prosopagnosia: A family study. *Journal of Neuropsychology, 2*(1), 99–117.

Schweinberger, S. R., Burton, A. M., & Kelly, S. W. (1999). Asymmetric dependencies in perceiving identity and emotion: Experiments with morphed faces. *Perception & Psychophysics, 61*(6), 1102–1115.

Shah, P., Gaule, A., Sowden, S., Bird, G., & Cook, R. (2015). The 20-item prosopagnosia index (PI20): A self-report instrument for identifying developmental prosopagnosia. *Royal Society Open Science, 2*, 140343.

Shakeshaft, N. G., & Plomin, R. (2015). Genetic specificity of face recognition. *Proceedings of the National Academy of Sciences of the United States of America, 112*, 12887–12892.

Song, S., Garrido, L., Nagy, Z., Mohammadi, S., Steel, A., Driver, J., et al. (2015). Local but not long-range microstructural differences of the ventral temporal cortex in developmental prosopagnosia. *Neuropsychologia, 78*, 195–206.
Thomas, C., Avidan, G., Humphreys, K., Jung, K. J., Gao, F., & Behrmann, M. (2009). Reduced structural connectivity in ventral visual cortex in congenital prosopagnosia. *Nature Neuroscience, 12*(1), 29–31.
Towler, J., Gosling, A., Duchaine, B., & Eimer, M. (2012). The face-sensitive N170 component in developmental prosopagnosia. *Neuropsychologia, 50*(14), 3588–3599.
Tsantani, M., & Cook, R. (2020). Normal recognition of famous voices in developmental prosopagnosia. *Scientific Reports, 10*(1), 1–11.
Tsantani, M., Gray, K. L. H., & Cook, R. (2020). Holistic processing of facial identity in developmental prosopagnosia. *Cortex; A Journal Devoted To the Study of the Nervous System and Behavior, 130*, 318–326.
Tsantani, M., Podgajecka, V., Gray, K. L. H., & Cook, R. (2022). How does the presence of a surgical face mask impair the perceived intensity of facial emotions? *PLoS One, 17*(1), Article e0262344.
Tsantani, M., Vestner, T., & Cook, R. (2021). The Twenty Item Prosopagnosia Index (PI20) provides meaningful evidence of face recognition impairment. *Royal Society Open Science, 8*(11), Article e202062.
Vestner, T., Gray, K. L. H., & Cook, R. (2021). Visual search for facing and non-facing people: The effect of actor inversion. *Cognition, 208*, Article 104550.
Vestner, T., Gray, K. L., & Cook, R. (2022). Sensitivity to orientation is not unique to social attention cueing. *Scientific Reports, 12*(1), e5059.
Vestner, T., Over, H., Gray, K. L. H., & Cook, R. (2021). Objects that direct spatial attention produce the search advantage for facing dyads. *Journal of Experimental Psychology: General, 151*(1), 161–171.
Wilmer, J. B., Germine, L., Chabris, C. F., Chatterjee, G., Williams, M., Loken, E., et al. (2010). Human face recognition ability is specific and highly heritable. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 5238–5241.
Winston, J. S., Henson, R. N. A., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of Neurophysiology, 92*(3), 1830–1839.
Woods, A. T., Velasco, C., Levitan, C. A., Wan, X., & Spence, C. (2015). Conducting perception research over the internet: A tutorial review. *PeerJ, 3*, Article e1058.