# Investigating the influence of autism spectrum traits on face processing mechanisms in developmental prosopagnosia

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Declarations of interest: none

## Abstract

Autism traits are commonly used as exclusionary criteria in studies of developmental prosopagnosia (DP). We investigated whether autism traits result in qualitatively different face processing in 43 DPs with high vs. low autism quotient (AQ) scores and 27 controls. Compared to controls, behavioral face recognition deficits were similar between the high and low AQ DP groups aside from worse emotion recognition in the high AQ DPs. Both DP groups showed reduced face selectivity in task-based fMRI, although higher AQ DPs showed decreased face selectivity in the posterior superior temporal sulcus. Resting-state fMRI showed similar face network connectivity between DP groups. This suggests that face processing is similar between the DP groups, with additional emotion processing deficits in higher AQ DPs.


**Keywords:** developmental prosopagnosia; autism quotient; face memory; holistic processing; emotion recognition

Autism spectrum disorders (ASD), defined in the DSM-5 as a group of developmental disabilities affecting communication and social behavior, often have co-occurring psychiatric and neurological conditions such as anxiety, depression, and attention deficit hyperactivity disorder (for a review, see Rosen, Mazefsky, Vasa, and Lerner, 2018). It has also been reported that those with ASD have a substantially higher rate of developmental prosopagnosia (DP; up to 36% [1], Minio-Palluelo, Porciello, Pascual-Leone, and Baron-Cohen, 2020), or severe lifelong face recognition deficits, than the general population prevalence of 2% (Kennerknecht et al., 2006; Behrmann and Avidan, 2005; Duchaine and Nakayama, 2006b; Susilo and Duchaine, 2013). However, the nature and causes of the co-occurrence between ASD traits and DP are poorly characterized (Cygan et al., 2018). The goal of the present study was to examine whether DPs with higher levels of autism traits (i.e., broader autism phenotype, Wheelwright, Auyeung, Allison, and Baron-Cohen, 2010; Landry and Chouinard, 2016) differ from DPs with lower levels of autism traits across a broad battery of assessments, including face memory, face perception, holistic face processing, eye and mouth processing, emotion recognition, and in their fMRI selectivity and connectivity of face processing regions.

Developmental prosopagnosia is considered to be a disorder that is selective to face perception and memory, with a subset of DPs potentially showing concurrent deficits in object recognition (Geskin and Behrmann, 2017; though see Fry et al., 2020). In contrast, ASD encompasses a much broader set of impairments that affect domains of social interaction and communication, including emotion recognition and face memory impairments in certain cases (Ozonoff et al., 2008; DSM-5). Although there is evidence that the deficits related to ASD and

[1] Although labeled ‘developmental prosopagnosics’, the diagnostic criteria were less strict than typically used in prosopagnosia studies and included individuals who did not self-report face recognition difficulties. Including individuals who had z-scores < -2 on the CFMT *and* who self-reported face recognition deficits on the PI20 would result in 12% of their sample having DP, which is still far greater than expected in the general population.

DP are dissociable (e.g., Duchaine et al., 2009), other results indicate that the impairments of the two disorders can overlap. In particular, Minio-Palluelo and colleagues (2020) recently showed that over a third of their sample of 80 adults with autism had significant face memory impairments on the Cambridge Face Memory Test (CFMT; Duchaine and Nakayama, 2006) that could not be explained by variance in general intelligence. As a field, DP researchers have generally assumed that individuals with comorbid DP and ASD have a different type of prosopagnosia (i.e., face recognition deficits due more to social aversion and lack of interest rather than more fundamental deficits in face perception or memory, see below) and have routinely excluded this sizeable group of DPs from their studies (Corrow, Dalrymple, and Barton, 2016; Shah et al., 2015; Dalrymple and Palermo, 2016; Bate et al., 2019). It has yet to be described in detail, however, the extent to which the presence of autism traits alters the neural and behavioral manifestation of DP.

When occurring in isolation, individuals with DP and ASD both demonstrate face memory deficits, though the mechanisms underlying these deficits may differ. Compared with typically developing controls, individuals with ASD demonstrate less interest in faces, worse face memory, and worse facial emotion recognition (Grelotti et al., 2002; Weigelt et al., 2013; Dwyer et al., 2018), largely thought to be due to avoidance of the eye region of the face and an aversion to social stimuli (Maddipakkam et al., 2017; Tanaka and Sung, 2016; Weigelt et al., 2012; Dalton et al., 2005). These characteristics contrast with findings from non-ASD DP studies showing that, despite severe face recognition deficits, the majority of DPs have intact emotion recognition ability (Humphreys, Avidan, and Behrmann, 2007; Duchaine, Parker, and Nakayama, 2003) or show more modest deficits in emotion recognition (Kress and Daum, 2003; Biotti and Cook, 2016; Tanaka et al., 2012). DPs notably demonstrate a wide range of face

processing deficits, many of which are characteristic of ASD, such as impairments in face memory and attention to the eyes (Bobak, Parris, Gregory, Bennetts, Bate, 2017), as well as other impairments not usually found in ASD, such as poor face matching ability (White, Rivolta, Burton, Al-Janabi, Palermo, 2017; Mishra et al., 2020) and holistic face processing deficits (DeGutis et al., 2012; Avidan et al., 2011; Palermo et al., 2011; though see Biotti et al., 2017). DPs' impairments in face recognition can also occur in the absence of impaired social cognition (e.g., reading social cues, body language, etc., though some show increased social anxiety; see Davis et at., 2011) or motivational impairment (Duchaine et al., 2010). This contrasts with the face processing pattern seen in ASD, wherein a number of studies have found intact holistic processing (using the part whole task, composite task, and the Thatcher illusion – see Weigelt et al., 2012 for a review) with only isolated studies finding reduced holistic processing (e.g., O'Brien, Spencer, Girges, Johnston, and Hill, 2014, using upright and inverted animated faces). The lack of consistent holistic face processing impairments in individuals with ASD further suggests face recognition impairments in the general autism population are not driven by impairments in face perception per se but are instead the result of atypical gaze patterns and/or reduced attention to the internal features of the face. In contrast, DP studies have demonstrated a consistent pattern of holistic processing deficits using the part whole task (DeGutis et al., 2012; Susilo et al., in press), face inversion tasks (Klargaard, Starrfelt, and Gerlach, 2018), and to a lesser degree, the composite face task (Avidan et al., 2011; Palermo et al., 2011; see Biotti et al., 2017 for an exception).

On a neural level ASD has typically been associated with broader network deficits than DP, which has shown deficits more specific to ventral occipito-temporal regions. In particular, individuals with ASD have shown reduced resting-state functional connectivity between the

posterior superior temporal sulcus (pSTS), a brain region involved in understanding social motivations and actions, and fronto-parietal regions in the 'action observation' network (Alaerts, Woolley, Steyaert, Di Martino, Swinnen, and Wenderoth, 2014). Additionally, fMRI studies have found reduced activation of the temporal parietal junction in autism, proposed to support 'theory of mind', while viewing socially awkward stimuli (Pantelis, Byrge, Tyszka, Adolphs, and Kennedy, 2015). ASD studies examining brain activation in face-selective regions such as the fusiform face area (FFA) and occipital face area (OFA) have found conflicting results. Whereas some studies found reduced FFA and OFA activation in response to faces (Schultz et al., 2003; Pierce et al., 2001; Grelotti et al., 2005; Humphreys et al., 2008), others have reported activation similar to typically developing controls (Jiang et al., 2013). These conflicting findings may be linked to the heterogeneity of ASD individuals.

In contrast to individuals with ASD, DPs frequently demonstrate reduced face selectivity in core (OFA, FFA, pSTS) and extended (anterior temporal) face regions during localizer tasks (Jiahui, Yang, and Duchaine, 2018; Gerlach, Klargaard, Alnaes, Kolskar, Karstoft, Westlye, and Starrfelt, 2019) as well as reduced FFA face adaptation (Furl, Garrido, Dolan, Driver, and Duchaine, 2011) and reduced resting-state connectivity amongst face-selective regions (Song et al., 2015) (but see: Behrmann, Avidan, Marotta, and Kimchi, 2005). Overall, ASD commonly implicates brain regions/networks involved in social cognition and social utilization of face information (e.g., pSTS) whereas DP is often associated with ventral occipito-temporal and anterior temporal regions more involved in face perception and identification (e.g., OFA, FFA, anterior temporal face area).

The established co-morbidity of and similarities between the two disorders raise the question of whether cases of co-morbid ASD and DP are the result of autism spectrum disorders

causing face recognition impairments (e.g., the strong interaction model), or whether the two are simply distinct but co-occurring disorders (e.g., the independent co-occurrence model). Prior studies investigating the relationship between social cognitive abilities and face recognition ability as well as impairments in these domains have shown both overlapping (Halliday et al., 2014) and distinct mechanisms (Barton et al., 2004; Minio-Palluelo et al, 2020). In a typically developing population, Halliday and colleagues (2014) investigated the reciprocal relationship between face recognition and ASD symptoms using separate hierarchical multiple regressions to determine which factors best predicted face recognition and AQ scores. They found that the two factors exhibited a bi-directional relationship: AQ scores reliably predicted face recognition scores, and face recognition performance uniquely contributed to scores on the AQ independently from gender, university major, and performance on an immediate memory object task. This study suggests that, within a healthy control sample, there is a reciprocal relationship where either autism traits (e.g., eye avoidance, aversion to faces/social stimuli) may lead to a decrement in face processing ability, or face recognition impairments may heighten the symptoms of autism related to social cognition.

Other studies have directly examined the link between face recognition and social abilities. Barton and colleagues (2004) compared the face recognition performance of 24 adults with social developmental disorder[2] (SDD) with a typically developed control group and a group of 12 prosopagnosics (9 acquired, 3 developmental) to determine the severity of face deficits, if present. They found that while two-thirds of the SDD participants had face recognition impairments (*d*' ranging from .75 to 2.25 on a Famous Faces Test, compared with a *d*' range of 2.19 to 3.88 in the control sample and .37 in the prosopagnosic sample), this subset with face recognition impairment

[2] SDD in this study encompasses autism, Asperger's, and pervasive developmental disorder - not otherwise specified.

did not differ from the remainder of the SDD group on the Social Skills Inventory (Riggio, 1992), indicating that severity of face processing impairments did not affect severity of social impairments in the group with SDD. This finding suggests that, while face processing deficits often co-occur with social developmental disorders, face processing deficits are not an inevitable result of social developmental disorders, nor are they necessarily modulated by the severity of the disorder. Another study by Minio-Palluelo and colleagues (2020) measured face recognition impairments in a sample of 80 adults with autism, and found that the subset of 29 individuals with ASD and z-scores < -2 on the CFMT did not differ from those with autism and unimpaired face memory on any measures of autism symptom severity, including the Autism Diagnostic Observation Schedule (Gotham, Pickles, and Lord, 2009), the AQ, Reading the Mind in the Eyes (RMET; Baron-Cohen, Wheelwright, Hill, Raste, and Plumb, 2001), or the Wechsler adult intelligence scale (Wechsler, 2008). This further suggests that face recognition impairments in adults with autism are largely unrelated to the severity of social impairments. Taken together, these studies suggest the interesting possibility that face recognition and social cognition may be related in the typically developing population but may not be as closely linked once a certain level of impairment is reached in either social cognition or face recognition ability.

Although these studies provide insights into the reciprocal relationship between face recognition and social functioning, less is known about the manner in which autism traits affect the expression of face recognition impairments when DP is the primary disorder (though Barton et al., 2004 used a small sample of prosopagnosics as an impaired control group to measure face performance in their SDD group, their social skills were not assessed). Because DP is typically diagnosed using face memory performance and self-report questionnaires (Bowles et al., 2009; Shah et al., 2015) rather than face perception assessments, individuals with very high levels of

social impairment may reach the cut-off for prosopagnosia based on poor face memory alone, though their impairment may be due to social aversion and lack of visual input rather than face processing-specific deficits. Given this, one possible model of DP/ASD is that the expression of face impairment in DP is related to AQ score (as seen in the typically developing population; Halliday et al., 2014) and thus follows different behavioral patterns when accompanied by high levels of autism traits (strong interaction model). This might reflect, as some researchers suggest (Riby et al., 2009; Dalton et al., 2005), that face recognition impairments in conjunction with high levels of autism traits are more associated with external factors such as diminished gaze fixation rather than fundamental deficits in face perception or memory. In other words, similar to face recognition deficits found in ASD, more severe face recognition deficits in DPs with ASD traits may be due to a lack of attention to faces, where general perception and holistic processing are intact but face recognition suffers due to lack of eye attention and face information input (e.g., memory deficits in the absence of impaired holistic processing; Weigelt et al., 2013). A second possibility is that when the population is strongly impaired in one domain (in this case, faces) ASD traits and DP more independently co-occur and the level of autism traits does not impact either the severity or manner of face recognition impairments (independent co-occurrence model). This would align more closely with Barton and colleagues' (2004) finding that adults with SDD and co-occurring facial recognition impairments do not differ in their symptoms of social impairment. This would result in DPs with high levels of autism traits showing a behavioral face recognition profile similar to that of DPs with unimpaired social cognition.

In the current study, our goal was to investigate how the presence of autism traits relates to the manifestation of DP in adults. We recruited 43 developmental prosopagnosics and 27 typically developing control subjects. DPs were categorized into low or high autism trait levels based on

their Autism Quotient score (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, and Clubley, 2001; Wheelwright et al., 2010). To more effectively measure face processing impairments in the two groups, we collected data across a range of domains including face perception, face memory, emotion recognition, holistic processing, fMRI localizer scans of face-, body-, object- and scene-selective regions, and resting-state fMRI. This was done to create a more complete profile of the deficits seen across groups. While many of the tasks provided direct insights into our hypothesized outcomes (e.g., face memory and holistic processing), others were more exploratory in nature (e.g., object memory, body- and scene-selectivity) to examine potential group differences in other domains.

If the two disorders present themselves independently, we would expect to see a similar behavioral profile between the high AQ and low AQ DPs, reflecting that DPs' facial recognition impairments are not modulated by the presence of autism traits. Also, because ASD may particularly affect the social utilization of face information, we predict that we would see differences between high and low AQ DPs in regions of the brain involved in social cognition and emotion interpretation, such as the pSTS, while showing similar face selectivity in the OFA and FFA. Conversely, if DPs with high levels of autism traits demonstrate a different type of facial processing deficit than DPs with low autism traits, then we would expect to find variations in behavioral performance between the groups. Specifically, we would expect to see better holistic processing abilities in the high AQ group (Ventura et al., 2017; Weigelt et al., 2012), along with impaired face memory and perceptual sensitivity to the eyes compared to typically developing controls (Maddipakkam et al., 2017; Tanaka and Sung, 2016). Across both the strong interaction and independent co-occurrence models, we would expect to see worse emotion recognition in the higher AQ group (Smith et al., 2010; Bolte and Poustka, 2003; Celani et al., 1999). By comparing

these groups on a large battery of face perception, memory, and fMRI tasks, we can better characterize the impact that autism traits have on the behavioral and neural outcomes of DP.

## Methods

### *Participants*

Participants were 43 developmental prosopagnosics and 27 typically developed controls between the ages of 18 and 70 years old. Developmental prosopagnosics were recruited from our database of previous DP participants in the Boston area, references from other research labs (Dr. Matthew Peterson, Massachusetts Institute of Technology; Dr. Brad Duchaine, Dartmouth College, www.faceblind.org), and individuals who responded to our advertisement on the Massachusetts Bay Transportation Authority subway system. Control subjects were recruited and tested at the Harvard Decision Science Laboratory in Cambridge, Massachusetts.

Developmental prosopagnosics reported lifelong face recognition deficits (all but one scored > 60 on the PI-20) in the absence of significant neurological disorders or moderate/severe traumatic brain injury (TBI) or mild TBI in the past 6 months. The majority of DPs scored 44 or below (z-score < -2) on the original CFMT (see supplementary materials; Duchaine and Nakayama, 2006), indicating severe objective face recognition deficits. We also included six participants that we consider to be mild DPs who scored between 44-48 on the CFMT (-2 < z-score < -1.5), since the rest of their profiles were consistent with prosopagnosia (e.g., PI-20 > 60, famous faces < .65). Notably, removing these participants had no appreciable effects on the key analyses. Typically developing controls did not report any face recognition deficits and all scored 45 or above on the CFMT. Participants were also pre-screened and excluded if they had musculoskeletal impairments that would hinder performance on computer tasks, a lack of English proficiency, any current psychiatric disorders, intellectual impairments, or current

alcohol or substance dependence. All participants had normal or corrected-to-normal vision and scored within the normal range on the Leuven Perceptual Organization Screening Test (L-POST; Torfs, Vancleef, Lafosse, Wagemans, & de-Wit, 2014) to rule out other causes of poor face recognition.

Informed consent was obtained for all participants prior to data collection according to the Declaration of Helsinki. Participants were compensated for their time at a rate of $10 per hour. The study was approved by the VA Boston Healthcare System and Harvard Medical School Institutional Review Boards, and all study tasks were completed at the VA Boston Healthcare System in Jamaica Plain, Massachusetts or the Harvard Decision Science Lab in Cambridge, Massachusetts.

*Autism Traits*

Our measure of autism traits in the population was the widely used, validated Autism Quotient questionnaire (AQ; Baron-Cohen et al., 2001). The AQ is a 50-item self-report questionnaire designed to identify symptoms of autism spectrum disorder in adults. Participants are instructed to respond either "definitely agree", "slightly agree", "slightly disagree" or "definitely disagree" to each item, with approximately half of the items designed to evoke an “agree” response from a neurotypical adult. The questionnaire covers the domains of social skills, communication, imagination, attention to detail, and attention switching and for the purposes of the current study, the total score was used (Baron-Cohen et al., 2001).

Categorization of low vs. high AQ was based on the broader autism phenotype (BAP; Wheelwright, Aeyeung, Allison, and Baron-Cohen, 2010). While not a diagnostic label, the broader autism phenotype describes a subclinical set of characteristics that are qualitatively similar to features of autism and was initially developed to study family members of individuals

with autism (Landry and Chouinard, 2016). Common characteristics of the BAP include mild impairments in social and communication skills that resemble those seen in autism spectrum disorders (Gerdts and Bernier, 2011). Based on Wheelwright and colleagues' 2010 study, a score of 23 or above on the AQ is >1 SD above the normative mean and thus constitutes the broader autism phenotype. Using this criterion, in the current study a score of 23 or above was classified as an "AQ+ DP" (N=15) while a score of below 23 was classified as an "AQ- DP" (N = 28). This cut-off allowed us to examine the relevant features typical of autism spectrum disorders while retaining large enough group sizes for meaningful group-level comparisons.

*Cambridge Face Memory Test*

The Cambridge Face Memory Test (Duchaine and Nakayama, 2006) is a highly validated and widely used face memory task. During the learning phase, participants are shown each target face from three different viewpoints for three seconds each, and are then asked to select which face they just viewed from a selection of three faces using the number keys. This learning trial repeats for each of the six target faces. After the learning phase, participants are shown all six target faces again for a total of 20 seconds. They are then given 30 forced-choice trials where they must select from among three faces which one was one of the six target faces they just learned. After these 30 test trials, participants again are shown all six faces for another 20 seconds, and the final 24 trials include Gaussian noise intended to obscure the internal facial features. The dependent variable is the total correct trials out of 72.

*Old/New Face Recognition Task*

During the study phase of the Old/New task, participants are shown 60 cropped and grayscale faces and are instructed to study the faces for a later memory test. Faces were presented in the center of the screen for 1.5 seconds each, and each face repeated a second time

in the same order. All subjects received the same order of faces. Immediately after the study phase, participants were presented with the 60 target and 60 lure faces randomly intermixed, and on each trial were asked to rate on a scale of 1 – 6 their level of confidence in classifying each face as "old" or "new" (1 – Confident Old, 2 – Somewhat Sure Old, 3 – Guessing Old, 4 – Guessing New, 5 – Somewhat Sure New, 6 – Confident New). Confidence ratings appeared directly below each face. Participants were instructed to try and use all confidence ratings when responding. Recollection and familiarity parameters were calculated using the Matlab ROC toolbox (see Stumps et al., 2020). "Recollection" is reflective of a participant's "recollection of newness", or their ability to recall a face as seen previously with context specific to its prior viewing. "Familiarity", on the other hand, reflects a participant's belief that they saw a face before without recalling the specific instance in which they viewed the face. DPs have been shown to rely more strongly on familiarity than recollection (Stumps et al., 2020).

*Novel Object Memory Test*

The Novel Object Memory Test (NOMT) mirrors the structure of the CFMT using novel objects (Ziggerins) instead of faces (Richler et al., 2017), and omitting the noise trials in the latter half of the test to better equate scores between the two tasks. This task is a useful measure of domain-general object memory separate from face recognition ability. Similar to the CFMT, the dependent variable is the total correct trials out of 72.

