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Article:
Epihova, Gabriela, Cook, Richard and Andrews, Timothy J. (2022) Recognition of pareidolic objects in developmental prosopagnosic and neurotypical individuals. Cortex. pp. 21-31. ISSN: 1973-8102

https://doi.org/10.1016/j.cortex.2022.04.011

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CORTEX 153 (2022) 21–31

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Research Report

Recognition of pareidolic objects in developmental prosopagnosic and neurotypical individuals

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ARTICLE INFO

Article history:
Received 2 August 2021
Reviewed 24 November 2021
Revised 2 February 2022
Accepted 5 April 2022
Action editor Stefan Schweinberger
Published online 22 April 2022

Keywords:
Face recognition
Object recognition
Developmental prosopagnosia
Neurodevelopmental disorders
Visual perception

ABSTRACT

Developmental prosopagnosia (DP) is a neurodevelopmental disorder associated with difficulties in the perception and recognition of faces. However, the extent to which DP affects non-face object is an ongoing debate. In this study, we asked whether pareidolic objects (which give rise to the perception of a face) are also affected in DP. First, we compared performance in DPs ($n = 30$) and controls ($n = 27$) on a recognition task with faces, pareidolic objects and non-pareidolic objects (bottles). The pareidolic objects had either similar or dissimilar image statistics to faces. Consistent with our understanding of DP, we found that the pattern of recognition across items between DPs and controls was lowest for faces. Interestingly, there was also a low correlation between DPs and controls for pareidolic-similar objects that was similar to faces. In contrast, there were higher correlations between DPs and controls for pareidolic-dissimilar objects and bottles, which were both significantly different to faces. These findings suggest that the deficit in DP involves processing image properties that are common to faces. Next, using an individual differences approach across a large group of neurotypical adults ($n = 94$), we found that face recognition covaried with the recognition of pareidolic-similar objects, but not with pareidolic-dissimilar objects or non-pareidolic objects. Together, these findings support the idea that a representation based on image properties plays an important role in the perception and recognition of objects and faces and that the deficit in the perception of some object categories in DP could be explained by their similarity to the image properties found in faces.

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https://doi.org/10.1016/j.cortex.2022.04.011

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1. Introduction

The extent to which the underlying cognitive processes involved in face and object recognition are specific for each category (domain-specific) or shared between categories (domain-general) is an ongoing debate in psychology and neuroscience (Behrmann & Plaut, 2014; Kanwisher, 2010). Support for a domain-specific organisation has been demonstrated in neuropsychological disorders, such as prosopagnosia in which lesions to the temporal lobe can result in severe deficits in face recognition but leave object recognition relatively intact (McNeil & Warrington, 1993). Conversely, other lesions are reported to affect non-face object processing, but leave face perception intact (Moscovitch, Winocur, & Behrmann, 1997). Further support for domain specificity is found in fMRI studies that have shown discrete regions in the temporal lobe respond selectively to faces (Kanwisher, McDermott, & Chun, 1997), whereas other regions are selective for different categories of non-face objects (Downing, Jiang, Shuman, & Kanwisher, 2001; Epstein & Kanwisher, 1998).

Other evidence supports a domain-general neural organization of the visual brain. In cases of acquired prosopagnosia, individuals develop typical face recognition ability, but subsequently experience face recognition difficulties following a brain injury (McNeil & Warrington, 1993; Renzi De, Faglioni, Grossi, & Nichelli, 1991). However, there is now growing evidence that these individuals also acquire deficits in the recognition of non-face objects (Behrmann & Plaut, 2013, 2014). There are also individuals in the general population who experience lifelong face recognition difficulties without any history of brain injury (Duchaine & Nakayama, 2006). This condition is often referred to as developmental prosopagnosia (DP), to reflect the fact that the disorder is lifelong in duration. The degree to which deficits in DP are face-specific or involve more general processing mechanisms has been the subject of debate (Behrmann & Plaut, 2013; Susilo & Duchaine, 2013). Some behavioural studies suggest that individuals with DP have preserved object recognition abilities (Bate, Bennetts, Tree, Adams, & Murray, 2019; Duchaine & Nakayama, 2006; Duchaine, Yovel, Butterworth, & Nakayama, 2006; Garrido, Duchaine, & DeGutis, 2018), whereas other studies report deficits in object recognition (Behrmann, Avidan, Marotta, & Kimchi, 2005; Biotti, Gray, & Cook, 2017; Geskin & Behrmann, 2018; Gray, Biotti, & Cook, 2019).

Further support for a domain-general neural organization can also be found in neuroimaging studies. For example, fMRI studies using multivariate analysis methods (in which the pattern, rather than the magnitude, of response is compared) show that overlapping patterns of response across the entire ventral temporal cortex may be important for the discrimination of different object categories (Harris, Rice, Young, & Andrews, 2015; Haxby et al., 2001; Rice, Watson, Hartley, & Andrews, 2014). The potential importance of the pattern is demonstrated by the fact that the ability to discriminate particular object categories is still evident when the most category-selective regions are removed from the analysis (Haxby et al., 2001). For example, the pattern can still discriminate faces when the most face-selective regions are removed from the analysis. These findings suggest a distributed domain-general representation could underlie the perception of faces and non-face objects in ventral temporal cortex.

A key problem in understanding whether prosopagnosia is a domain-general disorder is that there has not been a clear theoretical rationale for which objects to test (Bate et al., 2019). This has led to the use of a diverse range of object categories. As objects vary widely in both their visual and semantic properties (Coggan et al., 2019; Rice et al., 2014), it is difficult to compare results across different studies and this may account for some of the discrepancies in the literature. It also makes it difficult to draw wider conclusions about the perceptual or cognitive origins of the disorder.

The aim of this study is to determine whether objects with similar visual or semantic properties are affected in the DP. To test this prediction, we used an old/new recognition paradigm using objects that give rise to the perception of faces (pareidolia). Pareidolic objects not only give rise to the perception of a face, but they also elicit face-like patterns of neural response (Decramer et al., 2021; Taubert, Wardle, & Ungerleider, 2020; Wardle, Taubert, Teichmann, & Baker, 2020) and can engage higher-level semantic properties, such as gender, age, and emotional expression (Wardle, Paranjape, Taubert, & Baker, 2022). To determine the importance of visual and semantic properties, we selected pareidolic images that had either similar or dissimilar image statistics to faces. In Experiment 1, we compared the representational pattern similarity and performance on the recognition memory tasks for each condition with DPs and control participants. If semantic properties are important, we would expect the recognition of pareidolic objects to depend on perceived facial appearance. However, if image properties are important, we would only expect recognition to be affected for the pareidolic images with similar image statistics to faces. In Experiment 2, we used an individual differences approach with a larger analysis of neurotypical participants. We compared individual differences in performance on the face recognition task with performance with pareidolic objects. If image properties are important, we would only expect covariation in performance between faces and pareidolic images with similar image statistics to faces. On the other hand, if semantic properties are important, we would expect covariation between faces and all pareidolic images.

2. Methods

2.1. Participants

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Sample size was determined based on similar group studies investigating object recognition in DP (Bate et al., 2019; Biotti et al., 2017; Malaspina, Albonico, Toneatto, & Daini, 2017). In Experiment 1, there were 30 participants with DP (M_{age} = 41.17, SD_{age} = 11.04, 21 females) and 27 control participants (M_{age} = 36.93, SD_{age} = 11.31, 16 females). There was

no significant difference in age [t (55) = 1.43, p = .158, two-tailed] or gender [X^2 (1) = .72, p = .396, two-sided] between the two groups. All participants were over 18 years-old, had normal or corrected-to-normal vision and had no history of neurological conditions, schizophrenia or Autism Spectrum Disorder). All participants provided written informed consent and were fully debriefed after the experimental procedure. In Experiment 2, 95 participants (M_{age} = 19.05, SD_{age} = .98, 81 females) were recruited via an opportunity sample. One participant was excluded from the study for reporting face recognition difficulties (PI20 score >65). All participants were over 18 years-old, had normal or corrected-to-normal vision and had no history of psychiatric or neurological conditions. All participants provided written informed consent and were fully debriefed after the experimental procedure. All experiments presented were approved by the Psychology Research Ethics Committee at the University of York.

2.1.1. *Diagnostic tests*

DP participants were recruited through www.troublewithfaces.org. Diagnostic evidence for the presence of DP was collected using the PI20 questionnaire - a 20-item self-report measure of face recognition abilities - https://www.troublewithfaces.org/pi20_printable.pdf (Shah, Gaule, Sowden, Bird, & Cook, 2015) and the Cambridge Face Memory Test (CFMT) – an objective measure of face recognition (Duchaine & Nakayama, 2006). CFMT consists of a learning stage where a target face is presented from 3 viewpoints for 2 s per viewpoint and 500 ms. ISI. There were 3 types of test stages: 1) identical stage – target is presented the same as in the learning stage among 2 distractors; 2) novel stage – target is presented in a different viewpoint from the learning stage among 2 distractors; 3) noise stage – target is presented in a different viewpoint from the learning stage among 2 distractors and visual noise is added to all images. To be classified with DP, a participant had to score both >65 on the PI20 and <65% on the CFMT (Supplementary Table 1). The use of convergent diagnostic evidence from self-report and objective computer-based measure of face recognition ability is thought to provide reliable identification of DP; for example, less than 2% of the population score >65 on the PI20 and <65% on the CFMT (Gray, Bird, & Cook, 2017).

2.1.2. *Additional tests*

In order to assess face perception and car recognition abilities participants who were classified into controls and DPs based on their pre-screening scores completed the Cambridge Face Perception Test (CFPT) (Duchaine, Germine, & Nakayama, 2007), assessing the ability to perceive similarity between faces. Each trial required participants to arrange 6 faces morphed to different degrees according to their perceived similarity to a target face. Half of the trials were comprised of upright faces and half of inverted faces. Participants had 60 s to complete each trial. Performance was calculated as a deviation from the correct ordering of images across the upright and inverted trials (higher scores indicate more deviation and lower performance). All participants completed the Models Face Matching Test (MFMT) (Dowsett & Burton, 2015) assessing unfamiliar face matching abilities. The MFMT entails seeing 90 pairs of face images and assessing whether the 2 faces within a pair are the same or different identity. Half of the pairs contained faces of the same identity and the other half had faces with different identities. Participants also completed the Cambridge Car Memory Test (CCMT) (Dennett et al., 2012) – a well-validated test for car recognition abilities with the same task structure and demands as CFMT. As expected, there were significant differences in performance between DPs and Controls for tests of upright face processing (Table 1). Participants with DP showed significant differences from controls on the PI20, t (55) = 16.8, p < .0001, CFMT, t (55) = 12.55, p < .0001, MFMT, t (55) = 4.66, p < .0001, CFPT Upright, t (55) = 5.94, p < .001. However, there were no significant differences on the control tests: CFPT Inverted, t (55) = 1.49, p = .143; CCMT, t (55) = 1.55, p = .127.

2.1.3. *Old/new recognition task*

The old/new recognition test consisted of 4 conditions: 1) faces, 2) pareidolic objects with similar visual properties to faces, 3) pareidolic objects with dissimilar visual properties to faces, and 4) non-pareidolic objects (bottles). Face images were from young-adult, male, Caucasians and were taken from the MFMT (Dowsett & Burton, 2015). Images of pareidolic objects and bottles were taken from a variety of freely available Internet sources. Our rationale for choosing bottles as a control condition was threefold: (1) a category with exemplars that were similar to each other; (2) a category with dissimilar image properties to faces; (3) a category in which the neural response to bottles is dissimilar to faces (Coggan et al., 2016). All images were presented in gray-scale and had a resolution of 256 × 256 pixels.

A GIST descriptor was used to determine the image similarity of pareidolic images to faces (Torralba & Oliva, 2001). The GIST descriptor is an image analysis tool that captures the spectral and spatial properties of an image. Each image is spatially divided into 16 (4 × 4) locations. The GIST descriptor calculates low-level properties by convolving the image with 32 Gabor filters at 4 spatial scales, each with 8 orientations, producing 32 feature maps for each of the 16 spatial locations. This produces a total of 512 values describing the low-level properties of each image.

Table 1 – Mean scores (±1 SE) on the Twenty-Item Prosopagnosia Index (PI20), Cambridge Face Memory Test (CFMT), Models Face Matching Test (MFMT), Cambridge Face Perception Test (CFPT) – Upright and Inverted, and Cambridge Car Memory Test (CCMT) for control (n = 27) and DP (n = 30) participants • reverse scored.

Test	Controls (n = 27)	DPs (n = 30)	Significance	Effect size (Cohen's d)
PI20 •	39.6 ± 1.9	77.2 ± 1.2	***	4.40
CFMT %	83.8 ± 2.0	54.0 ± 1.4	***	3.30
MFMT %	72.9 ± 1.3	64.0 ± 1.4	***	1.24
CFPT Upright •	29.5 ± 1.8	47.9 ± 2.5	***	1.59
CFPT Inverted •	64.0 ± 2.6	69.1 ± 2.2	*n.s.*	.39
CCMT %	70.2 ± 2.4	65.6 ± 1.8	*n.s.*	.41

***P < .001, *n.s.* not significant.

First, we measured the GIST for all 60 face images to generate an average GIST descriptor for faces. Next, we measured the GIST of 120 pareidolic images and correlated the resulting vector with the average face vector. Based on the correlation values, the 20 pareidolic images with highest correlations to the 20 face targets were selected as targets for the face-like similar condition. The 20 pareidolic images with the lowest correlations to the 20 target faces were selected as targets for the face-like dissimilar condition. We compared the low-level properties of bottles with the average face vector. Fig. 1 illustrates example images of each condition and their correlation with the average GIST descriptor of faces. A one-way ANOVA indicated that there were significant differences in the similarity with faces across the different conditions (F (3,76) = 739.4, $p < .001$). *Post-hoc* multiple comparisons (FDR-corrected) showed that pareidolic-similar images had a higher correlation with faces ($M = .58$, $SD = .07$) compared to the pareidolic-dissimilar images ($M = .08$, $SD = .06$), t (76) = 26.75, $p < .001$) and bottles ($M = .29$, $SD = .07$, t (76) = 15.25, $p < .001$).

To select the distractors, we ran a cluster analysis of the pareidolic objects, which produced a matrix of similarity of each image to all other images. Based on the cluster analysis we chose the PS and PD distractor images from the clusters that contained the PS and PD targets. This allowed us to ensure that both targets and distractors in each condition had similar image properties. We also calculated low-level similarity of all 60 PS (targets and distractors) and 60 PD images to the face targets. Together, PS targets and distractors were the most face-like based on their image properties. PD targets and distractors were the least face-like based on their image properties. An independent *t*-test showed that low-level similarity to faces was significantly higher for the pareidolic-similar ($M = .41$, $SD = .15$) compared to pareidolic-dissimilar condition ($M = .26$, $SD = .15$), t (118) = 5.82, $p < .0001$).

To determine whether the observed low-level similarity of PS and PD images to faces generalises to a more diverse set of images, we calculated low-level similarity to faces from two other face databases (Supp Fig.1): Radboud face database (Langner et al., 2010) and the London face dataset (DeBruine et al., 2017). This analysis shows that PS images ($M = .43$, $SD = .08$) were significantly more similar to faces from the Radboud database than the PD images ($M = .08$, $SD = .15$), t (38) = 9.28, $p < .0001$. Similarly, PS images ($M = .31$, $SD = .13$) were more similar to faces from the London dataset compared to the PD images ($M = .05$, $SD = .14$), t (38) = 5.89, $p < .0001$).

The old/new recognition task involved a learning phase and a test phase. In the learning phase of each condition participants were presented with 20 target images for 2 s each with a 1 s inter-stimulus-interval. Participants were instructed to remember the images. During the recognition phase the 20 target images were presented along with 40 distractor

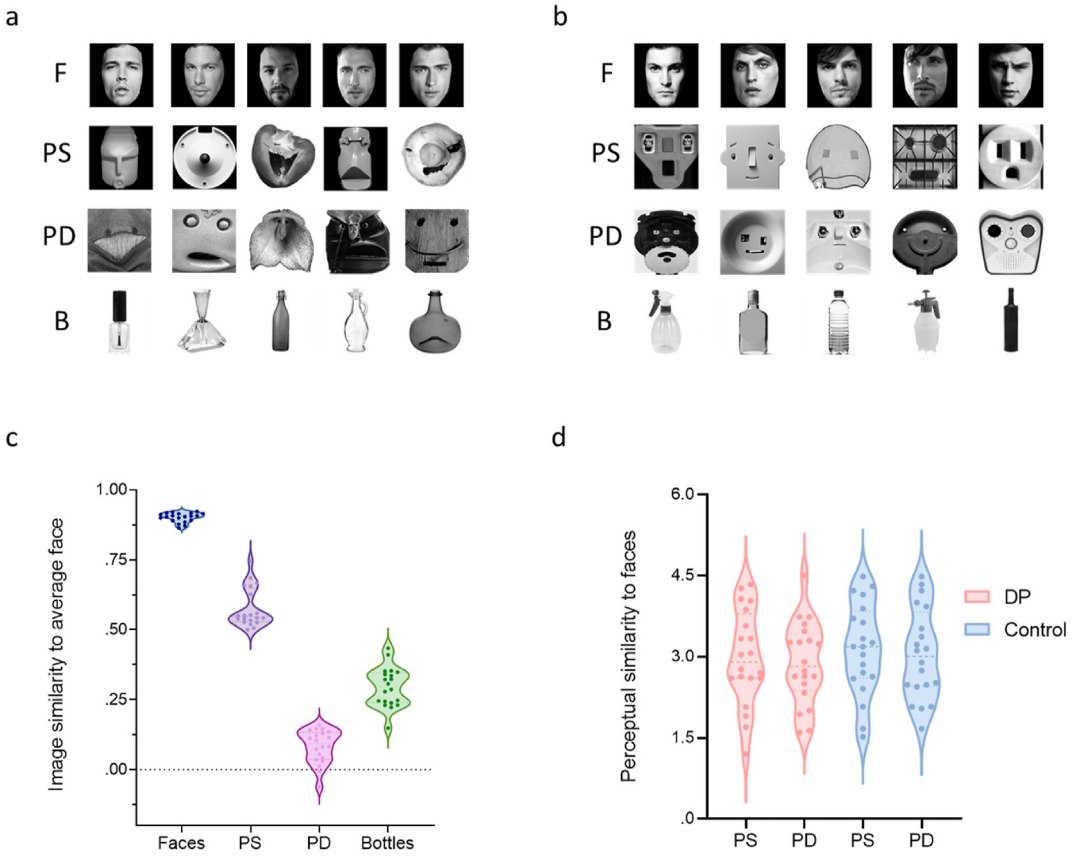

Fig. 1 – Example target (a) and distractor (b) images from F) Faces, PS) Pareidolic-Similar, PD) Pareidolic-Dissimilar and B) Bottles conditions. (c) Correlation in low-level properties (Pearson's *r*) between the images from each condition and the average face descriptor. (d) Mean face resemblance rating for PS and PD targets in DP and Control participants.

images. Conditions were counterbalanced and the order of image presentation in the recognition phase within each condition was randomised. Distractor images in each condition were from the same category as the target images. Participants were instructed to indicate by a button press whether the image was old or new. Images stayed on screen until participants made a response.

3. Results

3.1. *Experiment 1*

First, we performed an item analysis to determine whether there were differences in the way DPs and control participants represent images from the different conditions. To do this, we calculated the average accuracy for each item in the recognition task across all participants in either the DP or the control group, thus constructing a multi-item discriminability pattern for each task (Fig. 2). The mean and the range for each condition are shown in Table 2 and Supp Fig 1. The internal reliabilities are shown in Supp. Table 2. These are similar for the PS and PD conditions. We then correlated the average item values across the two groups for each condition. Correlations were then compared statistically using Fisher' z. A power analysis revealed that to detect an estimated correlation of $r = .54$, the required sample size is 24, (alpha = .05 and power = .80). Thus, the number of items ($n = 60$) used in the current analysis is sufficient for this analysis.

Table 2 – Mean (±1SEM) recognition accuracy for the old/new recognition tasks in Control ($n = 27$) and DP participants ($n = 30$).

	Controls	DPs	Significance	Effect size (Cohen's *d*)
Faces	.77 ± .02	.68 ± .02	***	.56
PS	.93 ± .01	.90 ± .01	*	.40
PD	.89 ± .01	.87 ± .01	*n.s.*	.20
Bottles	.84 ± .02	.83 ± .02	*n.s.*	.07

***P < .001, **P < .01, *P < .05, *n.s.* $p > .05$.

The multi-item pattern for faces showed the lowest correlation between DP and control participants. This is consistent with a general deficit in face perception in DPs. The correlation between DPs and control participants was significantly higher for bottles ($z = -3.29$, $p = .001$) and for pareidolic-dissimilar objects ($z = -2.09$, $p = .036$) compared to faces. However, there was no significant difference between DPs and controls for pareidolic-similar objects compared to faces

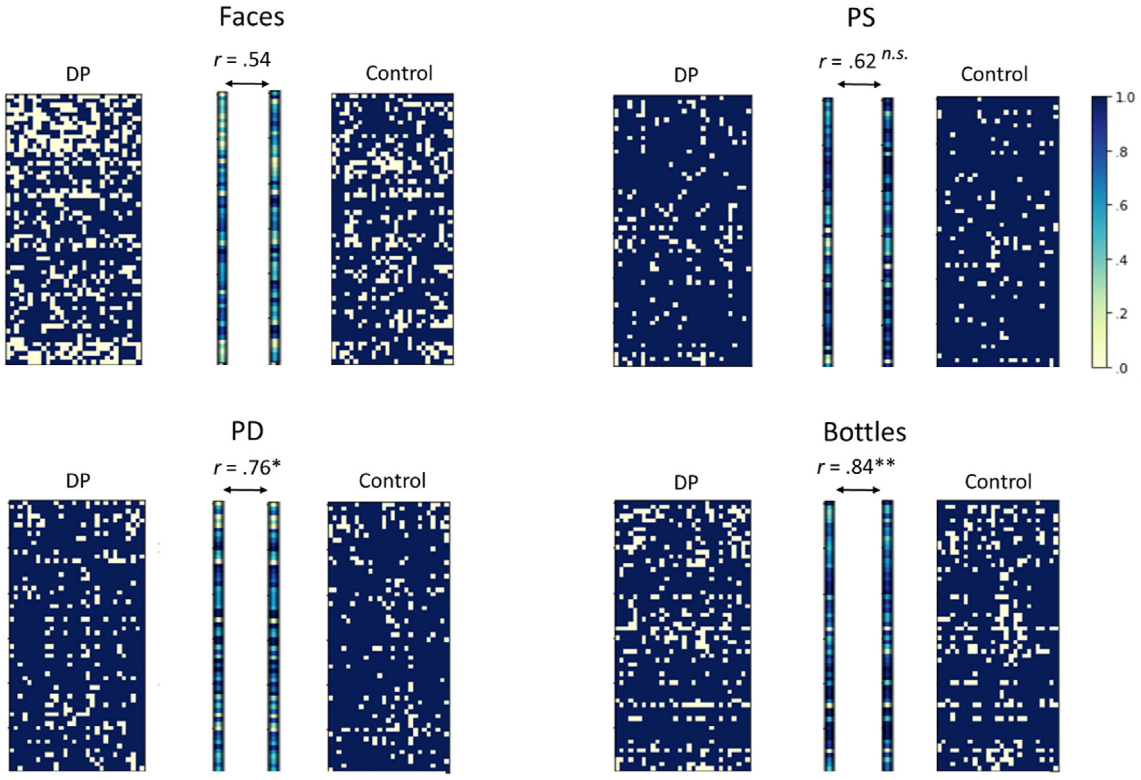

Fig. 2 – Correlations of multi-item patterns between DPs and controls for each recognition task. Each matrix shows participants on the x-axis and trials on the y-axis. Blue cells show correct responses and white cells show incorrect responses. The average values for each participant group were calculated for each trial and the corresponding item analysis correlated between DP and controls. The correlation between DPs and controls for faces was not significantly different to that of pareidolic similar (PS) but was significantly different to pareidolic dissimilar (PD) and Bottles. Significance values reflect whether each correlation is significantly different from the correlation value for faces ***P < .001, **P < .01, *P < .05, *n.s.* $p > .05$.

($z = -.65$, $p = .519$). The correlation between DPs and controls for pareidolic-similar objects was, however, significantly lower than for bottles ($z = -2.65$, $p = .008$). There was no significant difference between bottles and pareidolic-dissimilar objects ($z = -1.20$, $p = .229$). These findings suggest a difference in the way DPs represent faces and objects with similar image properties to faces compared to objects with dissimilar image properties to faces.

To determine whether these results could be explained by perceptual similarity to faces, participants rated the 20 pareidolic-similar and 20 pareidolic-dissimilar targets for their resemblance to faces on a 5 point scale (1: very low resemblance to faces to 5: very high resemblance to faces) at the end of the testing session. A 2-way mixed ANOVA with Group (DPs and Controls) as the between-subject factor and Image (PS, PD) as the within-subject factor. There was a significant main effect of Group (F (1, 38) = 9.80, $p = .003$). However, there was no effect of Image (F (1, 38) = .16, $p = .694$) or any interaction between Group and Image, F (1, 38) = .01, $p = .921$. *Post-hoc* multiple comparisons (FDR-corrected) revealed that DP participants ($M = 2.98$, SD = .88) reported lower face-like ratings for PS images compared to controls ($M = 3.14$, SD = .85, t (38) = 2.23, $p = .032$, Cohen's $d = .18$). PD images were also rated lower by DP ($M = 2.88$, SD = .76) than control ($M = 3.04$, SD = .84) participants (t (38) = 2.20, $p = .034$, Cohen's $d = .20$). This shows that the difference between pareidolic-similar and pareidolic-dissimilar objects did not reflect a difference in face likeness.

As a further test of whether perceptual similarity might explain the pattern of data, we reanalysed the data with the 20 'most face-like' ($M = 3.68$, SD = .44) and 20 'least face-like' ($M = 2.34$, SD = .45) pareidolic images, irrespective of the image properties. The correlation between the multi-item patterns of DPs and controls for the 20 most face-like images was r (18) = .71, $p < .0001$ and for least face-like images, r (18) = .66, $p = .002$. In order to compare these values to the correlations with faces, PS, PD and bottles from Experiment 1, we repeated the analysis with the 20 target images from the original conditions. The correlation between control and DP participants (restricted to the 20 target images) were as follows: faces ($r = .51$, $p = .021$), PS (r (18) = .48, $p = 0.032$), PD (r (18) = .79, $p < .0001$ and bottles (r (18) = .66, $p = .002$). Consistent with the original analysis, when pareidolic images are separated based on low-level properties, the correlation for faces ($r = .51$) is similar to PS ($r = .48$), but is different from PD ($r = .79$) (Supp Table 3). However, when the pareidolic images are separated based on perceived similarity to faces, the 'most face-like' and 'least face-like' conditions are higher (showing more similarity between DPs and Controls) and more similar to each other.

Next, we compared recognition accuracy for DP and control participants in the old/new recognition task. Item scores were entered into a 2 (group: DP and Control) x 4 (condition: face, pareidolic-similar, pareidolic-dissimilar and bottle images) repeated measures ANOVA. There were significant main effects of group (F (1, 236) = 33.26, $p < .0001$, $\eta p^2 = .12$) and condition (F (3, 236) = 34.05, $p < .0001$, $\eta p^2 = .30$). The interaction between group and condition was also significant (F (3, 236) = 7.06, $p < .001$, $\eta p^2 = .08$). To explore the interaction in more detail, we performed *post-hoc* comparisons (FDR-corrected) between DPs and controls for all tasks (Table 2). We found a significant difference between DPs ($M = .68$, SD = .18) and controls ($M = .77$, SD = .14) on the face condition, (t (236) = 6.79, $p < .0001$), $BF_{10} = 10.99$). There was also a significant difference in accuracy between DPs ($M = .90$, SD = .08) and controls ($M = .93$, SD = .07) on the pareidolic-similar condition (t (236) = 2.27, $p = .049$), $BF_{10} = 1.35$. However, there were no significant differences between DP ($M = .87$, SD = .10) and control participants ($M = .89$, SD = .10) on the pareidolic-dissimilar (t (236) = 1.51, $p = .178$, $BF_{10} = .34$) and the bottles, ($M_{DP} = .83$, $SD_{DP} = .15$, $M_C = .84$, $SD_C = .14$, t (236) = .97, $p = .331$, $BF_{10} = .22$).

We also analysed the heterogeneity of performance in the DP group across the 4 conditions (Suppl. Fig. 3). We found that the number of DPs who performed 1SD below the mean of the control group was 43.3% in the face task, 30% for the PS task, 20% for the PD task and only 13.3% for bottle task. This means that in the DP group, there were more DP individuals who had problems with recognising pareidolic-similar, compared with pareidolic-dissimilar images.

We calculated reaction time (RT) for all correct trials. There was a significant interaction between group and task (F (3, 220) = 2.73, $p = .045$). *Post-hoc* multiple comparisons (FDR-corrected) showed that RT was significantly higher for faces in the DP group ($M = 2.31$, SD = .69, $BF_{10} = 25.26$) compared to Controls ($M = 1.74$, SD = .55) (t (220) = 4.62, $p < .0001$). However, there was no difference between DPs and controls for pareidolic-similar ($M_{DP} = 1.41$, $SD_{DP} = .39$; $M_C = 1.28$, $SD_C = .31$, t (220) = 1.04, $p = .299$, $BF_{10} = .58$), pareidolic-dissimilar ($M_{DP} = 1.58$, $SD_{DP} = .47$; $M_C = 1.37$, $SD_C = .34$,t (220) = 1.70, $p = .091$, $BF_{10} = 1.19$), or bottles ($M_{DP} = 1.46$, $SD_{DP} = .45$; $M_C = 1.29$, $SD_C = .35$, t (220) = 1.34, $p = .182$, $BF_{10} = .70$).

Finally, we analysed the data using an individual differences approach. We calculated the correlation between individual performance with faces with performance on the other conditions. For controls, accuracy scores for faces were significantly correlated with PS, ($r_s = .53$, $p = .005$, $BF_{10} = 8.96$), but not with PD ($r_s = .31$, $p = .115$, $BF_{10} = .69$) or bottles ($r_s = .37$, $p = .057$, $BF_{10} = 1.29$). For DPs, there was no significant correlation between performance with faces and PS ($r_s = .03$, $p = .883$, $BF_{10} = .47$), PD ($r_s = .25$, $p = .192$, $BF_{10} = .35$) or bottles ($r_s = -.26$, $p = .158$, $BF_{10} = .67$). This shows similar individual variation between faces and PS in controls, but not in DPs.

3.2. *Experiment 2*

Experiment 2 used an individual differences approach to compare performance on tasks of face and object processing in a large group of neurotypical adults. First, we compared performance on the standard diagnostic tests used in Experiment 1 (scores on tests in which lower scores indicate better performance were reverse-coded). Fig. 3a shows the individual variation in all the tests: CFMT ($M = 80.0$, SD = 12.9), CFPT Upright ($M = 31.9$, SD = 13.1), and Inverted ($M = 62.9$, SD = 14.7), MFMT ($M = 70.4$, SD = 8.9) and CCMT ($M = 66.2$, SD = 11.5).

Fig. 3c shows a correlation matrix across all the diagnostic tests. We found that the CFMT had the highest correlation with the other tests of upright face perception, namely the CFPT upright (r_s (92) = .50, $p < .0001$, $BF_{10} = 31705.2$) and the

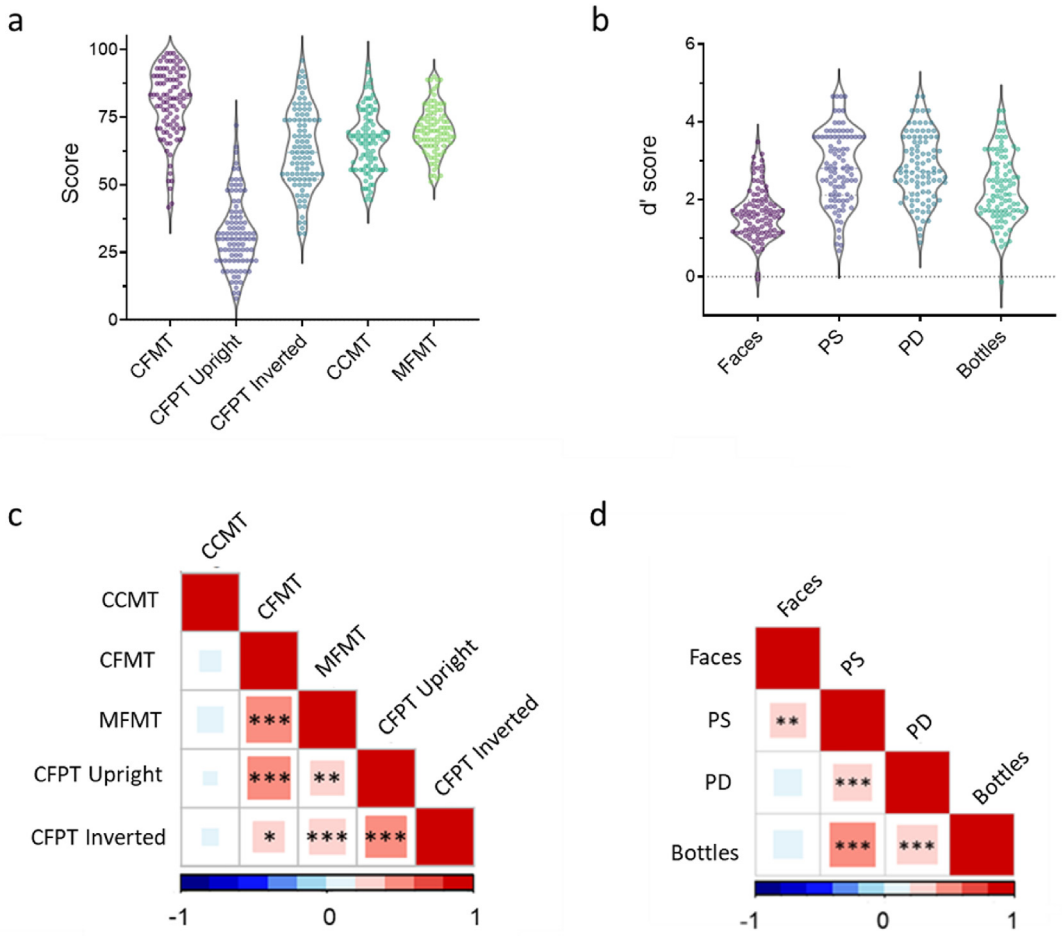

Fig. 3 – (a) Individual variation of scores on the diagnostic tests. (b) Individual variation of d' scores on the 4 conditions of the old/new recognition paradigm. (c) Correlation matrix between the diagnostic tests. (d) Correlation matrix between the *d'* values for Faces, PS, PD and Bottles conditions in the old/new recognition task ***P < .001, **P < .01, *P < .05.

MFMT (r_s (92) = .56, $p < .0001$, $BF_{10} = 382025.1$). The CFMT was also correlated with the CFPT inverted (r_s (92) = .26, $p = .011$, $BF_{10} = .88$). The MFMT correlated positively with both CFPT upright (r_s (92) = .34, $p = .001$, $BF_{10} = 27.9$) and inverted conditions (r_s (92) = .34, $p = .0009$, $BF_{10} = 29.1$). Finally, there was a significant positive correlation between the upright and inverted CFMT (r_s (92) = .46, $p < .0001$, $BF_{10} = 57853.1$). In contrast, the CCMT was not correlated with any of the tests at $p < .05$. These findings show that the significant inter-individual variation across participants covaries with tasks involving upright faces.

Performance for each participant on the old/new recognition tasks was calculated with *d'*, by using the hit rate (correctly recognising an image as a target) and false alarm rates (incorrectly mistaking an image for a target). In cases where hit rate was 1 and/or false alarm rate was 0, *d'* was calculated by decreasing the hit rate to .99 and increasing the false alarm to .01. Fig. 3b shows there was significant individual variation in the *d'* scores on the face ($M = 1.65$, $SD = .66$), pareidolic-similar ($M = 2.83$, $SD = .94$), pareidolic-dissimilar ($M = 2.83$, $SD = .85$) and bottles conditions ($M = 2.27$, $SD = .88$). Although there was significant variation in performance across the 4 conditions, F (3, 279) = 63.26, $p < .0001$, there was no significant difference in overall performance between the critical PS and PD conditions (t (93) = .01, $p = .990$, FDR-corrected).

Next, we compared individual variation on the recognition tasks (Fig. 3d). There was a significant positive correlation between recognition accuracy on the face condition and the pareidolic-similar condition (r_s (92) = .30, $p = .004$, $BF_{10} = 6.91$). In contrast, there was no correlation between performance on the face condition and pareidolic-dissimilar (r_s (92) = .18, $p = .081$, $BF_{10} = 2.16$) or bottle (r_s (92) = .20, $p = .054$, $BF_{10} = 1.39$) conditions. Recognition of pareidolic-similar and pareidolic-dissimilar objects was positively correlated (r_s (92) = .34, $p < .001$, $BF_{10} = 50.2$) and recognition performance with bottles was correlated positively with both pareidolic-similar objects (r_s (92) = .49, $p < .001$, $BF_{10} = 93179.7$), and PD objects, (r_s (92) = .39, $p < .001$, $BF_{10} = 231.6$).

4. Discussion

The aim of the study was to investigate the extent to which individuals with developmental prosopagnosia also exhibit impaired recognition of objects. Although some studies

suggest that individuals with DP have preserved object recognition abilities (Bate et al., 2019; Garrido et al., 2018), there is now growing evidence that individuals with DP have deficits in the recognition of some non-face objects (Geskin & Behrmann, 2018). A key issue that has not been resolved is why some objects appear to be affected whereas others are not. In this study, we asked whether objects with similar visual or semantic properties to faces are more likely to be affected in DP. To do this, we used the phenomenon of face pareidolia, in which inanimate objects give rise to the perception of faces (Alais, Xu, Wardle, & Taubert, 2021; Decramer et al., 2021; Keys, Taubert, & Wardle, 2021; Liu et al., 2014; Omer, Sapir, Hatuka, & Yovel, 2019; Wardle et al., 2020; Wardle et al., 2022).

We compared pareidolic objects with similar image properties to faces to pareidolic objects with dissimilar image properties to faces. In Experiment 1, we used an item-wise correlation analysis to determine the pattern of performance for DP and match-control participants. For each recognition condition, we first measured the mean accuracy for each item across all individuals within a group (DPs and neurotypical controls). The accuracy across the different items gives rise to the multi-item pattern. We measured the similarity of these multi-item patterns in DPs and controls for each condition. We found that the similarity between DPs and controls was significantly lower for faces compared to the control non-pareidolic object condition (bottles). This demonstrates a clear difference in the way that faces and non-face objects are represented in DPs and is consistent with a recent study using a similar item-wise correlation method (Xue et al., 2020). The key novel finding in this study is that the similarity in the multi-item pattern between DPs and controls was also lower for pareidolic objects with similar image properties to faces. In contrast, the similarity in the item analysis was greater for pareidolic objects with dissimilar image properties and with bottles. This suggests that these objects are perceived more similarly in DPs and controls. Importantly, the ranges and reliability for PS and PD scores were comparable.

A possible alternative explanation of the data could be that the pareidolic objects with more similar image properties were also perceived to be more 'face-like'. To address this issue, we measured the perceived 'face-likeness' of pareidolic objects with similar and dissimilar image properties to faces. We found that both pareidolic similar and pareidolic dissimilar objects were perceived to have a similar face-likeness. This allows us to differentiate between low-level and high-level properties in the main analysis of the data. We also reanalysed the data by separating the pareidolic images into the 'most face-like' and 'least face-like'. We found that the item-wise correlation was similar in these two conditions and was higher than for faces. Together, this suggests that the deficit in DP is better explained by the visual properties of the images.

We also found that DPs were impaired in the recognition of faces and pareidolic objects that had similar image statistics to faces. However, there was no difference in performance between DPs and controls for pareidolic objects that had dissimilar low-level image properties or non-pareidolic objects (bottles). The group difference in recognition accuracy for pareidolic similar objects was significant, but it was smaller compared to faces. There was also no difference in response time. There are two reasons for why there might be a smaller effect on overall recognition with pareidolic similar objects between DPs and controls. The first is that, although the image properties are similar, they are not identical to faces. This is consistent with previous studies have also shown that neural response to pareidolic objects is similar, but not identical to faces (Alais et al., 2021; Decramer et al., 2021; Keys et al., 2021; Liu et al., 2014; Omer et al., 2019; Wardle et al., 2020). Another reason for the smaller difference in pareidolic similar objects might be the higher accuracy for the pareidolic objects in the old/new recognition task, which may have masked the effect of group.

In Experiment 2, we tested a large group of neurotypical adults on the recognition tasks. One hypothesis about the deficit in DP is that it reflects the lower end of the normal distribution of face processing abilities (Barton & Corrow, 2016). With this theoretical perspective, we used an individual differences approach to ask whether recognition performance on faces could be predicted by recognition performance on other objects. Although some studies have found correlations between face and object tasks (Biotti et al., 2017; Malaspina et al., 2017; Zhao et al., 2016), other studies have failed to report significant covariation between faces and non-face objects (Bate et al., 2019). Here, we report that performance on the face recognition task was only correlated with performance on the pareidolic-similar object task. There was no correlation between faces and pareidolic-dissimilar objects or bottles. We performed a similar individual differences analysis on the data in Experiment 1, albeit with a smaller sample size. Consistent with the findings from Experiment 2, we found the highest correlation between faces and PS in control participants. Interestingly, there was no correlation between faces and PS in DPs. Together these findings suggest that variation in previous studies comparing the perception of faces and objects may reflect variance in the image statistics. Again, this suggests that performance on these recognition tasks is linked to the representation of the image properties.

One interesting result we observed from the additional tasks is that there was no group difference between DPs and controls for inverted faces (CFPT Inverted task) in Experiment 1 and this task showed the weakest correlations with other face tasks in Experiment 2. This fits with a previous study that found a reduced face inversion effect in DPs that reflected poorer performance on upright faces compared to controls (Klargaard, Starrfelt, & Gerlach, 2018). Most studies using inverted faces suggest that the difference in performance is explained by an absence of configural or holistic processing in inverted faces (Carey & Diamond, 1977). However, when faces are inverted, their low-level properties do not match those of upright faces. The role of low-level properties might be an alternative framework for future studies when trying to explain face and object inversion effects.

The importance of image statistics in the recognition of faces and objects shown across the two experiments raises important questions about the underlying neural representations of complex objects. Although the ventral visual pathway is directly involved in the perception and recognition of objects (Haxby et al., 1991; Milner & Goodale, 1995), the extent to which the neural representation of objects in this

region reflects low-level or high-level properties remains unresolved. Patterns of response in higher-visual areas of the ventral visual pathway have been linked to higher–level properties of objects, such as category (Connolly et al., 2012; Haxby et al., 2001), animacy (Kriegeskorte et al., 2008), semantics (Naselaris, Prenger, Kay, Oliver, & Gallant, 2009) and real-world size (Konkle & Oliva, 2012). However, it remains unclear how these representations emerge from the image-based representations found in early visual areas. One possibility is that the patterns of response in high-level visual areas reflect an underlying representation that is based on more fundamental properties of the stimulus (Andrews, Watson, Rice, & Hartley, 2015a). Recent studies have shown that differences in image properties of objects can explain a significant amount of the variance in high-level regions of visual cortex (Coggan et al., 2019; Rice et al., 2014; Sormaz, