

Dissociations between face identity and face expression processing in developmental prosopagnosia

Lauren Bell^a, Brad Duchaine^b, Tirta Susilo^{a,*}

^a Victoria University of Wellington, New Zealand

^b Dartmouth College, USA

ARTICLE INFO

Keywords:

Developmental
Prosopagnosia
Face
Identity
Expression
Dissociation

ABSTRACT

Individuals with developmental prosopagnosia (DPs) experience severe and lifelong deficits recognising faces, but whether their deficits are selective to the processing of face identity or extend to the processing of face expression remains unclear. Clarifying this issue is important for understanding DP impairments and advancing theories of face processing. We compared identity and expression processing in a large sample of DPs ($N = 124$) using three different matching tasks that each assessed identity and expression processing with identical experimental formats. We ran each task in upright and inverted orientations and we measured inversion effects to assess the integrity of upright-specific face processes. We report three main results. First, DPs showed large deficits at discriminating identity but only subtle deficits at discriminating expression. Second, DPs showed a reduced inversion effect for identity but a normal inversion effect for expression. Third, DPs' performance on the expression tasks were linked to autism traits, but their performance on the identity tasks were not. These results constitute several dissociations between identity and expression processing in DP, and they are consistent with the view that the core impairment in DP is highly selective to identity.

1. Background

Developmental prosopagnosia (DP) is a neurodevelopmental condition defined by the lifelong inability to recognise faces (McConachie, 1976). DP research has made notable progress in recent decades (Albonico & Barton, 2019; Bate & Tree, 2017; Biotti & Cook, 2016; Susilo & Duchaine, 2013), but whether DP deficits are selective to the processing of facial identity is unclear. Some people with DP (DPs) appear to have deficits that disrupt only identity processing (e.g., Duchaine, Yovel, Butterworth, & Nakayama, 2006), but other DPs can have additional deficits processing other facial information such as expression (e.g., Biotti & Cook, 2016), gender or sex (e.g., Marsh, Biotti, Cook, & Gray, 2019), and trustworthiness (e.g., Todorov & Duchaine, 2008). Some DPs can also have trouble discriminating exemplars of non-face objects (e.g., Geskin & Behrmann, 2018). While these findings may reflect the genuine heterogeneity of DP, they are mostly based on small-sample studies, which tend to produce imprecise estimates and prevent strong conclusions to be drawn. To address this issue more decisively, we need a series of high-powered, large-sample DP studies that compare identity processing against a range of other face processing skills and relevant neurocognitive functions. Here we report such a

study, focusing on the contrast between identity and expression processing.

Leading neurocognitive models of face processing (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000; Duchaine & Yovel, 2015) posit that identity and expression analyses proceed along separate pathways. Patients with acquired prosopagnosia can have impaired identity processing but intact expression processing (e.g., Fox, Hanif, Iaria, Duchaine, & Barton, 2011; Mattson, Levin, & Grafman, 2000), whereas patients with impaired expression processing can have normal identity processing (Adolphs, Tranel, Damasio, & Damasio, 1994; Calder et al., 1997; Humphreys, Donnelly, & Riddoch, 1993; Young, Hellowell, Van De Wal, & Johnson, 1996). Electrophysiological and neuroimaging data show that identity and expression processing are carried out at different time courses (Eimer & Holmes, 2002; Holmes, Vuilleumier, & Eimer, 2003) and in different brain regions (Haxby et al., 2000; Winston, Henson, Fine-Goulden, & Dolan, 2004). However, identity and expression processing can also interact. Interference studies show that task-irrelevant expression information can hinder identity processing and vice versa (Fisher, Towler, & Eimer, 2016; Ganel & Goshen-Gottstein, 2004), and modelling studies show that identity and expression information can be extracted from common image statistics

* Corresponding author at: School of Psychology, Victoria University of Wellington, NZ.

E-mail address: tirta.susilo@vuw.ac.nz (T. Susilo).

<https://doi.org/10.1016/j.cognition.2023.105469>

Received 31 October 2021; Received in revised form 21 April 2023; Accepted 24 April 2023

Available online 20 May 2023

0010-0277/© 2023 Elsevier B.V. All rights reserved.

(Calder, Burton, Miller, Young, & Akamatsu, 2001). Identity and expression processing may also develop along a common trajectory, as shown by similar improvements in children's identity and expression processing skills (Dalrymple, di Oleggio Castello, Elison, & Gobbin, 2017).

Several studies have investigated expression processing in DP. Some found normal processing (e.g., Döbel, Bölte, Aicher, & Schweinberger, 2007; Duchaine, Parker, & Nakayama, 2003; Humphreys et al., 1993; Lee, Duchaine, Wilson, & Nakayama, 2010; Palermo et al., 2011), while others found impaired processing (e.g., Biotti & Cook, 2016; Burns, Martin, Chan, & Xu, 2017; Djouab et al., 2020; Duchaine et al., 2006; Schmalzl, Palermo, & Coltheart, 2008; Tsantani, Gray, & Cook, 2022). Overall, these results may be taken as evidence that DP deficits are not selective to identity, and that expression processing may or may not be impaired in DP depending on individual heterogeneity. However, such conclusion is uncertain because many of these studies are single-case studies, and the group studies tested relatively small samples (the largest N is 34 in Tsantani et al., 2022; the second largest is 17 in Biotti & Cook, 2016; the rest tested 12 or less DPs). Moreover, many studies only used one or two tasks to measure expression processing, often without parallel tasks that measure identity processing in the same way.

To provide more decisive results, we ran a study that offers four methodological improvements. First, we tested an unprecedentedly large sample of 124 DPs. This large sample size increases the statistical power of our study to detect and clarify the status of expression processing in DP. Second, we used three different matching tasks that each assessed identity and expression processing under identical experimental procedures. This design allowed us to better isolate and compare identity and expression processing. The matching format was chosen to make the identity and expression tasks as simple as possible, and to minimise the contribution of long-term memory or semantic knowledge. Third, we ran each task in upright and inverted orientations. This setup allowed us to measure a face inversion effect (Yin, 1969), which we used to index the integrity of upright-specific processes involved in identity or expression analyses. Finally, we measured the presence of subthreshold autism traits in the DP group. This approach allowed us to explore whether identity or expression deficits in DP are linked to neurodevelopmental traits that may co-vary with DP such as autism.

2. Methods

2.1. Participants

2.1.1. DP participants

DP participants were sourced from Prosopagnosia Research Center (faceblind.org) as part of our ongoing research programme on DP. We restricted participation to individuals aged 18–52 years to avoid testing older individuals, which can exhibit reduced performance on a range of cognitive tasks (e.g., Deary et al., 2009; Hartshorne & Germine, 2015). Following typical diagnostic practice (e.g., Barton & Corrow, 2016), our inclusion criteria were (1) subjective complaints of lifetime problems recognising faces, (2) an impaired score on the Prosopagnosia Index 20-item (Shah, Gaule, Sowden, Bird, & Cook, 2015), (3) an impaired score on the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006), and (4) an impaired score on a famous faces test (Duchaine & Nakayama, 2005). Exclusion criteria were (1) a reported history of brain damage or (2) an impaired score on the Leuven Perceptual Organisation Screening Test (Torfs, Vancleef, Lafosse, Wagemans, & de-Wit, L., 2014). We also measured the presence of autism traits using the Subthreshold Autism Trait Questionnaire (SATQ; Kanne, Wang, & Christ, 2012), but we did not exclude participants on this basis.

A total of 128 DPs completed the study. We excluded four DPs because three attempted the tasks once prior to fully completing them, and one reported being disrupted for an extended period while completing the tasks. The final sample comprised 124 DPs (80 women,

39 men, 5 other). Their diagnostic scores are presented in Table 1. The mean age was 38.07 years old ($SD = 9.48$, range 20–52 years old). Most DPs lived in the USA ($n = 89$); the rest lived in the UK ($n = 18$), Canada ($n = 10$), Germany ($n = 6$) and France ($n = 1$).

2.1.2. Control participants

A total of 251 individuals located in North America participated via Amazon Mechanical Turk (www.mturk.com). Following completion of the experimental tasks, controls also completed the CFMT, which we used to screen out potential DP. Controls were excluded if they were older than 52 years of age at the time of testing ($n = 43$) or scored within the DP range (raw score below 43) on the CFMT ($n = 35$). To enhance data quality, we also screened out controls who showed poor engagement with the experimental tasks, as reflected by accuracy at or below chance level for any task ($n = 40$).

The final control group comprised 133 individuals (89 woman, 44 men). The mean age was 36.88 years old ($SD = 7.58$, range 21–52 years old), which was similar to the mean age of the DPs, $t(255) = 1.12$, $p = .266$, $d = 0.14$. The controls' gender distribution was also similar to the DPs', $\chi^2(1) = 0.39$, $p = .531$, $hp2 < 0.01$. Relative to controls, DPs had much lower CFMT scores (control $M = 59.31$, control $SD = 7.66$; DP $M = 35.50$, DP $SD = 4.28$), $t(255) = 30.60$, $p < .001$, $d = 3.82$. The mean CFMT score of the control group is very similar to the original mean (Duchaine & Nakayama, 2006) and previous control means in large-sample DP studies (e.g., $M = 61.2$, $SD = 10.42$ in Biotti & Cook, 2016), indicating that our control group has been selected appropriately. That said, because we screened controls using only the CFMT, it is possible that the control group might have included individuals with undiagnosed DP, and that control performance might have been slightly underestimated.

All participants completed the study online on Testable (www.testable.org, Rezlescu, Danaila, Miron, & Amariei, 2020), a web-based platform for running sensitive behavioural experiments. They provided consent to participate by clicking an 'agree' button presented below the digital consent form. On completing the tasks, participants were linked to a debriefing form. The study was approved by Victoria University of Wellington's Human Ethics Committee.

2.2. Materials and procedure

We used three different tasks: simultaneous matching, sequential matching, and sorting (Fig. 1). All tasks were administered online on Testable (Rezlescu et al., 2020). Each task had an identity version and an expression version, and each was run upright and inverted. Orientation was blocked for the simultaneous and the sequential matching tasks and intermixed for the sorting tasks. Raw data are available at OSF <https://osf.io/uwk9y/>

2.2.1. Simultaneous matching task

This task was adapted from Palermo, O'Connor, Davis, Irons, and McKone (2013). Participants viewed three faces and selected the 'odd-identity' (identity task) or 'odd-expression' (expression task) out (Fig. 1A). Stimuli were shown for 4500 ms. An inter-trial-interval (ITI) of

Table 1

DP diagnostic scores. Norm data for the CFMT and FFT were sourced from a separate sample of Amazon Turk participants. PI-20 control data was sourced from Shah et al. (2015).

Diagnostic test	Diagnostic cut-off	Score M (SD)	Range	Norm data n , M (SD)
CFMT	< 42	35.55 (4.18)	17–41	$n = 97$, 54.3 (7.27)
FFT	< 58	28.88 (13.16)	0–57.14	$n = 97$, 78.65 (11.60)
PI-20	> 60	81.43 (6.27)	64–93	$n = 242$, 38.90 (10.88)

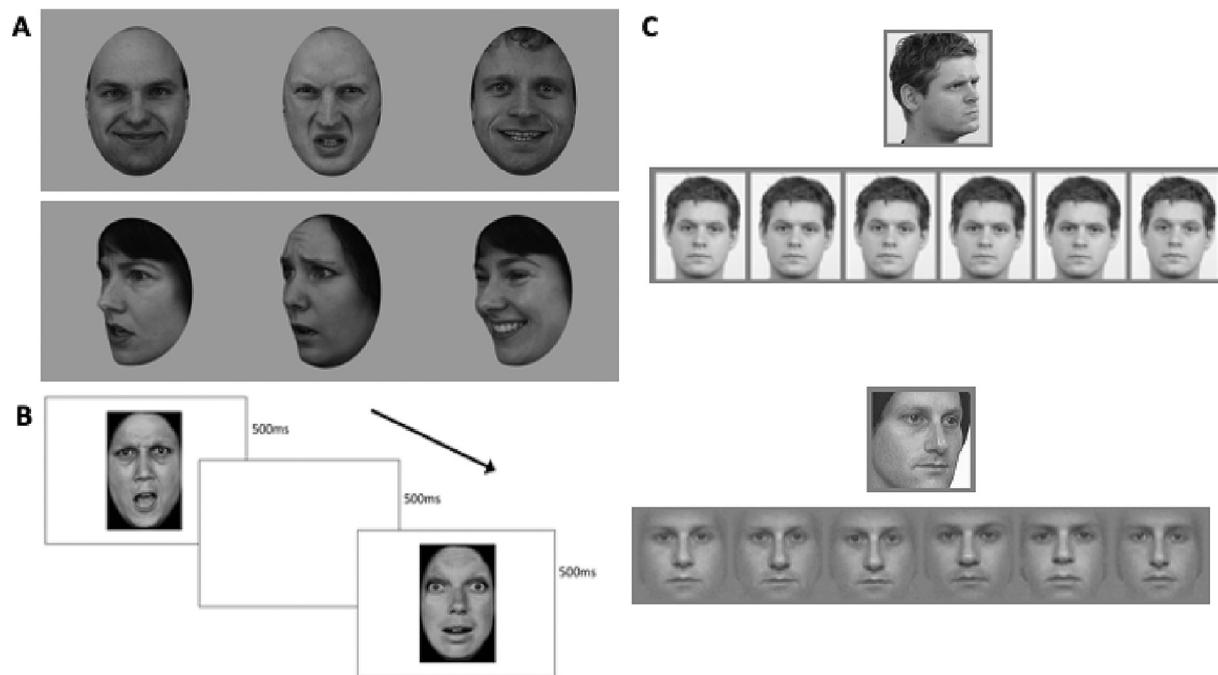


Fig. 1. A. Example from the simultaneous matching task for expression (top) and identity (bottom). B. Example from the sequential matching task. C. Example trials from the sorting task for expression (top) and identity (bottom).

500 ms separated trials. Participants completed 120 trials (60 upright, 60 inverted) for each version of the task. In the identity version, the faces displayed three different expressions. Two faces belonged to the same individual, and the other face belonged to a different individual of the same sex. All stimuli were from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998). In the expression version, the three faces were from different identities. Two faces displayed the same expression, and one displayed a different expression. The expressions were happy, sad, angry, surprised, disgusted, or fearful.

2.2.2. Sequential matching task

This task was created by Garrido et al. (2009). Participants viewed two faces in quick succession and judged whether they showed the same or different identities (identity task) or expressions (expression task) (Fig. 1B). The first face was shown for 500 ms, followed by a 500 ms inter-stimulus interval (ISI), then the second face for 500 ms. An ITI of 500 ms separated trials. Stimuli were 36 greyscale images of six females displaying the six basic expressions. Participants completed 144 trials (72 upright, 72 inverted) for each version of the task. In the expression version, participants had to ignore the identities of the faces and focus on their expressions. The expressions were happy, sad, angry, surprised, disgusted, or fearful. On every trial, the identities of the two faces differed. In the identity version, participants had to ignore the expressions displayed on the faces and focus on their identities. On every trial, the expressions displayed on the two faces differed.

2.2.3. Sorting task

This task used the Cambridge Face Perception Test (CFPT, Duchaine, Germine, & Nakayama, 2007) format. A target face ($\frac{3}{4}$ viewpoint) was presented above six randomly ordered morph faces (full-front viewpoint). Participants were asked to sort the six faces with regards to their similarity in identity or expression to the target face (Fig. 1C). The identity task was the original CFPT (Duchaine et al., 2007). The expression task was created to match the CFPT. The target face displayed an expression at full intensity (e.g., anger at 100% intensity) and the six morph faces showed the same individual with the same expression at differing intensities between the target expression and neutral (as in Janik, Rezlescu, & Banissy, 2015). Target expressions were angry, sad,

happy, or fearful. Participants had to sort the morph faces from most to least similar (left to right) within 40 s. Participants completed 16 trials (8 upright, 8 inverted) for each identity and expression versions separately.

3. Results

3.1. Simultaneous matching task

We first compared DPs' performance with identity and expression on upright trials. A 2×2 ANOVA on upright accuracy data (Fig. 2) revealed an interaction $F(1,255) = 17.7, p < .001$, where DPs performed worse than controls with identity (control = 77%, DP = 70%), $t(255) = 5.33, p < .001$, but not with expression (control = 78%, DP = 76%), $t(255) = 1.31, p = .559$. The same analysis with response time data also revealed an interaction ($F(1,255) = 6.39, p = .012$, with DPs being slower than control with identity (control = 2215 ms, DP = 2901 ms), $t(255) = 8.83, p < .001$, and with expression but to a lesser extent (control = 2136 ms, DP = 2657 ms), $t(255) = 7.23, p < .001$. These results suggest that DPs have more trouble with identity than expression. The results also suggest that DPs might have minor problems with expression as reflected by the numerically slower and less accurate performance, but they were statistically comparable.

We next analysed the inversion effect. A 2×2 ANOVA on accuracy inversion effect (accuracy upright – accuracy inverted; Fig. 2B) showed an interaction $F(1,255) = 10.1, p = .002$, where DPs showed a reduced inversion effect for identity (control = 11%, DP = 6%), $t(255) = 4.08, p < .001$, but not expression (control = 7%, DP = 7%), $t(255) = 0.08, p = 1.000$. A 2×2 ANOVA on response time (response time inverted – response time upright) also showed an interaction, $F(1,255) = 6.25, p < .013$, with controls showing a larger inversion effect for identity than expression (identity = 177 ms, expression = -93 ms), $t(255) = 5.01, p < .001$, but DPs showing similar inversion effects for both face information (identity = 55 ms, expression = -20 ms), $t(255) = 1.36, p = .524$. These results suggest that DPs have impaired inversion effect for identity but a largely intact inversion effect for expression.

Overall, findings from the simultaneous matching task shows that DPs are more impaired at discriminating identity than expression, with

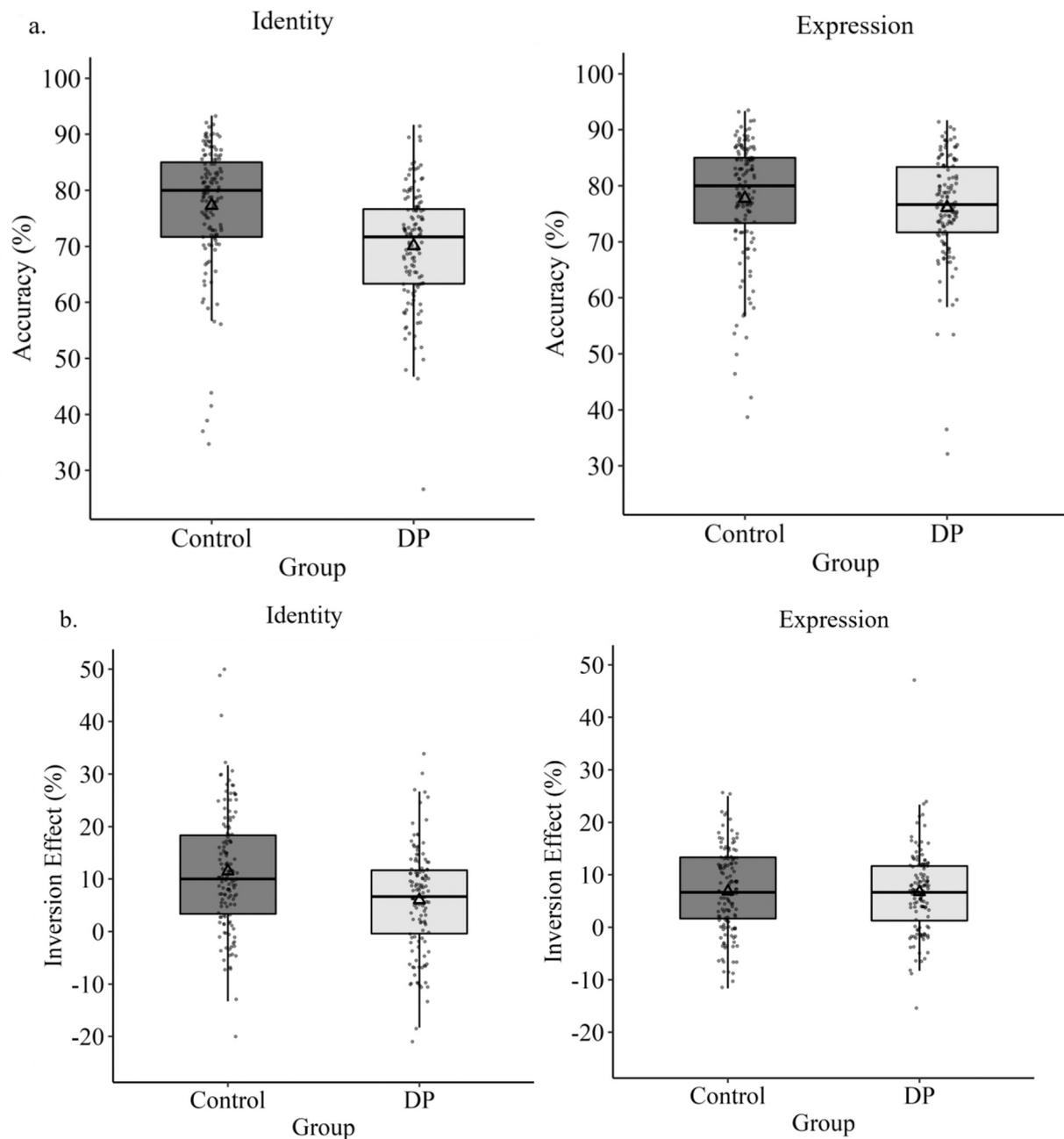


Fig. 2. (A) Upright accuracy data from the simultaneous matching task. Dots represent individual data. Triangles represent group means. (B) Inversion accuracy data from the simultaneous matching task. Dots represent individual data. Triangles represent group means.

some indication for potentially subtle problems with expression. DPs also show impaired inversion effect but only for identity, suggesting that their identity deficits might be driven by disruptions of orientation-selective mechanisms dedicated for identity.

3.2. Sequential matching task

A 2×2 ANOVA on upright accuracy data (Fig. 3A) revealed an interaction $F(1,255) = 27.8, p < .001$, where DPs performed worse than controls with identity (control = 75%, DP = 66%), $t(255) = 7.55, p < .001$, but not with expression (control = 77%, DP = 75%), $t(255) = 1.44, p = .473$. Response time analysis only revealed a main effect of group, $F(1,255) = 103, p < .001$, with DPs being slower than controls for both face information. No other effects were significant. These results suggest that DPs have more trouble with identity than expression, but they

might also have subtle problems with expression since they were slower than controls and numerically worse on accuracy.

The same-different response format of this task allowed us to run additional analyses of sensitivity (d') and response bias (c). A 2×2 ANOVA on upright d' -prime data revealed an interaction $F(1,255) = 20.0, p < .001$. Consistent with the accuracy analysis, DPs performed worse than controls on identity (control = 1.45, DP = 0.92), $t(255) = 7.10, p < .001$, but not expression (control = 1.64, DP = 1.50), $t(255) = 1.72, p = .315$. A 2×2 ANOVA on upright response bias data revealed no significant effects (all c values are close to zero, range = -0.04 to 0.05), suggesting unbiased responses by both groups.

For the inversion effect, a 2×2 ANOVA on accuracy data (accuracy upright – accuracy inverted; Fig. 3B) showed an interaction $F(1,255) = 13.35, p < .001$, where DPs showed a reduced inversion effect for identity (control = 6%, DP = 3%), $t(255) = 3.78, p = .001$, but not

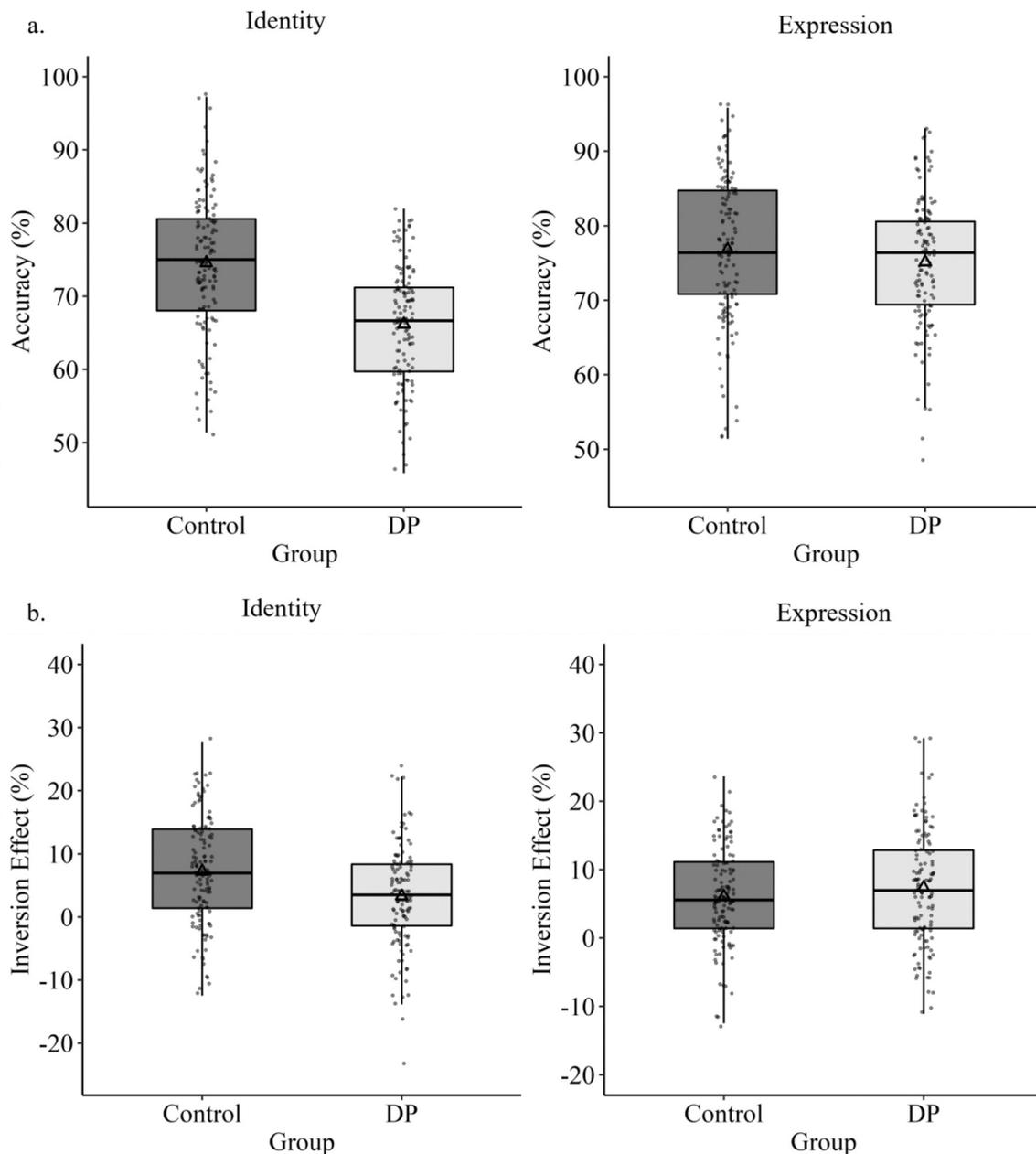


Fig. 3. (A) Upright accuracy data from the sequential matching task. Dots represent individual data. Triangles represent group means. (B) Inversion accuracy data from the sequential matching task. Dots represent individual data. Triangles represent group means.

expression (control = 6%, DP = 7%), $t(255) = 1.35, p = .531$. A 2×2 ANOVA on response time (response time inverted – response time upright) revealed no significant effects, with comparable numbers across all conditions (control identity = 36 ms, control expression = 34 ms, DP identity = 29 ms, DP expression = 20 ms). These results suggest that DPs have impaired inversion effect for identity but not expression.

Similar to the results from the simultaneous matching task, the results from the sequential matching task suggests that DPs have more trouble with identity than with expression. There was also an indication for minor problems with expression. The inversion effect was again reduced for identity but not expression, indicating disruptions of orientation-selective face processing specific to identity.

3.3. Sorting task

A 2×2 ANOVA on upright accuracy data (Fig. 4A) revealed an interaction $F(1,255) = 16.2, p < .001$, where DPs performed worse than

controls with identity (control = 72%, DP = 60%), $t(255) = 9.73, p < .001$, as well as expression but to a lesser degree (control = 65%, DP = 60%), $t(255) = 3.12, p = .011$. Response time analysis only revealed a main effect of group, $F(1,255) = 54.7, p < .001$, with DPs being slower than controls for both face information. No other effects were significant. These results suggest that DPs have more trouble with identity than expression, but they also have minor problems with expression.

A 2×2 ANOVA on accuracy inversion effect (accuracy upright – accuracy inverted; Fig. 4B) showed an interaction $F(1,255) = 5.20, p = .023$, where DPs showed a reduced inversion effect for identity (control = 19%, DP = 10%), $t(255) = 7.13, p < .001$, and also expression but to a lesser extent (control = 21%, DP = 16%), $t(255) = 3.10, p = .011$. A 2×2 ANOVA on response time (response time inverted – response time upright) revealed only a group difference, $F(1,255) = 6.30, p = .013$, with DPs showing smaller inversion effect overall. No other effects were significant. These results suggest that DPs have reduced inversion effect for both identity and expression, but the reduction is greater for identity.

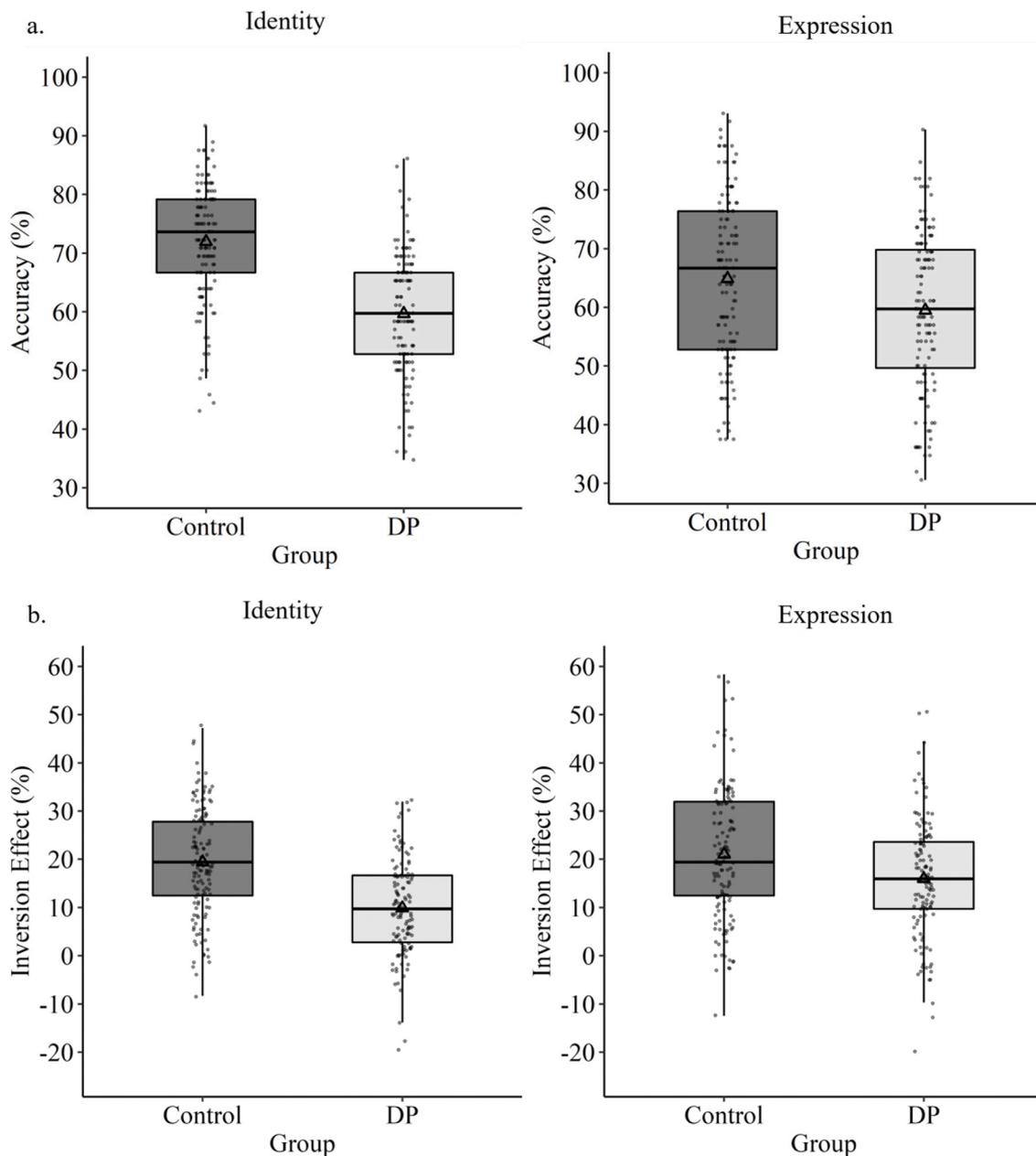


Fig. 4. (A) Upright accuracy data from the sorting task. Dots represent individual data. Triangles represent group means. (B) Inversion accuracy data from the sorting task. Dots represent individual data. Triangles represent group means.

Overall, results from the sorting task indicates that DPs are more impaired with identity than with expression, but DPs also have subtle impairment with expression. Inversion effect analyses again show that DPs have impaired inversion effect for identity, but they also present with slightly reduced inversion effect for expression. These findings suggest a dissociation between orientation-selective disruptions in DP, with greater disruptions for identity processing than for expression processing.

3.4. Aggregate analyses

The three tasks are consistent in showing that DPs have more trouble with identity than expression, and that they show a pronounced reduction of inversion effect for identity but not expression. But there is a slight difference between the tasks regarding the expression data. The sorting task revealed that DPs have minor problems with expression (5%

accuracy drop that is significant), whereas the two matching tasks did not (2% accuracy drops that are not significant). Similarly, the sorting task revealed that DPs have reduced inversion effect for expression (5% smaller than controls), but the two matching tasks did not (0–1% larger than controls). These differences might seem to suggest that the sorting task is more sensitive at detecting expression deficits than the other tasks. To test whether this is the case, we ran a $3 \times 2 \times 2$ ANOVA with task, face information, and group as factors. If the sorting task is statistically more sensitive at picking up expression deficits than the other tasks, we would expect to find a significant 3-way interaction.

For upright accuracy data, the 3-way interaction was not significant, $F(2,510) = 0.28, p = .752$. This result suggests that the sorting task is not statistically more sensitive than the other tasks. For a thorough analysis, we followed up this lack of 3-way interaction by collapsing data across tasks and analysed the aggregate accuracy (Fig. 5A). A 2×2 ANOVA on accuracy data revealed an interaction $F(1, 255) = 51.00, p < .001$, with

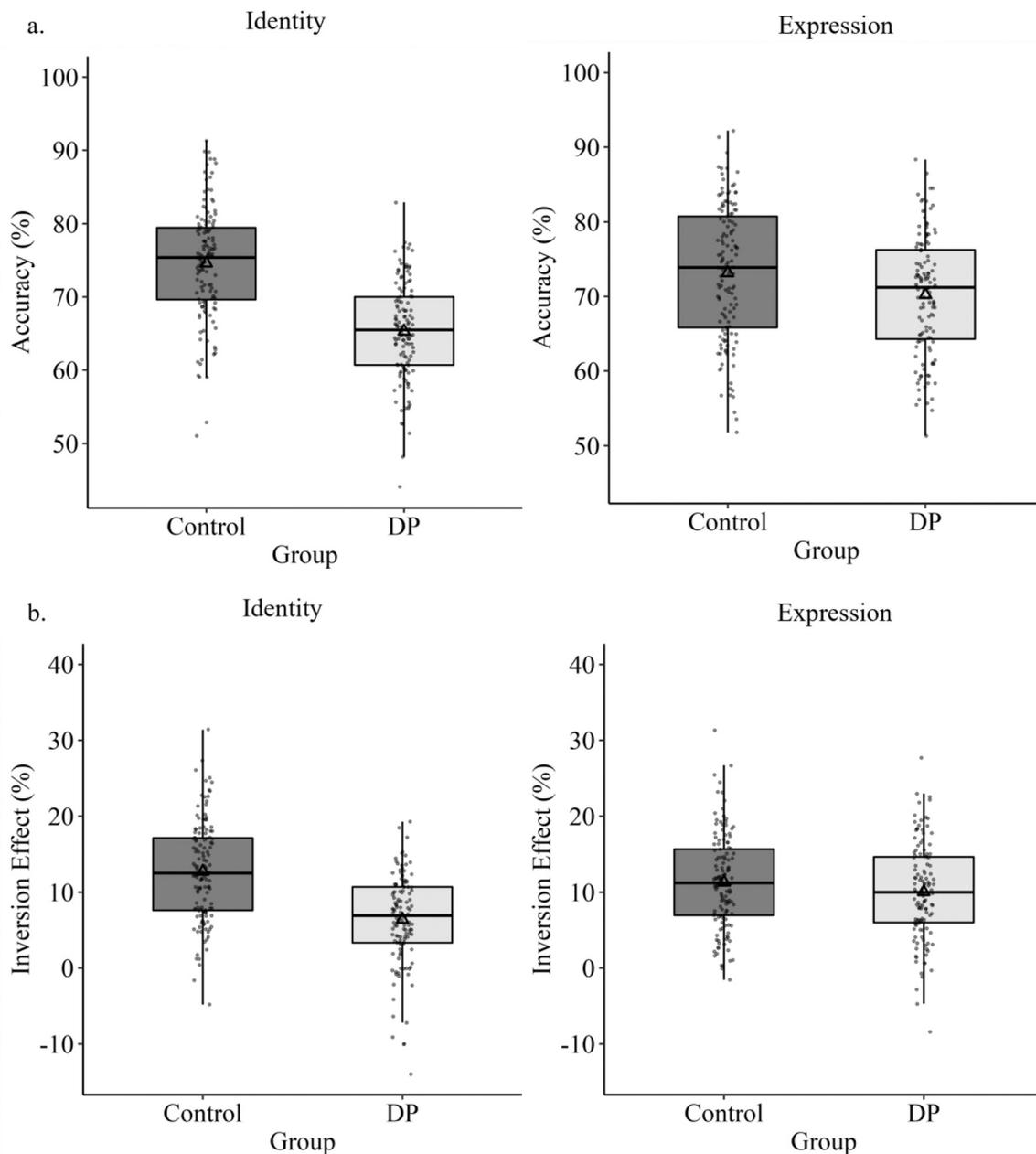


Fig. 5. (A) Upright accuracy data on aggregate across all tasks. Dots represent individual data. Triangles represent group means. (B) Inversion accuracy data on aggregate across all tasks. Dots represent individual data. Triangles represent group means.

DPs showing impaired performance with identity (control = 75%, DP = 65%), $t(255) = 10.30$, $p < .001$, as well as expression but less so (control = 73%, DP = 70%), $t(255) = 2.74$, $p = .033$. A 2×2 ANOVA on aggregate response time revealed no interaction, only a main effect of group (controls = 8430 ms, DP = 11,557), $F(1, 255) = 62.20$, $p < .001$, and a main effect of face information (identity = 10,255 ms, expression = 9595 ms). This result suggests that across all tasks, DPs have more trouble with identity than expression, but they also show subtle problem with expression.

For the inversion effect data, the 3-way interaction was again not significant, $F(2,510) = 0.08$, $p = .912$. We again analysed aggregate data, where a 2×2 ANOVA (Fig. 5B) revealed an interaction $F(1,255) = 23.22$, $p < .001$. DPs showed a reduced inversion effect for identity (control = 13%, DP = 6%), $t(255) = 8.07$, $p < .001$, but a normal inversion effect for expression (control = 11%, DP = 10%), $t(255) = 1.63$, $p = .366$. A 2×2 ANOVA on aggregate response time (Fig. x)

revealed only a main effect of group, $F(1,255) = 6.58$, $p = .011$, with DPs showing a smaller inversion effect overall than controls. These results suggest that across all tasks, DPs show impaired inversion effect for identity, but largely intact inversion effect for expression.

Together, the task-specific analyses and the aggregate analyses paint a coherent set of findings. First, DPs are more impaired with identity than with expression. Second, DPs show minor impairment with expression, and this minor impairment may appear more pronounced on the sorting task. Finally, DPs show a dissociation of inversion effect. DPs consistently showed large reductions of inversion effect for identity, but mostly intact inversion effect for expression.

3.5. Identity-expression correlation within each task

To further examine the extent to which identity and expression processing dissociate in DP, we ran a correlation analysis. This analysis

relies on the following logic – if identity and expression processing dissociate in DP to an unusual degree, then identity and expression data should produce a weaker correlation in DPs than in controls. Control data show that all tasks have moderate-to-good reliabilities as indicated by Cronbach's Alphas between 0.631 and 0.813 (simultaneous matching identity = 0.805, simultaneous matching expression = 0.813, sequential matching identity = 0.742, sequential matching expression = 0.783, sorting identity = 0.631, sorting expression = 0.743). These reliabilities suggest that the tasks are suitable for correlation analyses.

Table 2 presents the identity-expression correlation for each task in control and DP groups, accompanied by Fisher's *r* to *z* tests that directly test whether the correlations in the two groups are statistically different.

Across all tasks, identity and expression data in controls consistently correlate at a moderate size, ranging from 0.464 to 0.495. The correlations are less consistent in DPs, producing a greater range from 0.219 to 0.507. Critically, the Fisher's *r* to *z* tests indicate that the identity-expression correlation is weaker in DPs than in controls for sequential matching ($p = .01$) and sorting ($p = .05$) tasks. These weaker correlations provide another evidence for the dissociation between identity and expression processing in DP.

3.6. Cross-task correlations for identity and expression separately

We performed another correlation analysis to measure how the tasks correlate with each other for identity and expression separately. These correlations reflect the extent to which the different tasks capture common mechanisms relevant for each face information. Impaired processing of a particular face information in DP predicts weaker correlations for that face information in DPs than in controls. Table 3 presents the correlations, again with the Fisher's *r* to *z* tests that directly test for group differences.

For identity, controls consistently show a small-to-moderate correlations, ranging from 0.298 to 0.391. In contrast, DPs show a non-significant correlation for two of the three task pairs (simultaneous matching-sorting at 0.123; sequential matching-sorting at 0.171). However, Fisher's tests revealed that the correlations in DPs are statistically comparable to those in controls, so these results require careful interpretations. For expression, controls again consistently show a small-to-moderate correlations, ranging from 0.315 to 0.494. DPs also show a range of small-to-moderate correlations, ranging from 0.254 to 0.396. However, one of the Fisher's tests came out significant (for the sequential matching-sorting pair), potentially reflecting a disruption of expression processing in DP. Overall, these results accord with other analyses in showing that identity and expression processing are both impaired in DP, albeit to a different degree.

3.7. Subthreshold autism traits

We next investigated whether identity and expression processing in DP dissociate in terms of their relationship to subthreshold autism traits. The motivation is two-fold. First, autism traits and DP may co-vary (Kracke, 1994; Minio-Paluello, Porciello, Pascual-Leone, & Baron-Cohen, 2020; Pietz, Ebinger, & Rating, 2003). Second, autism traits have been linked to expression deficits (e.g., Loth et al., 2018), although the overall evidence appears mixed (Harms, Martin, & Wallace, 2010) and the existing effects tend to be small (e.g., Uljarevic & Hamilton, 2013). These motivations raise the possibility of a selective link between autism traits and expression deficits but not identity deficits. To test this

Table 2
Identity-expression correlations for each task in control and DP groups.

Identity-expression	Control	DP	Fisher's <i>r</i> to <i>z</i>	<i>p</i> -value
Sim matching	0.495***	0.507***	-0.13	0.45
Seq matching	0.479***	0.219*	2.37	0.01
Sorting	0.464***	0.291**	1.6	0.05

Table 3

Cross-task correlations for identity and expression in control and DP groups.

Identity	Control	DP	Fisher's <i>r</i> to <i>z</i>	<i>p</i> -value
Sim matching and seq matching	0.391***	0.442***	-0.49	0.31
Sim matching and sorting	0.298***	0.123	1.45	0.07
Seq matching and sorting	0.322***	0.171	1.28	0.10
Expression	Control	DP	Fisher's <i>r</i> to <i>z</i>	<i>p</i> -value
Sim matching and seq matching	0.418***	0.396***	0.21	0.42
Sim matching and sorting	0.315***	0.356***	-0.37	0.36
Seq matching and sorting	0.494***	0.254**	2.23	0.01

possibility we ran correlations between SATQ (a measure of sub-threshold autism that we collected as part of DP diagnosis) and the aggregate identity and expression data from DPs (Fig. 6). SATQ was correlated with expression ($r = -0.29$, $p = .001$) but not identity ($r = 0.03$, $p = .734$), Fisher's *r* to *z* = 3.18, $p = .001$. This result shows that the higher the autism score in DP, the more likely the expression deficits.

This finding survives four robustness checks. First, we reran the same correlations excluding three SATQ items that explicitly ask about expression ("I respond appropriately to other people's emotions (for example, comforting someone who is upset)", "I am good at knowing what others are feeling by watching their facial expressions or listening to the tone of their voice", "I can sense that someone is not interested in what I'm saying by reading their facial expressions"). We obtained the same result, with a SATQ-expression correlation of -0.28 and a SATQ-identity correlation of 0.04. Second, we reran the correlations excluding the three expression items as well as four additional "social" items that may be impacted by expression deficits ("I seek out and approach others for social interactions", "I enjoy social situations where I can meet new people and chat (i.e. parties, dances, sports, games)". "Others consider me warm, caring, and/or friendly", "I make eye contact when talking with others."). Again we found the same result, with a SATQ-expression correlation of -0.27 and a SATQ-identity correlation at 0.07. Third, we excluded 30 DPs who met the autism threshold for SATQ (score > 40, Kanne et al., 2012), in case they might have had undiagnosed autism. We reran the correlations with the remaining sample ($N = 94$), with and without the three expression items and the four social items. We found slightly smaller but still significant correlations for expression (range = -0.10 to -0.16) but not identity (range = 0.02 to 0.07). Finally, we computed the correlations between SATQ and each task format separately, with and without expression and social items excluded. As shown in Table 4, the overall pattern of findings persists. SATQ is negatively correlated with expression tasks but not with identity tasks. A potential exception is the sorting tasks, which produced no significant correlations despite showing similar trends, but this result should be taken cautiously because the sorting tasks have the lowest number of trials and the lowest reliabilities.

Overall, these multiple checks demonstrate that our finding of a link between autism traits and expression processing in DP is robust and cannot be explained by select items in SATQ, a subset of DPs, or particular task formats.

3.8. Specific expressions

A subset of our data allowed us to look deeper into the expression results. We examined whether the minor expression deficits in DP are driven by specific expressions. To address this question, we analysed data from the simultaneous matching task and the sorting task, both of which presented trials with individual expressions. We did not use the sequential matching task because the task combines two expressions in half of the trials. A 2×6 ANOVA (group: DP, control; expression: anger,

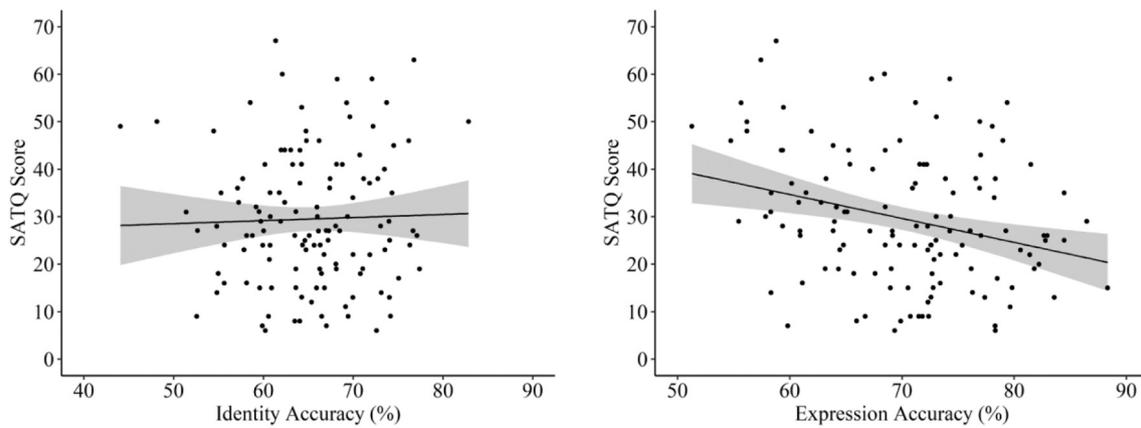


Fig. 6. Correlations between SATQ and identity and expression processing in DP.

Table 4

Correlations between SATQ and each identity and expression tasks.

SATQ versions	Face info	Sim matching	<i>p</i> -value	Seq matching	<i>p</i> -value	Sorting	<i>p</i> -value
All items	Expression	−0.35	0.00	−0.24	0.01	−0.11	0.22
	Identity	0.05	0.58	−0.10	0.26	0.09	0.32
Without 3 expression items	Expression	−0.35	0.00	−0.24	0.01	−0.09	0.32
	Identity	0.06	0.51	−0.10	0.26	0.11	0.22
Without 3 expression items and 4 social items	Expression	−0.33	0.00	−0.24	0.01	−0.08	0.38
	Identity	0.09	0.32	−0.09	0.32	0.12	0.18

disgust, fear, happy, sad, surprise) on the simultaneous matching task revealed no interaction, $F(5, 1275) = 1.05, p = .388$. Similarly, a 2×4 ANOVA (group: DP, control; expression: anger, fear, happy, sad) on the sorting task also revealed no interaction, $F(3, 765) = 1.28, p = .282$. These results indicate that the minor expression deficits we observed were not driven by some expressions more than others, but rather reflect a more general problem with any type of expression.

3.9. Inverted trials

Finally, we analysed data from the inverted trials only. To the extent that performance with inverted faces may reflect the integrity of some aspects of object processing (Moscovitch, Winocur, & Behrmann, 1997; Pitcher, Duchaine, Walsh, Yovel, & Kanwisher, 2011), this data may shed some light on the classic question of whether DP deficits are restricted to faces, or whether DP may also disrupt processing of non-face objects (Susilo, 2018; Geskin & Behrmann, 2018). This data is also relevant to the question of whether face processes that are orientation-invariant and can be applied to inverted faces (e.g., local part analysis) are impaired in DP. We compared the aggregate inverted accuracy data for DPs and controls for identity and expression trials separately. For identity, controls ($M = 62\%$, $SD = 8$) outperformed DPs ($M = 59\%$, $SD = 7\%$) by small margin, $t(255) = 3.19, p < .001$. Similarly for expression, controls ($M = 62\%$, $SD = 8\%$) again outperformed DPs by a small margin ($M = 60\%$, $SD = 7$), $t(255) = 1.76, p = .04$. These small margins did not result from floor effects, since DP performance was far above chance level (about 40%). This result suggests that DP may be linked to a minor disruption of object processing, a minor impairment of orientation-invariant face processing, or both.

4. Discussion

We assessed identity and expression processing in DP with a large-sample experiment ($N = 124$ DPs). We used three different tasks, each contrasting identity and expression processing under identical experimental formats. We report three main results. First, DP deficits are selective to identity, where they showed marked deficits with identity but

only subtle deficits with expression. Second, DPs showed reduced inversion effects for identity but not for expression, indicating impaired upright-specific processing of identity but not expression. Third, sub-threshold autism traits in DP are related to expression discrimination but not identity discrimination. Together, these results constitute several important dissociations between identity and expression processing in DP.

Our study extends and corroborates previous findings of dissociations between identity and expression processing in DP (e.g., Duchaine et al., 2003; Lee et al., 2010; Palermo et al., 2011). Our sample size is unprecedentedly large, and our tasks vary considerably in terms of experimental procedures (e.g., the sorting task showed all stimuli at once and allow 40s of completion time; the sequential matching task flashed each stimulus for 500 ms). These methodological strengths increase the generalisability of our results. Both task-specific and aggregate analyses produce coherent findings with only minor variations, and together they present clear and compelling dissociations between identity and expression in DP.

Reports of aberrant expression processing in DP are growing (Biotti & Cook, 2016; Burns et al., 2017; Djouab et al., 2020; Tsantani et al., 2022). Our study adds to these reports by showing that the extent of the expression deficits is minor, compared to the large identity deficits. This result accords with another study that also used the same experimental task with identity and expression and found subtle deficits for expression (Djouab et al., 2020). The other studies that found impaired expression (Biotti & Cook, 2016; Burns et al., 2017; Tsantani et al., 2022) did not assess identity processing with the same experimental tasks, but the size of the expression deficits also appear small (e.g., a 6% drop in accuracy on a 4AFC task in Biotti & Cook, 2016). Overall, the emerging picture is that DP is associated with expression deficits, but the expression deficits are minor compared to the identity deficits.

There is a slight difference between the three tasks regarding the expression result. The sorting task produced a small but statistically significant deficit in DPs, whereas the two matching tasks produced reduced performance that was not statistically significant. Although the difference between the tasks is not statistically significant, the trend for the sorting task to be more sensitive than the other tasks accords with

reports that expression deficits in DP tend to occur when assessed with challenging stimuli, such as face-morphs (Biotti & Cook, 2016; Burns et al., 2017; Djouab et al., 2020), partial faces (Biotti & Cook, 2016), or masked faces (Tsantani et al., 2022). This finding may also explain why DPs rarely report expression deficits in daily life, where they mostly encounter natural faces exhibiting natural expressions. Future investigations of expression processing in DP would benefit from the use of challenging stimuli and tasks.

A novel finding is the dissociation between inversion effects for identity and expression in DP. The reduced inversion effect for identity in DP has been found before (Avidan, Tanzer, & Behrmann, 2011; Klargaard, Starrfelt, & Gerlach, 2018; Russell, Duchaine, & Nakayama, 2009), but the finding of largely intact inversion effect for expression is novel. This finding indicates that the core impairment in DP is highly circumscribed, disrupting upright-specific processing of information relevant for identity while sparing upright-specific processing of information relevant for expression. This finding also helps mitigate the possibility that DPs might have used atypical, orientation-invariant strategies that might have worked better with expression than with identity, resulting in their much smaller deficits for expression than for identity.

Our analysis of the inverted data show that DPs were slightly outperformed by controls, in line with previous results (Klargaard et al., 2018; Russell et al., 2009). This finding is important for two key issues in DP research. First is whether DP deficits are restricted to faces or extend to non-face objects (Geskin & Behrmann, 2018; Susilo, 2018). Since inverted faces have been shown to capture aspects of object processing (Moscovitch et al., 1997; Pitcher et al., 2011), this finding supports the view that DP deficits are selective to faces but they can also impact object processing to a minor extent. The other issue is whether DP deficits are restricted to upright-specific face processes or extend to other face processes that can operate on inverted faces. Inverted faces engage face-selective regions (Kanwisher, Tong, & Nakayama, 1998; Pitcher et al., 2011) and face-selective neurons (Freiwald, Tsao, & Livingstone, 2009), and they can capture rapid attention (Little, Jenkins, & Susilo, 2021) and be analysed somewhat holistically (Susilo, Rezesescu, & Duchaine, 2013; Murphy, Gray, & Cook, 2020). These findings suggest that inverted face deficits in DP may also indicate an impairment of orientation-invariant face processes, which are not well-understood and would require more research.

Another novel finding is the link between subthreshold autism traits and expression deficits in DP. This finding supports the notion that while marked identity deficits are a primary symptom of DP, minor expression deficits may be conceptualised as a secondary symptom that can occur depending on co-varying traits. This finding fits nicely within the view that people with DP may be more prone to developing other neurodevelopmental conditions due to neural migration errors (Susilo & Duchaine, 2013) or common risk factors (Gray & Cook, 2018). The effect size for this link is relatively small (the correlation values are 0.2–0.3), but the link survives multiple robustness checks and so it would benefit from systematic follow-ups. For example, while some studies have reported a direct link between autism and expression deficits (e.g., Loth et al., 2018), others have suggested that such link can be accounted by co-varying alexithymia in the autism population (e.g., Cook, Brewer, Shah, & Bird, 2013). In any case, what this finding illustrates is the value of measuring traits relevant to DP and including them in the main analyses, rather than just using them as an exclusion criterion (Barton & Corrow, 2016; Dalrymple & Palermo, 2016). Such approach may yield novel insights about DP, and perhaps about other conditions and neurodevelopmental disorders in general.

Turning to theoretical implications, our study dovetails with leading neurocognitive models of face perception that feature segregated pathways for identity and expression processing (Bruce & Young, 1986; Haxby et al., 2000; Duchaine & Yovel, 2015). Our results extend these models in two ways. First, the dissociation we found between inversion effects for identity and expression suggests that both pathways carry out

face-specific operations that are distinct and dissociable. This finding is in line with the notion that face-specific processes are not singular but rather heterogeneous (e.g., Rezesescu, Susilo, Wilmer, & Caramazza, 2017), and that distinct face-specific processes may be needed for different kinds of face information. The second extension is developmental. Assuming that the DP deficits with identity have an early onset (Dalrymple et al., 2017; Dalrymple, Garrido, & Duchaine, 2014), our study suggests that identity and expression pathways dissociate relatively early during development. Alternatively, identity and expression pathways are associated during most of development, but DP deficits are selective to identity because expression discrimination is easier to compensate for than identity discrimination, likely using non face-specific strategies. However, this alternative interpretation is unlikely because our identity and expression tasks are comparable in terms of difficulty and size of inversion effects.

Finally, our study sheds new light on the functional locus of the DP impairment. It has been suggested that the presence of both identity and expression deficits in DP are indicative of an early impairment in the face processing stream, before the identity and expression pathways diverge (e.g., Biotti & Cook, 2016). Our results provide a partial support for this “early locus” view. We found both identity and expression deficits, and our analysis of specific expressions indicates an early impairment that would disrupt processing of all expressions. However, our data also provide evidence for a dissociation between identity and expression. In our DP sample, the expression deficits are smaller and inconsistent compared to identity deficits, the reduced inversion effect is negligible for expression but pronounced for identity, and the link with autism traits is found for expression but not identity. These results suggest that there is a later and likely more severe impairment that selectively disrupts the identity processing pathway. These “early locus” and “later locus” views are not mutually exclusive, and future research is needed to clarify their contributions to DP.

CRedit authorship contribution statement

Lauren Bell: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Visualization. **Brad Duchaine:** Conceptualization, Methodology, Resources. **Tirta Susilo:** Conceptualization, Methodology, Formal analysis, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Data availability

Data are available at OSF

Acknowledgments

This work was supported by the Royal Society of New Zealand Marsden Fund 16-VUW-175 to Tirta Susilo. We thank Lucia Garrido and Romina Palermo for sharing their tasks and Lizzie Collyer for helping with manuscript preparation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2023.105469>.

References

- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, 372(6507), 669. <https://doi.org/10.1038/372669a0>
- Albonico, A., & Barton, J. (2019). Progress in perceptual research: The case of prosopagnosia. *F1000Research*, 8. <https://doi.org/10.12688/f1000research.18492.1>. F1000 faculty Rev-765.

- Avidan, G., Tanzer, M., & Behrmann, M. (2011). Impaired holistic processing in congenital prosopagnosia. *Neuropsychologia*, 49(9), 2541–2552.
- Barton, J. J. S., & Corrow, S. L. (2016). The problem of being bad at faces. *Neuropsychologia*, 89, 119–124. <https://doi.org/10.1016/j.neuropsychologia.2016.06.008>
- Bate, S., & Tree, J. J. (2017). The definition and diagnosis of developmental prosopagnosia. *Quarterly Journal of Experimental Psychology*, 70(2), 193–200. <https://doi.org/10.1080/17470218.2016.1195414>
- Biotti, F., & Cook, R. (2016). Impaired perception of facial emotion in developmental prosopagnosia. *Cortex*, 81, 126–136. <https://doi.org/10.1016/j.cortex.2016.04.008>
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, 77(3), 305–327. <https://doi.org/10.1111/j.2044-8295.1986.tb02199.x>
- Burns, E. J., Martin, J., Chan, A. H., & Xu, H. (2017). Impaired processing of facial happiness, with or without awareness, in developmental prosopagnosia. *Neuropsychologia*, 102, 217–228. <https://doi.org/10.1016/j.neuropsychologia.2017.06.020>
- Calder, A. J., Burton, A. M., Miller, P., Young, A. W., & Akamatsu, S. (2001). A principal component analysis of facial expressions. *Vision Research*, 41(9), 1179–1208. [https://doi.org/10.1016/S0042-6989\(01\)00002-5](https://doi.org/10.1016/S0042-6989(01)00002-5)
- Calder, A. J., Young, A. W., Karnat, A., Sprengelmeyer, R., Perrett, D. I., & Rowland, D. (1997). Selective deficits in emotional expression recognition following brain damage. *International Journal of Psychophysiology*, 1(25), 69. Retrieved from <http://www.infona.pl>. Retrieved from.
- 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. <https://doi.org/10.1177/0956797612463582>
- Dalrymple, K., & Palermo, R. (2016). Guidelines for studying developmental prosopagnosia in adults and children. *Wiley Interdisciplinary Reviews: Cognitive Science*, 7, 73–87. <https://doi.org/10.1002/wcs.1374>
- Dalrymple, K. A., di Oleggio Castello, M. V., Elison, J. T., & Gobbini, M. I. (2017). Concurrent development of facial identity and expression discrimination. *PLoS One*, 12(6). <https://doi.org/10.1371/journal.pone.0179458>. e0179458.
- Dalrymple, K. A., Garrido, L., & Duchaine, B. (2014). Dissociation between face perception and face memory in adults, but not children, with developmental prosopagnosia. *Developmental Cognitive Neuroscience*, 10, 10–20. <https://doi.org/10.1016/j.dcn.2014.07.003>
- Deary, I. J., Corley, J., Gow, A. J., Harris, S. E., Houlihan, L. M., ... Marioni, R. E. (2009). *StarrAge-associated cognitive decline* British Medical Bulletin, 92, 135–152.
- Djouab, S., Albonico, A., Yeung, S. C., Malaspina, M., Mogard, A., Wahlberg, R., ... Barton, J. J. (2020). Search for face identity or expression: Set size effects in developmental prosopagnosia. *Journal of Cognitive Neuroscience*, 32(5), 889–905. https://doi.org/10.1162/jocn_a_01519
- Dobel, C., Bölte, J., Aicher, M., & Schweinberger, S. R. (2007). Prosopagnosia without apparent cause: Overview and diagnosis of six cases. *Cortex*, 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. <https://doi.org/10.1080/02643290701380491>
- Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience*, 17(2), 249–261. <https://doi.org/10.1162/0898929053124857>
- Duchaine, B., & Nakayama, K. (2006). Developmental prosopagnosia: A window to content-specific face processing. *Current Opinion in Neurobiology*, 16(2), 166–173. <https://doi.org/10.1016/j.conb.2006.03.003>
- Duchaine, B., Parker, H., & Nakayama, K. (2003). Normal recognition of emotion in a prosopagnosic. *Perception*, 32(7), 827–838. <https://doi.org/10.1068/p5067>
- Duchaine, B., & Yovel, G. (2015). A revised neural framework for face processing. *Annual Review of Vision Science*, 1, 293–416.
- Duchaine, B., Yovel, G., Butterworth, E. J., & 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. <https://doi.org/10.1080/02643290500441296>
- Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport*, 13(4), 427–431. Retrieved from <http://journals.lww.com>.
- Fisher, K., Towler, J., & Eimer, M. (2016). Facial identity and facial expression are initially integrated at visual perceptual stages of face processing. *Neuropsychologia*, 80, 115–125. <https://doi.org/10.1016/j.neuropsychologia.2015.11.011>
- Fox, C. J., Hanif, H. M., Iaria, G., Duchaine, B. C., & Barton, J. J. (2011). Perceptual and anatomic patterns of selective deficits in facial identity and expression processing. *Neuropsychologia*, 49(12), 3188–3200. <https://doi.org/10.1016/j.neuropsychologia.2011.07.018>
- Freiwald, W. A., Tsao, D. Y., & Livingstone, M. S. (2009). A face feature space in the macaque temporal lobe. *Nat. Neurosci.*, 12, 1187–1196.
- Ganel, T., & Goshen-Gottstein, Y. (2004). Effects of familiarity on the perceptual integrity of the identity and expression of faces: The parallel-route hypothesis revisited. *Journal of Experimental Psychology: Human Perception and Performance*, 30(3), 583. <https://doi.org/10.1037/0096-1523.30.3.583>
- Garrido, L., Furl, N., Draganski, B., Weiskopf, N., Stevens, J., Tan, G. C.-Y., ... Duchaine, B. (2009). Voxel-based morphology reveals reduced grey matter volume in the temporal cortex of developmental prosopagnosics. *Brain*, 132(12), 3443–3455. <https://doi.org/10.1093/brain/awp271>
- Geskin, J., & Behrmann, M. (2018). Congenital prosopagnosia without object agnosia? A literature review. *Cognitive Neuropsychology*, 35(1–2), 4–54. <https://doi.org/10.1080/02643294.2017.1392295>
- Gray, K. L. H., & Cook, R. (2018). Should developmental prosopagnosia, developmental body agnosia, and developmental object agnosia be considered independent neurodevelopmental conditions? *Cognitive Neuropsychology*, 35(1–2), 59–62.
- Harms, M., Martin, A., & Wallace, G. (2010). Facial Emotion Recognition in Autism Spectrum Disorders: A Review of Behavioral and Neuroimaging Studies. *Neuropsychology Review*, 20(3), 290–322.
- Hartshorne, J. K., & Germine, L. T. (2015). When does cognitive functioning peak? The asynchronous rise and fall of different cognitive abilities across the life span. *Psychological Science*, 26(4), 433–443.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223–233. [https://doi.org/10.1016/S1364-6613\(00\)01482-0](https://doi.org/10.1016/S1364-6613(00)01482-0)
- Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Cognitive Brain Research*, 16(2), 174–184. [https://doi.org/10.1016/S0926-6410\(02\)00268-9](https://doi.org/10.1016/S0926-6410(02)00268-9)
- Humphreys, G. W., Donnelly, N., & Riddoch, M. J. (1993). Expression is computed separately from facial identity, and it is computed separately for moving and static faces: Neuropsychological evidence. *Neuropsychologia*, 31(2), 173–181. [https://doi.org/10.1016/0028-3932\(93\)90045-2](https://doi.org/10.1016/0028-3932(93)90045-2)
- Janik, A. B., Rezesleu, C., & Banissy, M. J. (2015). Enhancing anger perception with transcranial alternating current stimulation induced gamma oscillations. *Brain Stimulation: Basic, Translational, and Clinical Research in Neuromodulation*, 8(6), 1138–1143. <https://doi.org/10.1016/j.brs.2015.07.032>
- Kanne, S. M., Wang, J., & Christ, S. E. (2012). The subthreshold autism trait questionnaire (SATQ): Development of a brief self-report measure of subthreshold autism traits. *Journal of Autism and Developmental Disorders*, 42(5), 769–780. <https://doi.org/10.1007/s10803-011-1308-8>
- Kanwisher, N., Tong, F., & Nakayama, K. (1998). The effect of face inversion on the human fusiform face area. *Cognition*, 68, B1–B11.
- Klargaard, S. K., Starrfelt, R., & Gerlach, C. (2018). Inversion effects for faces and objects in developmental prosopagnosia: A case series analysis. *Neuropsychologia*, 113, 52–60.
- Kracke, I. (1994). Developmental prosopagnosia in Asperger syndrome: Presentation and discussion of an individual case. *Developmental Medicine & Child Neurology*, 36(10), 873–886. <https://doi.org/10.1111/j.1469-8749.1994.tb11778.x>
- 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*, 46(8), 949–964. <https://doi.org/10.1016/j.cortex.2009.07.012>
- Little, Z., Jenkins, D., & Susilo, T. (2021). Fast saccades towards faces are robust to orientation inversion and contrast negation. *Vision Research*, 125, 9–16.
- Loth, E., Garrido, L., Ahmad, J., Watson, E., Duff, A., & Duchaine, B. (2018). Facial expression recognition as a candidate marker for autism spectrum disorder: How frequent and severe are deficits? *Molecular Autism*, 9(1), 7. <https://doi.org/10.1186/s13229-018-0187-7>
- Lundqvist, D., Flykt, A., & Öhman, A. (1998). *The Karolinska directed emotional faces (KDEF)*. CD ROM from Department of Clinical Neuroscience, Psychology section. Karolinska Institutet.
- Marsh, J. E., Biotti, F., Cook, R., & Gray, K. L. H. (2019). The discrimination of facial sex in developmental prosopagnosia. *Scientific Reports*, 9, 1907.
- Mattson, A. J., Levin, H. S., & Grafman, J. (2000). A case of prosopagnosia following moderate closed head injury with left hemisphere focal lesion. *Cortex*, 36(1), 125–137. [https://doi.org/10.1016/S0010-9452\(08\)70841-4](https://doi.org/10.1016/S0010-9452(08)70841-4)
- McConachie, H. R. (1976). Developmental prosopagnosia. A single case report. *Cortex*, 12(1), 76–82. [https://doi.org/10.1016/S0010-9452\(76\)80033-0](https://doi.org/10.1016/S0010-9452(76)80033-0)
- Minio-Paluello, I., Porciello, G., Pascual-Leone, A., & Baron-Cohen, S. (2020). Face individual identity recognition: A potential endophenotype in autism. *Molecular Autism*, 11(1), 81. <https://doi.org/10.1186/s13229-020-00371-0>
- Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? *J. Cogn. Neurosci.*, 9, 555–604. <https://doi.org/10.1162/jocn.1997.9.5.555>
- Murphy, J., Gray, K. L. H., & Cook, R. (2020). Inverted faces benefit from whole-face processing. *Cognition*, 194, 104105.
- Palermo, R., O'Connor, K. B., Davis, J. M., Irons, J., & McKone, E. (2013). New tests to measure individual differences in matching and labelling facial expressions of emotion, and their association with ability to recognise vocal emotions and facial identity. *PLoS One*, 8(6). <https://doi.org/10.1371/journal.pone.0068126>. e68126.
- Palermo, R., Willis, M. L., Rivalta, 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. <https://doi.org/10.1016/j.neuropsychologia.2011.02.021>
- Pietz, J., Ebinger, F., & Rating, D. (2003). Prosopagnosia in a preschool child with Asperger syndrome. *Developmental Medicine and Child Neurology*, 45(1), 55–57. <https://doi.org/10.1017/S0012162203000100>
- Pitcher, D., Duchaine, B., Walsh, V., Yovel, G., & Kanwisher, N. (2011). The role of lateral occipital face and object areas in the face inversion effect. *Neuropsychologia*, 49, 3448–3453.
- Rezesleu, C., Danaila, I., Miron, A., & Amariei, C. (2020). Chapter 13 - More time for science: Using testable to create and share behavioral experiments faster, recruit better participants, and engage students in hands-on research. In B. L. Parkin (Ed.), *Vol. 253. Progress in brain research* (pp. 243–262). Elsevier. <https://doi.org/10.1016/bs.pbr.2020.06.005>
- Rezesleu, C., Susilo, T., Wilmer, J., & Caramazza, A. (2017). The inversion, part-whole, and composite effects reflect distinct perceptual mechanisms with varied relationships to face recognition. *Journal of Experimental Psychology: Human Perception and Performance*, 43, 1961–1973.
- Russell, R., Duchaine, B., & Nakayama, K. (2009). Super-recognizers: people with extraordinary face recognition ability. *Psychon. Bull. Rev.*, 16, 252–257.

- Schmalzl, L., Palermo, R., & Coltheart, M. (2008). Cognitive heterogeneity in genetically based prosopagnosia: A family study. *Journal of Neuropsychology*, 2(1), 99–117. <https://doi.org/10.1348/174866407X256554>
- 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(6), 140343. <https://doi.org/10.1098/rsos.140343>
- Susilo, T. (2018). The face specificity of lifelong prosopagnosia. *Cogn Neuropsychol*, 35(1–2), 1–3.
- Susilo, T., & Duchaine, B. (2013). Advances in developmental prosopagnosia research. *Current Opinion in Neurobiology*, 23(3), 423–429. <https://doi.org/10.1016/j.conb.2012.12.011>
- Susilo, T., Rezlescu, C., & Duchaine, B. (2013). The composite effect for inverted faces is reliable at large sample sizes and requires the basic face configuration. *Journal of Vision*, 13(13), 14.
- Todorov, A., & Duchaine, B. (2008). Reading trustworthiness in faces without recognizing faces. *Cognitive Neuropsychology*, 25(3), 395–410. <https://doi.org/10.1080/02643290802044996>
- Torfs, K., Vancleef, K., Lafosse, C., Wagemans, J., & de-Wit, L. (2014). The Leuven perceptual organization screening test (L-POST), an online test to assess mid-level visual perception. *Behavior Research Methods*, 46(2), 472–487. <https://doi.org/10.3758/s13428-013-0382-6>
- Tsantani, M., Gray, K. L., & Cook, R. (2022). New evidence of impaired expression recognition in developmental prosopagnosia. *Cortex*, 154, 15–26. <https://doi.org/10.1016/j.cortex.2022.05.008>
- Uljarevic, M., & Hamilton, A. (2013). Recognition of emotions in autism: A formal meta-analysis. *Journal of Autism and Developmental Disorders*, 43(7), 1517–1526. <https://doi.org/10.1007/s10803-012-1695-5>
- 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. <https://doi.org/10.1152/jn.00155.2004>
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81, 141–145.
- Young, A. W., Hellawell, D. J., Van De Wal, C., & Johnson, M. (1996). Facial expression processing after amygdalotomy. *Neuropsychologia*, 34(1), 31–39. [https://doi.org/10.1016/0028-3932\(95\)00062-3](https://doi.org/10.1016/0028-3932(95)00062-3)