*Part-Whole Task*

In the part-whole task (from Tanaka, Kiefer, & Bukach, 2004, used with permission of Jim Tanaka, University of Victoria), target faces were designed using a single Caucasian male face and inserting different features (eyes, nose, mouth) to create six unique target faces. During whole trials, foil faces were created by switching one of the features (eyes, nose, or mouth) with

a feature from a different target face. When only a single feature was shown during the test phase (part trials), foil stimuli were an isolated facial feature (eyes, nose, or mouth) from a different target face. One of the six target faces is presented in the center of the screen for 1,000 ms following a 500 ms fixation cross. Next, a scrambled face mask is displayed for 500 ms. During the test trials, participants are presented with a pair of images side by side, either whole faces (whole trials) or isolated features (part trials). One of the images matches the target they just viewed, and the other is a foil image. Stimuli remain on the screen until participants select either '1' to indicate that the left image is the target image, or '2' to indicate that the right image is the target. For whole trials, subjects must choose between the whole target face and a whole foil face. For part trials, subjects must choose between a single feature from the target face (eyes, nose, or mouth) and the same feature from one of the foil faces. Subjects did not know which feature they would be tested on during each trial. There were 72 trials (36 parts trials and 36 whole trials), with 24 trials for each feature category. We calculated the holistic advantage by first regressing the part trial 'control condition' from the whole trial 'condition of interest' (using the regression equation in the control sample, e.g., see DeGutis et al., 2013), and then applying this equation to calculate residuals for DPs and controls.

*Cambridge Face Perception Test*

The Cambridge Face Perception Test (CFPT) is a computerized sorting task in which participants arrange six front-view faces according to their similarity to a three-quarter view target face (Duchaine et al., 2007). Participants completed eight upright sorting trials and eight inverted sorting trials. The dependent variable is the sum of the deviations from the correct order across all sorting trials. We calculated the holistic advantage by first regressing the inverted trial 'control condition' from the upright trial 'condition of interest' (using the regression equation in

the control sample, e.g., see DeGutis et al., 2013), and then applying this equation to calculate residuals for DPs and controls.

*Georges Task*

The Georges task provides a measure of internal and external facial feature discrimination ability (Malcolm et al., 2004). On a single trial, participants are presented with frontal views of three same-identity anonymous faces in a triangular arrangement for two seconds, with the lower two faces slightly offset horizontally. Two faces are identical and one has a single feature manipulation. There were six possible manipulations spanning these three categories: internal feature position, feature size, and external contour. Each category of change had one manipulation in the upper face and one in the lower face. Feature position was manipulated with either a decrease in interocular distance or elevation of the mouth. Feature size was modified by increasing the vertical width of both eyes or increase in the vertical width of the mouth. External contour was modified by elevating the hairline or narrowing the chin. Participants indicated which of the three faces differed from the other two using the left, right, and up arrow keys. There were 108 trials, with six different face identities. Dependent variables were the percentage correct for each feature.

*Computerized Benton Face Recognition Task*

In this computerized version of the original Benton Face Recognition Task (Benton, 1968; Rossion and Michael, 2018), six grayscale photographs of unfamiliar faces (3 x 3.5 cm) are presented with the majority of external features cropped out. The target face is presented at the top of the screen with the six test faces below, in two rows of three. During the first six trials participants must select the face that matches the target exactly, and in the next 16 trials they are instructed to select which three faces are the same identity as the target face. During this portion

of the test the six test faces have either lighting changes or viewpoint changes. Lighting and viewpoint change trials are intermixed, and the stimuli are displayed until the participant completes their responses. Participants are instructed to make their responses as quickly as possible without losing accuracy.

*University of Southern California Face Perception Test*

The University of Southern California Face Perception Test (USCFPT) is a perceptual face-matching task that uses synthetic grayscale computer-generated faces. The face stimuli were generated using Facegen software and were provided by Irving Biederman (Yue *et al.*, 2012 ). The faces include no external cues such as hair or clothing . Each trial displayed a single target face (3.2 x 4.2 cm) at the top of a screen, and two test faces below it for a total of 5 seconds. The participant must then select which of the two test faces matches the top target face using either the left or right arrow key. Responses were recorded even after the faces disappeared. There was a total of 96 trials.

*Same/Different Face Matching Task*

The Same/Different Face Matching Task (SDFMT) is a simultaneous matching task where the participant must indicate whether two faces are the same identity or different identities from among different viewpoints (front view vs. 3/4 view) or changes in lighting (fully lit vs. lighting from the side). Face images are greyscale and cropped to remove external features such as hair or clothing. During each trial, a pair of faces is presented simultaneously for 3 seconds each and participants are instructed to respond ‘1’ if the faces are the same identity and ‘0’ if the faces are different identities. Foils were selected to have matching verbal descriptions (e.g., dark hair, thin nose, large eyes). There are seven different trial types: 1) Same identity from front view, 2) same identity with lighting change, 3) same identity with viewpoint change, 3) different

identity from front view, 4) different identity with lighting change, 5) different identity with viewpoint change, 6) same identity on a different day, 7) same identity and same day but cropped differently. There are 210 total trials, with 30 trials per trial type.

*Social Interaction Anxiety Scale*

The Social Interaction Anxiety Scale (SIAS; Mattick and Clarke, 1998) is a self-report scale designed to measure the amount of distress an individual experiences during social interactions with others. There are 20 items, each measured on a five-point Likert scale. Each item includes a statement about social interaction (e.g., "I am tense mixing in a group"). Individuals can respond whether they believe the characteristic is "not at all characteristic or true of me", "slightly characteristic or true of me", "moderately characteristic or true of me", "very characteristic or true of me", or "extremely characteristic or true of me". Three of the items are reverse-scored, and the points are then summed to create a total measure score. Only 22 DPs completed the SIAS.

*Reading the Mind in the Eyes*

The Reading the Mind in the Eyes Test (Baron-Cohen, Wheelwright, Hill, Raste, and Plumb, 2001) was designed to test the ability to decipher the emotions of others by viewing only the eyes. In this test, an image showing only the eye region of the face (eyes, eyebrows, bridge of nose) is presented along with four mood descriptors. The participant must choose which of the four words best describes the emotion the eyes are showing. The dependent variable was the total correct out of 36 items. Thirty-one DPs and none of the control sample completed the RMET test.

*20-item Prosopagnosia Index*

The 20-item Prosopagnosia Index (PI-20) is a self-report questionnaire that assesses difficulty with face recognition (Shah et al., 2015). Items are measured on a five-point scale from "Strongly disagree" to "Strongly agree", and include statements such as "I feel like I frequently offend people by not recognizing who they are" and "I often mistake people I have met before for strangers". The dependent variable is the total score out of 100, with 100 being the most severe prosopagnosia symptoms.

*fMRI Scanning Procedure*

Thirty-three DPs (six males, mean age 37.5 y) and 25 typically developing adults (11 males, mean age 33.6 y) participated in the fMRI section. 22 of the 27 AQ- DPs and 11 of the 15 AQ+ DPs completed the fMRI portion of the study. It should be noted that the resting-state and task-based fMRI results for overall DPs vs. controls were previously reported by Li et al. (2020) and for the for the purposes of the current study, DPs were further broken up into AQ+ DP and AQ- DP groups.

Using a 3-Tesla Siemens Prisma and 32-channel head coil, we performed the following scans for each participant: 1) high-resolution 3D anatomical MPRAGE, 2) one 6-minute resting-state fMRI scan, 3) four runs of dynamic localizer scans containing four visual categories (faces, scenes, bodies, and objects). Stimuli in the localizer were brief video clips of each category used in Jiahui et al. (2018). Each participant completed four runs, which comprised 18s category blocks of video clips, which in total lasted about 4 min (per run). Each visual category was displayed twice in each run in a quasi-random order across scans, with an exception for faces (4 blocks in total, with 2 blocks of non-famous faces and 2 blocks of famous faces, which was composed of video clips of Barack Obama and Donald Trump). Stimuli were presented using PsychoPy v1.85.4 and displayed to the participant via at the rear of the scanner.

*fMRI Processing and Analysis*

To promote replicability, we adopted the default pipeline offered by fMRIPrep (see detailed description in supplementary material) to preprocess both the resting-state and the dynamic localizer task fMRI data. The fMRIPrep preprocessed dynamic localizer scans were then smoothed at a 6mm kernel (see nilearn.image.smooth_img), and submitted to a GLM in SPM12 (welcome center human neuroimaging), with physiological noise regressors (i.e., CSF signal, white matter signal, head displacement, and six head-motion parameters [three rotations and three translations]) computed from fMRIPrep included. Contrasts between categories were subsequently added to examine the specialized tuning towards the face category at our regions of interest.

Category selectivity was used to measure how strongly tuned a cortical area was to a particular category. Using the dynamic localizer scans, selectivity for faces was defined as the difference between the response to faces (the combination of famous and non-famous) and the response to scenes. Similar to previous (e.g., Ramot et al., 2019), we chose the face vs. scene contrast to maximize our ability to localize robust face selective regions (e.g., greater sensitivity to detect occipital face area, Schwarz et al., 2019), though it should be noted that very similar results were found when examining the face vs. object contrast. The bilateral fusiform face area (FFA), occipital face area (OFA), posterior superior temporal sulcus (pSTS), and anterior temporal lobe (ATL) were individually identified for their specialized selectivity towards faces.

The four runs from the localizer task were divided into the localization runs and the test run to carry out a “leave-one-out” analysis. In each of the leave-one-out combinations, three of the four runs for a participant were used to localize the regions of interest (ROIs) for faces. To avoid the double-dipping problem, the responses of the selected ROIs to each stimulus condition

were then measured in the left-out run. All four combinations were analyzed and then averaged to produce the final result for each participant.

To avoid rater bias, each category selective ROI was individually defined with an automated pipeline. Specifically, using the Harvard-Oxford Atlas, an anatomical mask was created as a structural confinement for each ROI within each category. For example, for the right FFA, in each subject, the four runs' face vs. scene contrast map were first mapped to retain only the positive-valued voxels, i.e., voxels that were selectively responsive to faces in contrast to scenes. Then, the anatomical confinement for the right FFA was applied to each of the four runs' (face vs. scene) contrast map to retain the positive values only in the right ventral occiptal-temporal region (i.e. the anatomical area that contains the functional area of right FFA, regardless of individual variation). We then identified the largest most activated cluster within this region (see nilearn.plotting.find_xyz_cut_coords) for each run's contrast map. The center of mass for the identified cluster was computed for each run. The coordinates computed from the localization runs were averaged, over which a 6mm radius sphere was created from the left-out run's contrast map. The beta values within this sphere were averaged to index this individual's right FFA specialized tuning towards faces (i.e. face selectivity) in the current left-out run. This process was looped through the four leave-one-out combinations. Finally, the average of the four runs' right FFA face selectivity was used to index this individual's right FFA face selectivity.

*Resting State fMRI*

First-level models

Following the preprocessing steps outlined above, resting-state data were analyzed using general linear models (GLMs). Within first-level models, we modelled nuisance regressors including 6 rigid body motion regressors, framewise displacement between volumes, mean

timeseries extracted from white matter and cerebrospinal fluid, and a linear trend to account for slow drift throughout the scan session. To further minimize motion-related confounds, we censored TRs that exceeded 0.3mm framewise displacement as well as the immediately preceding TR. Within these first-level models, data were bandpass filtered (0.01 – 0.10 Hz) to remove additional noise associated with physiological processes of non-interest (e.g., respiration).

Whole-brain model

Using the residual outputs from first-level models, we extracted the cleaned timeseries for the left and right pSTS ROI defined by the face localizer task. For the left and right pSTS ROIs, we averaged and combined the timeseries to form a single bilateral ROI timeseries. We characterized group differences in voxel-wise connectivity across the brain using AFNI's 3dMVM program (Cox, 1996). Given our primary research aims, we focused on contrasting voxel-wise connectivity between the AQ+ and AQ- DP groups. To control family-wise error (FWE) in these exploratory analyses, we used a combined voxel-wise and cluster threshold approach. To determine the necessary cluster threshold at a nominal threshold of $p = 0.01$, we submitted the observed smoothness of the residual outputs to AFNI's more stringent non-parametric 3dClustSim function. Using a voxel-wise threshold of $p = 0.01$, a cluster threshold of 48 voxels controlled for FWE at $p < 0.05$. For clusters that survived whole-brain correction for the DP+ vs. DP- contrast, we extracted beta coefficients to characterize the pattern of group differences.

*Statistical Approach*

First, we performed independent-samples *t*-tests between the AQ+ and AQ- groups for each of the different behavioral test battery measures. Next, we compared both the AQ- and AQ+

DP groups to the typically developing control sample on each of the behavioral measures using independent-samples *t*-tests. For tasks that measured individual feature responses (part whole and Georges Task), we compared both the overall score as well as the results for the eyes and the mouth. An eye composite score was calculated by averaging participants' scores across the Georges eye size and eye horizontal position trials and the part whole 'whole eyes' and 'part eyes' trials. We calculated bivariate Pearson's correlations between the AQ scores and each of the behavioral measures within the entire DP sample to examine potential relationships between level of autism traits and different aspects of face recognition. Because 11 of the DPs in the AQ+ group had AQ scores below the standard clinical cut-off of 32 (Woodbury-Smith et al., 2005) suggestive of mild ASD traits, we also ran exploratory analyses on a smaller group of DPs with AQ scores equal to or above 32 (N = 4), comparing them with the AQ- group measures to evaluate if there were any behavioral differences in the group that fell above the clinical cut-off.

For the task-based fMRI analyses, we first conducted a 2 (DP/TD) x 4 (region) x 2 (hemisphere) ANOVA comparing category selectivity during task between the DP and TD groups for face, scene, object, and body selectivity across each of the regions. We then conducted a 2 (AQ+/AQ- DP) x 2 (hemisphere) ANOVA of pSTS selectivity to determine whether the two DP groups differed in the region typically implicated in emotion recognition (Isik et al., 2017; Shih et al., 2011; Alaerts et al., 2013), followed by a 2 (AQ+/AQ- DP) x 3 (remaining regions) x 2 (hemisphere) ANOVA.

To analyze resting state functional connectivity within the face network, we conducted a 2 (DP/TD) x 4 (region) x 2 (hemisphere) ANOVA between the DP and TD groups to determine whether the groups differed in their network connectivity for each node in the face network. We then conducted a 2 (AQ+/AQ- DP) x 2 (hemisphere) ANOVA of the pSTS, followed by a 2

(group) x 3 (region) x 2 (hemisphere) with the remaining face regions to determine if there were any differences between the AQ+ and AQ- DP groups. Finally, for the exploratory whole-brain STS analyses, we compared the connectivity of AQ+ and AQ- DPs for each of the regions that survived whole-brain correction using independent-samples *t*-tests.

## Results

*Participants*

The AQ+ DP group (n = 15) did not differ from the AQ- DP group (n = 28) in age [$t(41)$= -.62, $p$ = .542], education [t(40) = .78, $p$ = .443], or gender ($p$ = .116). The average AQ of the AQ+ group was significantly higher than that of the AQ- group ($t_{41}$=8.59, $p$ < .001). Similarly, the DP group did not differ from the typically developed control group in age, however, the TD group had a higher proportion of males than the low AQ group as well as a lower overall education level (see Table 1). Education has shown not to predict additional variance in general memory performance outside of age (West, Crook, and Barron, 1992), and face recognition abilities have shown to be independent from both education and IQ (Wilmer, 2017). Further, the gender imbalance between the groups would, if anything, decrease the DP/TD group differences in face recognition performance, as females have shown slightly better face recognition performance than males (Rennels and Cummings, 2013; Mishra, Likitlersang, Wilmer, Cohan, Germine, and DeGutis, 2019). The AQ scores of the AQ+ group were significantly higher than those of the TD group ($t_{40}$=4.63, $p$ < .001), and the average AQ score of the AQ- group was significantly lower than the TD group ($t_{53}$=3.18, $p$ = .002).

**Table 1** Group demographic means, standard deviations, and between-group ANOVA results

| | AQ+ DP | | AQ- DP | | TD | | ANOVA |
|---|---|---|---|---|---|---|---|
| | M | SD | M | SD | M | SD | p-values |
| Age | 39.87 | 11.38 | 37.11 | 15.20 | 42.37 | 10.29 | .313 |
| Gender (F:M) | 9:5 | - | 24:4 | - | 14:13 | - | .024* |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Education | 17.20 | 3.10 | 17.81 | 2.04 | 15.63 | 4.06 | .043* |
| AQ | 28.33 | 5.38 | 14.50 | 4.84 | 19.33 | 6.36 | < .001** |
| PI-20 | 80.80 | 10.81 | 82.71 | 7.56 | 36.89 | 7.06 | < .001** |
| CFMT | 40.40 | 3.77 | 39.64 | 4.71 | 58.78 | 7.92 | < .001** |

*Face and Object Memory*

We first compared AQ+ and AQ- performance on our battery of face and object memory tasks, expecting that AQ+ DPs would show similar levels of memory impairments to AQ- DPs, as all DPs were selected for poor face memory. The results of the AQ+ and AQ- DPs were similar across our broad array of memory measures. In particular, we found that the AQ+ group did not differ from the AQ- group on the CFMT ($M_{AQ+}$ = 40.40, $SD_{AQ+}$ = 3.77, $M_{AQ-}$= 39.64, $SD_{AQ-}$ = 4.71; $p$ = .598), the Old/New face recognition overall score ($M_{AQ+}$ = .63, $SD_{AQ+}$ = .05, $M_{AQ-}$ =.64, $SD_{AQ-}$ = .58; $p$ = .310) or recollection or familiarity parameters derived from the Old/New face recognition task. Further, both groups performed significantly worse on the CFMT and Old/New (accuracy, recollection, and familiarity) when compared to typically developing controls (see Table 2). Likewise, performance on the NOMT did not differ between the two groups ($M_{AQ+}$ = 58.40, $SD_{AQ+}$ = 7.57, $M_{AQ-}$ = 60.04, $SD_{AQ-}$ = 8.48; $p$= .535), and performance for both groups was not significantly different from typically developing controls.

Examining Pearson correlations in the DP group between the AQ and each of the memory measures demonstrated a similar pattern of results – the AQ showed little to no correlation with the CFMT, Old/New face recognition task (accuracy, recollection and familiarity), or NOMT, indicating that the degree of autism traits was unrelated to severity of face memory impairment (see Figure 1).

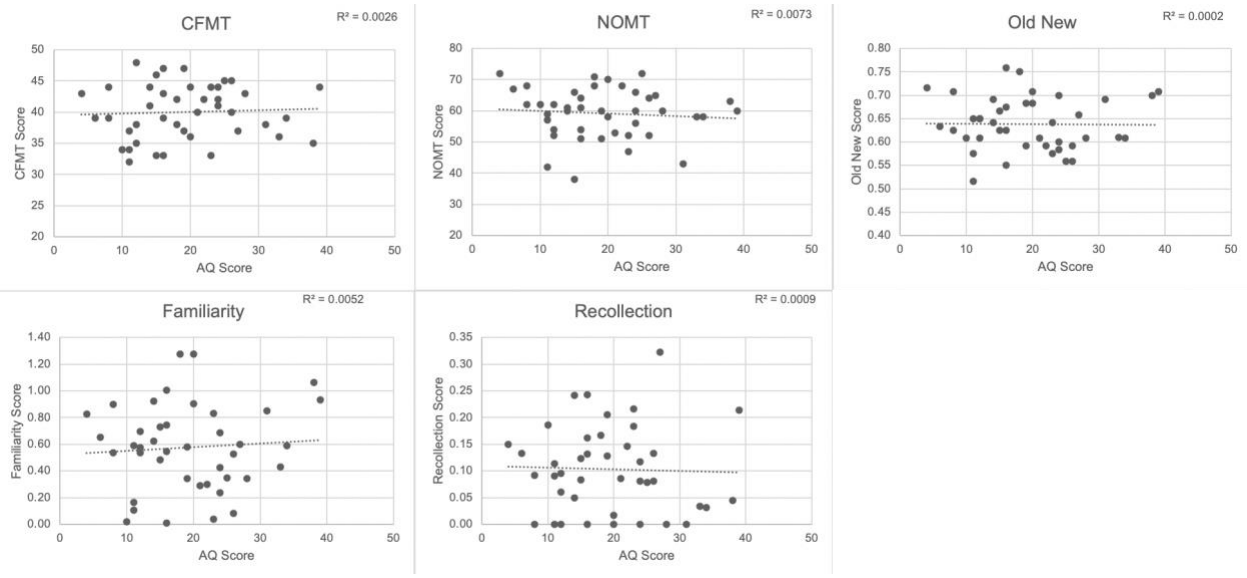


**Fig 1** Correlations between AQ scores and memory tasks in the entire DP population

*Face Matching, Holistic Processing, and Eye vs. Mouth Region Discrimination Performance*

We next considered face perception performance, hypothesizing, based on studies of face processing in ASD (Ventura et al., 2017; Weigelt et al., 2012), that AQ+ DPs, compared to AQ- DPs, would have less impaired face perception and holistic processing abilities. Interestingly, the results showed a very similar pattern of performance in AQ+ and AQ- DPs in terms of perceptual ability and holistic processing, with both groups showing significant deficits compared to controls (see Table 2). In terms of feature processing and feature attention, the AQ+ group did not differ from the AQ- group on any individual measures of feature sensitivity, nor did they differ in a composite measure of eye performance, comprised of eye trials from the part whole and Georges tasks. Notably, though the TD group performed significantly better on the eye vs. mouth composite ($M_{Eye}$ = 71.09, $SD_{Eye}$ = 11.33, $M_{Mouth}$= 63.44, $SD_{Mouth}$ = 9.47; $p < .001$), neither the AQ+ ($M_{Eye}$ = 63.03, $SD_{Eye}$ = 12.63, $M_{Mouth}$= 59.20, $SD_{Mouth}$ = 7.00; $p = .313$) nor the AQ- ($M_{Eye}$ = 61.28, $SD_{Eye}$ = 11.19, $M_{Mouth}$= 59.25, $SD_{Mouth}$ = 7.88; $p = .436$) DP group performed significantly better on eye versus mouth composite scores. This suggest that, compared to

controls, both AQ+ and AQ- DPs had reduced sensitivity to the eye region relative to the mouth region. Consistent with these results, correlations in the entire DP sample again showed that continuous measures of the AQ showed little to no correlation with the perceptual measures (SDFMT, CFPT, BFRT-c, USCFPT, Georges Task), holistic processing (part whole), or relative attention to the eye or mouth regions (see Figure 2). A summary of all the perceptual and memory differences between AQ+ DPs, AQ- DPs, and controls can be seen in Figure 4.[3]

[3] Because the control group was not given the RMET and z-scores were calculated using the control group as the normative data, the RMET is excluded from this figure.

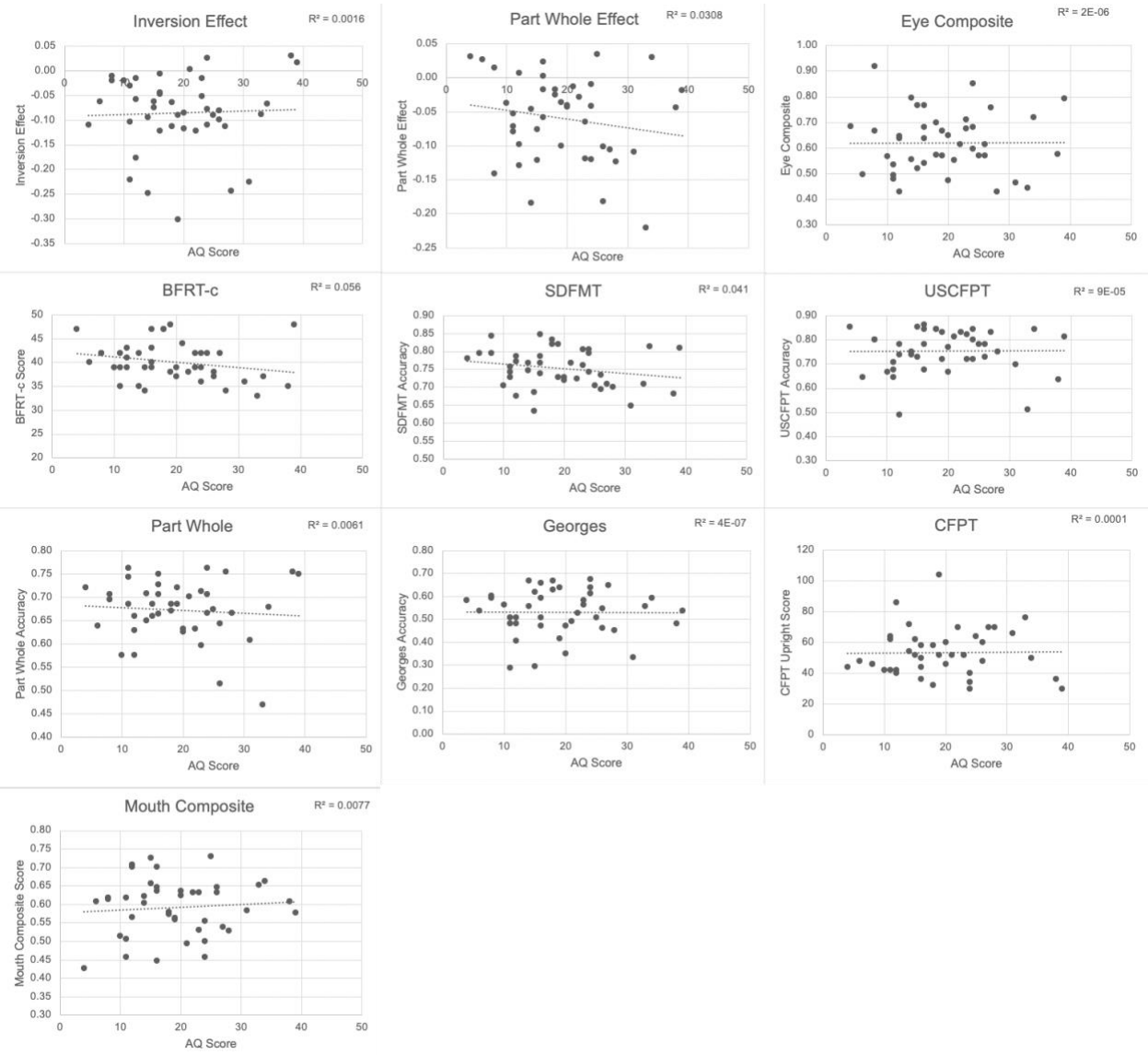


**Fig 2** Correlations between AQ scores and perceptual tasks in the entire DP population

**Table 2** AQ- DP, AQ+ DP, and control behavioral task performance

| **Measure** | **AQ- DP** | **AQ+ DP** | **TD** | ***p*-values and** | | |
|---|---|---|---|---|---|---|
| | **N=28** | **N=15** | **N=27** | **Cohen's *d*** | | |
| | | | | **AQ+ vs. AQ-** | **AQ- vs. TD** | **AQ+ vs. TD** |
| **Cambridge Face** | 39.64 ± 4.71 | 40.40 ± 3.77 | 58.78 ± 7.92 | $p = .598$ | $p < .001$** | $p < .001$** |
| **Memory Test** | | | | $d$=.18 | $d$=2.94 | $d$=2.96 |
| **PI-20** | 82.71 ± 7.56 | 80.80 ± 10.81 | 36.89 ± 7.06 | $p = .548$ | $p < .001$** | $p < .001$** |
| | | | | $d$=.20 | $d$=6.26 | $d$=4.81 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Famous Faces Memory Test** | 32.47 ± 15.05 | 41.57 ± 13.44 | 73.82 ± 16.09 | *p* = .063<br>*d*=.64 | *p* < .001**<br>*d*=2.65 | *p* < .001**<br>*d*=2.18 |
| **Cambridge Face Perception Test** | 54.36 ± 15.28 | 51.87 ± 15.45 | 40.54 ± 14.47 | *p* = .617<br>*d*=.16 | *p* = .001**<br>*d*=.93 | *p* = .024**<br>*d*=.76 |
| **Computerized Benton Face Recognition Test** | 40.96 ± 3.83 | 38.67 ± 3.96 | 45.65 ± 4.63 | *p* = .071<br>*d*=.59 | *p* < .001**<br>*d*=1.10 | *p* < .001**<br>*d*=1.62 |
| **USC Face Perception Test** | 74.52 ± 10.02 | 75.21 ± 9.02 | 78.63 ± 9.87 | *p* = .820<br>*d*=.07 | *p* = .132<br>*d*=.41 | *p* = .274<br>*d*=.36 |
| **Same/Different Face Matching Task** | 75.85 ± 5.09 | 74.10 ± 5.41 | 79.91 ± 6.58 | *p* = .298<br>*d*=.33 | *p* = .013**<br>*d*=.69 | *p* = .006**<br>*d*=.96 |
| **Part Whole Test** | 67.45 ± 4.97 | 66.39 ± 8.74 | 73.28 ± 15.79 | *p* = .614<br>*d*=.15 | *p* = .002**<br>*d*=.50 | *p* = .012**<br>*d*=.54 |
| **Whole Eyes** | 74.26 ± 11.79 | 75.28 ± 15.79 | 85.49 ± 14.54 | *p* = .811<br>*d*=.07 | *p* = .003**<br>*d*=.85 | *p* = .041**<br>*d*=.67 |
| **Part Eyes** | 70.09 ± 11.06 | 70.56 ± 11.94 | 82.87 ± 12.03 | *p* = .899<br>*d*=.04 | *p* < .001**<br>*d*=1.11 | *p* = .003**<br>*d*=1.03 |
| **Whole Mouth** | 77.53 ± 11.75 | 72.22 ± 14.32 | 79.63 ± 10.86 | *p* = .198<br>*d*=.40 | *p* = .495<br>*d*=.19 | *p* = .066<br>*d*=.58 |
| **Part Mouth** | 65.63 ± 13.96 | 66.94 ± 10.74 | 65.28 ± 15.59 | *p* = .752<br>*d*=.11 | *p* = .931<br>*d*=.02 | *p* = .715<br>*d*=.12 |
| **Georges Task** | 52.31 ± 10.32 | 54.63 ± 8.88 | 55.34 ± 10.83 | *p* = .467<br>*d*=.24 | *p* = .298<br>*d*=.29 | *p* = .830<br>*d*=.07 |
| **Eye Trials** | 50.40 ± 15.62 | 53.15 ± 18.06 | 57.80 ± 14.68 | *p* = .605<br>*d*=.16 | *p* = .079<br>*d*=.49 | *p* = .375<br>*d*=.28 |
| **Mouth Trials** | 46.83 ± 10.87 | 48.70 ± 9.44 | 53.53 ± 11.77 | *p* = .576<br>*d*=.18 | *p* = .034**<br>*d*=.59 | *p* = .184<br>*d*=.45 |
| **Eye Composite** | 61.28 ± 11.19 | 63.03 ± 12.63 | 71.09 ± 11.33 | *p* = .643<br>*d*=.15 | *p* = .002**<br>*d*=.87 | *p* = .042**<br>*d*=.67 |
| **Mouth Composite** | 59.25 ± 7.88 | 59.20 ± 7.00 | 63.44 ± 9.47 | *p* = .984<br>*d*=.01 | *p* = .079<br>*d*=.48 | *p* = .137<br>*d*=.51 |
| **Holistic Processing** | | | | | | |
| **Inversion Effect** | -.1052 ± .080 | -.093 ± .081 | -.018 ± .128 | *p* = .644<br>*d*=.15 | *p* = .004**<br>*d*=.82 | *p* = .048**<br>*d*=.70 |
| **Part Whole Effect** | -.0411 ± .056 | -.069 ± .072 | .0002 ± .076 | *p* = .170<br>*d*=.43 | *p* = .026**<br>*d*=.62 | *p* = .007**<br>*d*=.93 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Old New** | 64.48 ± 5.75 | 62.62 ± 5.32 | 70.96 ± 10.82 | $p$ = .310<br>$d$=.34 | $p$ = .009**<br>$d$=.75 | $p$ = .002**<br>$d$=.98 |
| **Recollection** | .109 ± .095 | .103 ± .095 | .269 ± .236 | $p$ = .819<br>$d$=.06 | $p$ = .002**<br>$d$=.89 | $p$ =.003**<br>$d$=.92 |
| **Familiarity** | .594 ± .333 | .532 ± .303 | .835 ± .568 | $p$ = .557<br>$d$=.19 | $p$ = .064<br>$d$=.52 | $p$ = .032**<br>$d$=.67 |
| **Reading the Mind in the Eyes** | 29.18 ± 2.92 | 26.36 ± 3.98 | - | $p$ = .028**<br>$d$=.81 | - | - |
| **Social Interaction Anxiety Scale** | 19.77 ± 7.91 | 23.11 ± 11.48 | 21.04 ± 13.60 | $p$ = .427<br>$d$=.34 | $p$ = .758<br>$d$=.11 | $p$ = .685<br>$d$=.16 |

*Note. Mean ± standard deviation. P-values are derived from independent-samples t-tests comparing groups with low vs. high AQ test scores. **Statistically significant at $p < 0.05$.*

*Emotion Recognition and Self-reported Social Functioning*

We next compared performance on measures of emotion recognition ability and self-reported social functioning, predicting that the AQ+ group would demonstrate worse emotion recognition and increased social anxiety compared to the AQ- group (Spain et al., 2018). Note that 31 DPs completed the RMET, 22 DPs completed the SIAS, and no controls were given these measures. As predicted, the AQ+ group scored significantly worse than the AQ- group on the RMET ($M_{AQ+}$ = 26.36, $SD_{AQ+}$ = 3.98, $M_{AQ-}$ = 29.18, $SD_{AQ-}$ = 2.92; $p$ = .028). However, the groups did not significantly differ on their SIAS scores ($M_{AQ+}$ = 23.11, $SD_{AQ+}$ = 11.48, $M_{AQ-}$ = 19.77, $SD_{AQ-}$ = 7.91; $p$ = .427), and further, the DP groups were not significantly different from the control group's SIAS scores. The AQ+ group did not self-report worse face recognition impairments according to their PI-20 scores ($M_{AQ+}$ = 80.80, $SD_{AQ+}$ = 10.81, $M_{AQ-}$ = 82.71, $SD_{AQ-}$ = 7.56; $p$ = .063), and both groups scored higher (higher indicating worse impairment) than typically developing controls.

Correlation analyses showed that, within DPs, the AQ was significantly negatively correlated with the RMET (r = -.516, $p$ = .002). However, the AQ did not significantly correlate

with either social anxiety (r = .261, $p$ = .240) nor self-reported face recognition difficulties (r = -.057, $p$ = .716; see Figure 3).

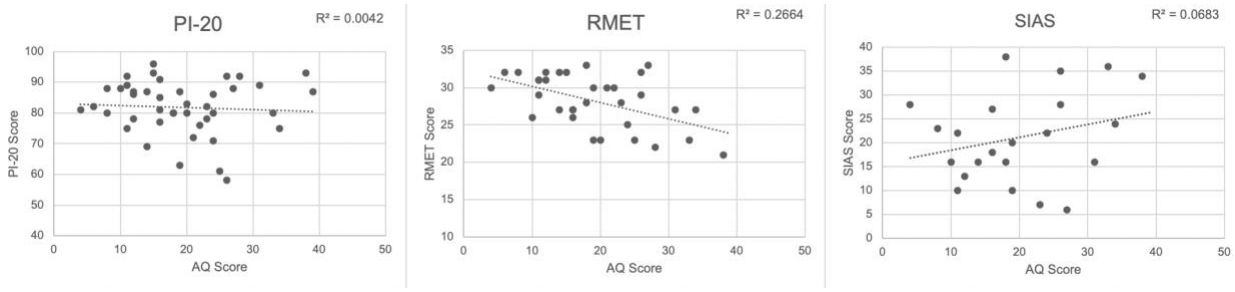


**Fig 3** Correlations between AQ scores and social and emotional measures in the entire DP population

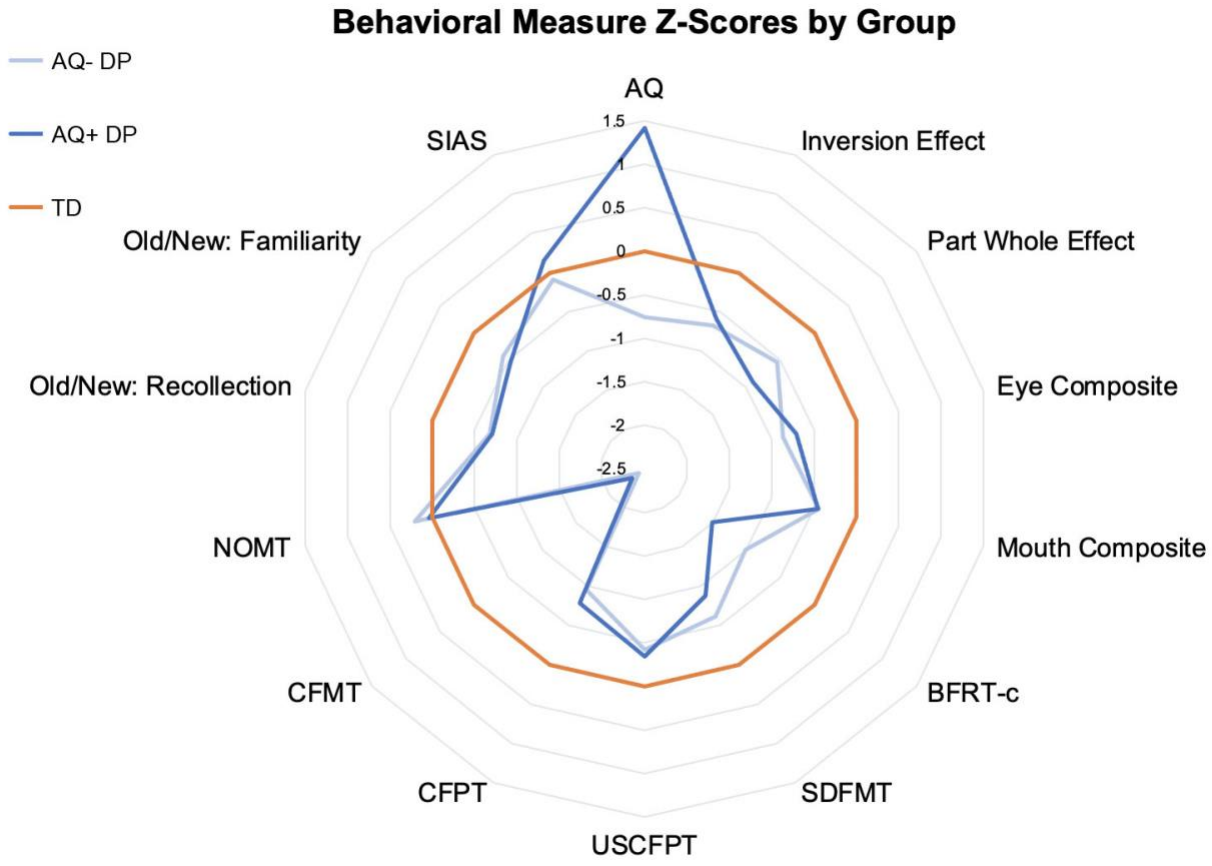


**Fig 4** Comparison of z-scores by group on behavioral task battery

*Exploratory Analyses of DPs with the highest Autism Quotient Scores*

Because 11 of the DPs in the AQ+ group had AQ scores below the standard clinical cut-off of 32 (Woodbury-Smith et al., 2005) suggestive of mild ASD traits, we ran exploratory analyses on a smaller group of DPs with AQ scores equal to or above 32 (N = 4) with the AQ- group. The average AQ score of the smaller sample (AQ++) significantly differed from that of the AQ- group ($M_{AQ++}$ = 36.00, $SD_{AQ++}$ = 2.94, $M_{AQ-}$ = 14.50, $SD_{AQ-}$ = 4.84; $p < .001$). The pattern of scores were very similar to that of the larger AQ+ group, with the smaller sample failing to significantly differ from the AQ- group on any measure of face perception, holistic processing, or featural measures (See supplementary table 1). Similarly, the two groups did not significantly differ on any measures of face or object memory. As with the larger AQ+ group, the RMET scores were significantly different from the AQ- group. The only variation from the larger AQ+ group was on self-reported social anxiety – while the AQ+ group was numerically but not significantly higher than the AQ- group on the SIAS, the smaller 4-person sample had significantly higher SIAS scores than the AQ- group ($M_{AQ++}$ = 31.33, $SD_{AQ++}$ = 6.43, $M_{AQ-}$ = 19.77, $SD_{AQ-}$ = 7.91; $d$ = 1.60). The two groups did not differ on self-reported face recognition difficulty as indexed by the PI-20.

*fMRI Category Selectivity*

Though the pattern of behavioral performance of AQ+ and AQ- DPs were very similar, it could be that the neural mechanisms underlying face processing differ between these groups. To test this possibility, we first examined face vs. scene selectivity during the fMRI localizer scan, focusing on individually-defined face-selective regions (OFA, FFA, pSTS, anterior temporal face area - aTFA). To identify significant DP/control differences, we began by comparing face selectivity in the entire group of DPs vs. controls, performing a 2 (DP/control) x 4 (region) x 2 (hemisphere) ANOVA. Though we did not find a significant main effect of group ($F(1,55)=1.11$,

p=.297), we did find a significant group x hemisphere x region interaction (F(3,53)=3.08, p=.035). This was driven by DPs demonstrating significantly reduced face selectivity compared to controls in the left OFA (t(56)=2.48, p=.016) and left FFA (t(55)=2.35, p=.022), while showing similar selectivity to controls in the other face-selective regions (see Figure 5).

We next compared AQ+ and AQ- DP groups in their face selectivity. Based on previous studies showing autism is particularly associated with regions involved in the social utilization of face information such as pSTS (Lahnakoski et al., 2012), we hypothesized that the pSTS selectivity would be reduced in our AQ+ DP group. We performed a 2 (AQ+ DP/AQ- DP) x 2 (hemisphere) ANOVA on the pSTS and found a significant main effect of group (F(1, 31)=6.95, p=.013) as well as hemisphere, with the rpSTS having greater selectivity than the lpSTS (F(1, 31)=7.46, p=.010), but no group x hemisphere interaction (F(1, 31)=.42, p=.521; see Figure 5). We next examined whether AQ+ and AQ- DPs differed in their face selectivity across the other face regions by running a 2 (AQ+ DP/AQ- DP) x 3 (region) x 2 (hemisphere) ANOVA. We did not find a significant main effect of group or any significant interaction with group (all p's>.11). Finally, since we found that the DP group as a whole showed reduced selectivity in the left OFA and left FFA, we sought to assess whether the AQ+ and AQ- DP groups showed a similar magnitude of effect. We performed Bayesian null hypothesis testing and found that comparing selectivity of the left FFA between the two DP groups yielded a Bayes Factor of 3.75, and comparing the selectivity of the left OFA between groups resulted in a Bayes Factor of 2.97, indicating slight to moderate evidence in favor of the null hypothesis.

We also performed an exploratory comparison between DPs and controls in their scene-, object-, and body-selectivity, focusing on the occipital place area (OPA), the posterior place area (PPA), the extrastriate body area (EBA), the fusiform body area (FBA), the lateral-occipital

cortex (LO), and the posterior fusiform sulcus (pFS), using a 2 (DP/control) x 6 (region) x 2 (hemisphere) ANOVA. We did not find a significant main effect of group ($F(1,55) = .01$, $p = .927$), nor did we find a significant group x hemisphere x region interaction ($F(1,55) = 1.47$, $p = .231$). We then compared the AQ+ and AQ- DP groups using a 2 (AQ+ DP/AQ- DP) x 6 (region) x 2 (hemisphere) ANOVA, and similarly found no significant main effects of group ($F(1,31) = 3.87$, $p = .058$) or group x hemisphere x region ($F(1,31) = 3.84$, $p = .059$).

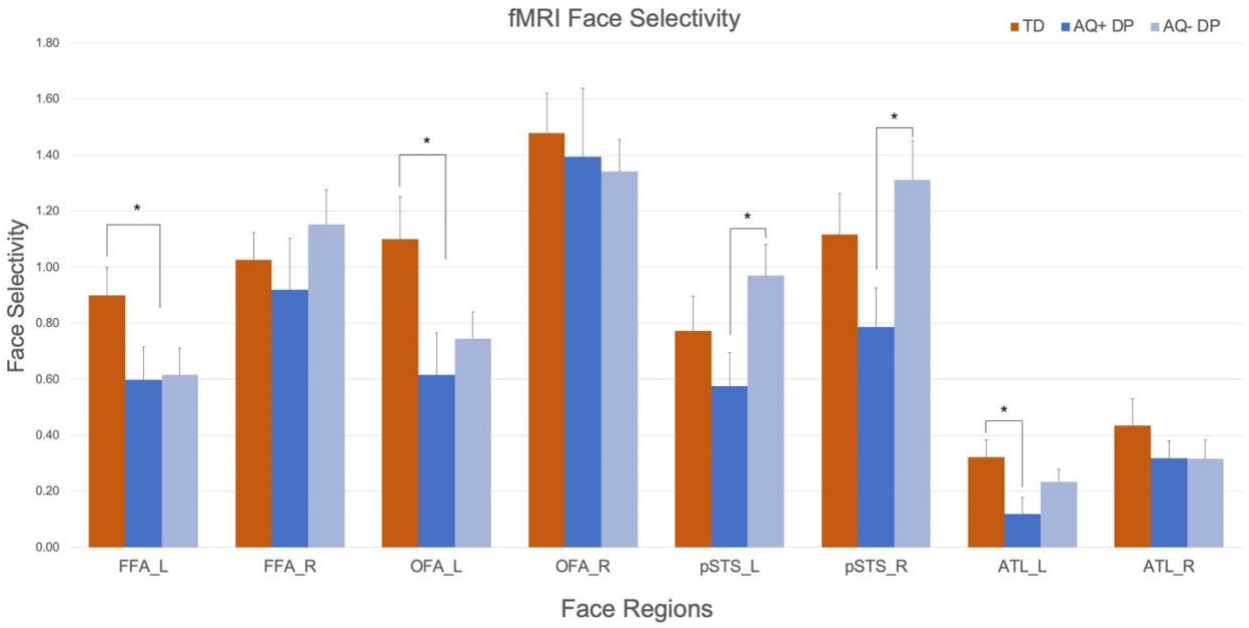


**Fig 5** Comparison of AQ-, AQ+, and TD face specificity in dynamic localizer fMRI task

*Resting-State Connectivity in the Face-selective Network*

To examine overall levels of connectivity between each of the regions within the face network (FFA, OFA, ATL, pSTS), we first compared average functional connectivity between the DP and control groups. A 2 (DP/control) x 4 (region) x 2 (hemisphere) ANOVA showed significant group effect ($F(1,54) = 8.99$, $p = .004$) but no significant interactions between group, hemisphere, and region. As can be seen in Figure 6, post-hoc *t*-tests showed significantly lower functional connectivity in the DP group across all regions (all p's < .05). To investigate whether

there were differences between the AQ+ and AQ- DPs' pSTS connectivity, we first performed a 2 (AQ+ DP/AQ- DP) x 2 (hemisphere) ANOVA on the pSTS and found no significant group effects ($F(1,30 = .26$, $p = .612$). We next investigated whether there were any differences in connectivity between the AQ+ and AQ- DP groups within the remaining face regions using a 2 (AQ+ DP/AQ- DP) x 3 (region) x 2 (hemisphere) ANOVA and found no main effect of group ($F(1,30) = .29$, $p = .594$) or significant group interactions. A Bayesian independent sample test between the AQ+ and AQ- DP groups for each of the regions yielded Bayes Factors ranging from 2.19 (left OFA) to 3.68 (left FFA), indicating slight to moderate support in favor of the null hypothesis.

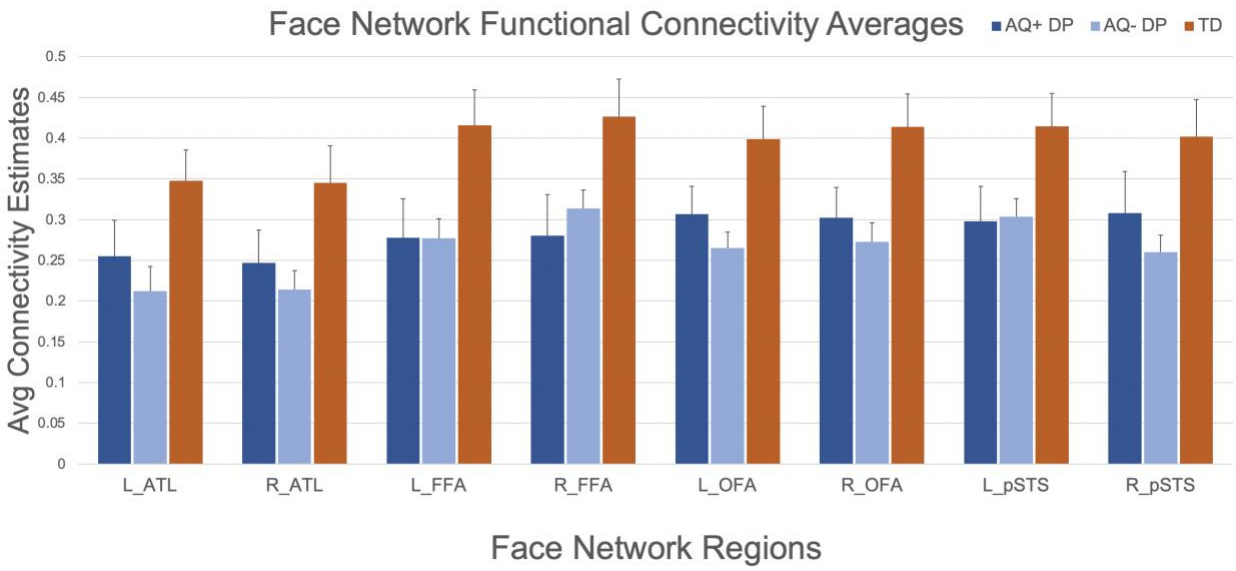


**Fig 6** Average functional connectivity of the face network across groups

*Exploratory Functional Connectivity of the Superior Temporal Sulcus*

Given the results of the face selectivity analysis, we next sought to examine if AQ+ vs. AQ- DPs showed any differences in connectivity between the bilateral STS and the rest of the brain. This could provide evidence that information in face processing regions may be processed or elaborated on differently in higher-level brain regions. When comparing the differences

between AQ+ and AQ- resting-state functional connectivity between the bilateral STS and the rest of the brain, we found that seven different regions survived whole-brain correction (corrected p<.05), including the left anterior middle temporal gyrus [$t(28)= 5.44$, uncorrected $p < .001$], the right inferior frontal gyrus [$t(11.5)= 3.58$, uncorrected $p = .001$, the right superior temporal gyrus [$t(28)= 5.32$, uncorrected $p < .001$], the right ventromedial prefrontal cortex [$t(28)= 5.63$, uncorrected $p < .001$], the right ventrolateral prefrontal cortex [$t(28)= 5.23$, $p < .001$], the left superior temporal gyrus [$t(28)= 5.51$, $p < .001$], and the left superior occipital gyrus [$t(28)= 4.38$, $p < .001$]. For all regions, the AQ+ group exhibited higher STS-ROI connectivity compared to the AQ- group with the exception of the left superior occipital gyrus, where the AQ+ group (M=-.06, SD=.12) showed lower connectivity than the AQ- group (M=.16, SD=.14). The RMET did not significantly correlate with any of the connectivity values of the above regions (all p's > .05).

## Discussion

The goal of this study was to compare the mechanistic similarities and differences between DPs with higher (AQ+ DPs) and lower (AQ- DPs) autism traits. To achieve this, we recruited a large sample of DPs (n=43) with a range of autism traits and a group of matched controls (n=27) and administered an extensive battery of face/object memory, face perception, emotion recognition, and self-reported face impairment and social functioning measures. We also had participants perform a face/scene/object/body localizer task and resting-state fMRI. Our findings demonstrate that the behavioral and neural face processing profiles of DPs with higher versus lower levels of autism traits were overall quite similar. The main differences between the two groups were significantly poorer face emotion recognition and reduced pSTS face selectivity in an fMRI dynamic localizer task in the AQ+ compared to AQ- DP group. Both DP groups

showed similarly reduced resting-state functional connectivity between regions of the face network when compared with typically developing controls. Interestingly, the AQ+ group showed significantly greater resting-state connectivity between the pSTS and several regions, including the inferior frontal gyrus, which has been implicated in face processing. Further, when examining the smaller group of DPs with the highest AQ scores, we found that they had both higher SIAS and RMET scores compared to the low AQ DPs, consistent with previous findings that individuals on the autism spectrum demonstrate higher levels of social anxiety (Spain, Sin, Linder, McMahon, and Happe, 2018). The overall pattern of results we observed is inconsistent with the notion that the presence of autism traits fundamentally changes the mechanisms of DP but rather supports a more independent co-occurrence model of ASD traits and DP. These findings have important implications for the study and treatment of developmental prosopagnosia with accompanying autism traits.

Diagnosed cases of autism have been described as having largely memory-based face recognition impairments, with intact holistic face processing and strong patterns of eye avoidance (Tanaka and Sung, 2016). In our sample of DPs, we found that in addition to the expected poor face memory performance, the AQ+ and AQ- DP groups were similarly impaired in their face perception performance across a wide array of tasks. Both groups demonstrated deficits in face matching and holistic processing and showed a similar pattern of reduced feature sensitivity/discrimination compared to controls. This suggests that not only do AQ+ and AQ- DPs have an equivalent degree of face perception deficits but also that the likely sources of these deficits, poorer holistic processing and reduced feature processing especially of the eye region, is comparable between the two groups. It also suggests that the relative levels of attention to the eye and mouth regions were commensurate between AQ+ and AQ- DPs, with both DP groups

demonstrating more attention to the mouth and less attention to the eyes when compared with the control group. The attentional pattern of eye avoidance seen in the AQ+ DPs is similar to that of both non-DP ASD individuals (Madipakkam et al., 2017) and of typical DPs (Bobak, Parris, Gregory, Bennetts, and Bate, 2017), while their poor holistic processing is more similar to typical DP patterns (e.g., Avidan et al., 2011; Palermo et al., 2011; DeGutis et al., 2012) and is less consistent with prior findings in ASD populations (Ventura et al., 2017; Weigelt et al., 2012).

In addition to their similar behavioral profiles, we also found similarities between the AQ+ and AQ- DP groups in terms of fMRI task activation in face-, scene-, object, and body-selective regions as well as in their resting-state functional connectivity. In particular, we found that during the face/scene/object/body localizer task, both AQ+ and AQ- DPs had similarly significantly reduced selectivity in face-selective regions compared to controls, particularly in the left OFA and left FFA, components of the core face processing network (Haxby et al., 2002). This reduced face-selectivity is consistent with previous studies (Jiahui et al., 2018) and the left FFA reduction in selectivity is consistent with a recent DP study by Gerlach et al. (2019). However, both AQ+ and AQ- DPs had normal selectivity in body-, scene-, and object-selective regions. During resting-state scans, both AQ+ and AQ- DPs had similarly significantly reduced functional connectivity amongst all face-selective regions compared to controls, and did not demonstrate AQ+ vs. AQ- differences in functional connectivity of any of the face-selective regions, including the pSTS. However, in an exploratory analysis, AQ+ DPs showed significantly stronger resting-state functional connectivity between the bilateral STS and several regions of the brain, including regions of the prefrontal cortex and temporal gyri, with the exception of the left superior occipital gyrus where they showed lower functional connectivity

with the STS. These results demonstrated notable similarities between the functional connectivity of the face regions of AQ+ and AQ- DPs, with the exception of the region responsible for socio-communicative functions (STS).

Despite such similar face memory, face perception, and fMRI results, it is notable that AQ+ DPs showed poorer face emotion recognition on the RMET and reduced pSTS activation to faces compared to AQ- DPs. AQ+ DPs' impairment on the RMET is consistent with previous findings that individuals on the autism spectrum often have difficulty recognizing basic emotions (Griffiths, Jarrold, Penton-Voak, Woods, Skinner, and Munafo, 2019). It is particularly notable that the AQ+ and AQ- DP groups did not differ in eye perception accuracy on the part whole or Georges task. This suggests that, in contrast to AQ+ DPs, AQ- DPs may be able to efficiently process eye-related information for highly overlearned categories such as emotions (though see Biotti and Cook, 2016), but have difficulty matching novel identities using the eyes in the part whole and Georges tasks. Additionally, the highest AQ++ group had significantly higher SIAS scores while the AQ+ group had numerically but not significantly higher self-reported levels of social anxiety. These results correspond with a meta-analysis that found links between social anxiety and autism (Spain et al., 2018). The AQ+ group's scores on the RMET and SIAS reflected the impaired emotion recognition and heightened social anxiety that we might expect to find in populations with social developmental disorders such as autism (Smith et al., 2010; Bolte and Poustka, 2003; Celani et al., 1999; Spain et al., 2018), which could reflect AQ+ DPs' impairment on social and emotional functioning and extracting socio-emotional information from faces. These findings are further supported by our fMRI category selectivity results where, compared to the AQ- DPs, AQ+ DPs had significantly reduced face selectivity in bilateral pSTS, a brain region consistently implicated processing dynamic aspects of faces (Pitcher et al, 2011),

facial expressions (Baseler et al., 2014), and emotion perception (Allison, Puce, and McCarthy, 2000).

The current results suggest that DPs with higher levels of autism traits do not demonstrate a different behavioral profile of holistic face processing, featural processing, or face memory deficits than DPs with lower levels of autism traits. In other words, the current results are inconsistent with a strong version of the autism phenotype x DP interaction model, where the presence of autism traits fundamentally changes the mechanisms and manifestation of DP. The current results provide support for a model where social developmental disorders such as autism and DP are more independent and additive. This is consistent with a previous study demonstrating that participants with diagnosed social developmental disorders (including autism, Asperger's syndrome, and PDD-NOS) and either the presence or absence of co-occurring face recognition impairments did not differ on the Social Skills Inventory (Barton et al., 2004), suggesting independence between face recognition impairments and social cognitive abilities (Minio-Palluelo et al., 2020). Our study demonstrates the reciprocal finding, where participants with DP and co-occurring autism traits do not differ from those without co-occurring autism traits on a wide array of face processing tasks. Just as the presence or absence of face recognition impairments did not result in differing social impairments in participants with SDD, the presence or absence of autism traits did not result in differing face processing impairments in our participants with DP, aside from the expected emotion recognition deficits.

Taken together, our results, along with previous studies on face recognition and social development (Barton et al., 2014; Halliday et al., 2014; Minio-Palluelo et al., 2020), provide converging evidence that the presence of social developmental disorders such as autism may not necessarily strongly interact with prosopagnosia symptoms and likewise, that the presence of

prosopagnosia may not necessarily interact with SDD symptoms. Still, this begs the question of why DP co-occurs at higher proportions in individuals with autism than in the general population. There are a few potential explanations, inspired by models proposed to explain high co-occurrence of ASD and ADHD (Leitner, 2014). The first hypothesis is that the two disorders are independent and a third environmental factor (e.g., advanced parental age at conception, Karimi, Kamali, Mousavi, and Karahmadi, 2017) influences the presence of both disorders. A second hypothesis is that there is a genetic basis for the co-occurrence, likely due to the heritable nature of both disorders as well as potential overlap of the genetic mechanisms. Their relative independence (e.g., cases where autism is present without DP, and vice versa) may be because DP affects more face-selective regions, while ASD affects the more social cognitive regions such as the pSTS and temporal parietal junction. Face recognition abilities are highly heritable (correlation of .70 on face recognition scores in monozygotic twins) and have shown to be separate from general visual and verbal abilities (Wilmer, Germine, Chabris, Chatterjee, Williams, Loken, Nakayama, and Duchaine, 2010). ASD similarly has a high estimated heritability (83%, Sandin, Lichtenstein, Kuja-Halkola et al., 2017). Further, the oxytocin receptor gene (OXTR) has been implicated in both DP (Cattaneo et al., 2016; Bate et al., 2013) and ASD (Loparo and Waldman, 2014; Jacob et al., 2007). Oxytocin plays an important role in social behaviors and bonding, and the administration of intranasal oxytocin has shown to improve face recognition, albeit temporarily, in DPs (Bate et al., 2013), indicating an important link to face recognition. The administration of intranasal oxytocin has also shown to increase eye contact in adult males with autism (Aeyung et al., 2015), providing further evidence of a mechanistic link between the two disorders. While ASD is a highly heterogeneous disorder, nonetheless, the

similarities in genetic determinants of ASD and DP may help explain why we see such high co-occurrence of these disorders (see Gray and Cook, 2018).

In addition to providing a better mechanistic understanding of DPs with ASD traits, the current results have important practical implications for including DPs with high autism traits in future studies. Even though between an estimated 15% and 35% of DPs in the general population have autism or high autism traits (based on estimates that 1 in 54 has autism, CDC 2020, and 12-36% with autism have DP, Minio-Palluelo et al., 2020), these individuals have been routinely excluded from DP studies (or have largely been studied separately from DP, see Murray et al., 2018; Corrow et al., 2016) under the assumption that DPs with high autism traits are mechanistically different from DPs with lower autism traits. The current findings suggest that high versus low AQ DPs are substantially more similar than they are different and future DP studies could benefit from including high AQ DP participants, both in terms of increasing overall study sample sizes as well as further testing the generalizability of findings between high and low AQ DPs. Another reason to include high AQ DPs is that it is possible that interventions that have been successful with low ASD DPs could help DPs with higher ASD traits as well. Previous studies have shown that holistic face training (DeGutis, Cohen, and Nakayama, 2014) and face morph training (Corrow et al., 2019) can improve face processing in non-ASD DPs. Additionally, several studies have found improvements through emotion recognition training of individuals on the autism spectrum (see Berggren, Fletcher-Watson, Milenkovic, Marschik, Bolte, and Jonsson, 2017 for a review), indicating that it is possible to train and improve face-related recognition deficits in this population. If face recognition impairments in AQ+ DPs are consistent with those seen in cases of AQ- DP, then similar training benefits may be achieved in individuals with higher levels of autism traits, and these individuals could benefit from future

inclusion in DP training programs. While previous studies have advocated for the exclusion of potential DPs with high levels of autism traits, these findings suggest that such exclusions may be unnecessary.

One limitation of this study is the lack of ASD diagnosis in the AQ+ group. Though the current study focused on the broader autism phenotype, which demonstrates social and communicative impairments that are qualitatively similar to those seen in diagnosed ASD, a study using a sample of DPs with and without a diagnosis of ASD would provide a more conclusive picture of the interaction between the disorders. While we did compare the AQ-sample to the DPs that scored above 32 on the AQ (a widely used cut-off score correctly identifying 76% of patients in a clinical sample; Woodbury-Smith et al., 2005) and found similar results, this sample size was very small and may not be representative of the ASD population. Additionally, this study was performed in adults and therefore may not generalize to children. Symptoms of autism can change from childhood to adulthood (Taylor and Seltzer, 2010; Marriage et al., 2009), and it is therefore possible that the pattern of face recognition deficits differs between children with DP and low autism traits and children with DP and high autism traits. Additionally, in the current study we could not differentiate attention to different facial features from perceptual sensitivity and examining eye movements in future studies would be useful. Future studies studying impaired face recognition in diagnosed cases of ASD would be useful to provide further insight into the effect, or lack thereof, that autism traits have on developmental prosopagnosia.

These results have important implications for the future of studying combined DP and autism traits. The notable similarities between DPs with high and low levels of autism traits suggest that the presence of autism traits does not necessarily result in a different type of DP

with regards to holistic face processing, featural processing, face memory abilities, and the neural mechanisms underlying these processes.

## Acknowledgements

We want to thank the developmental prosopagnosics and control participants for completing our challenging battery of tasks. This study was funded by R01 from the National Eye Institute grant #R01EY026057 awarded to JD.

## Data Accessibility

Upon acceptance of the manuscript, all data will made be publicly available on Dryad in accordance with NIH policy and with the approval of the VA Boston Healthcare System and Harvard Medical School IRBs.

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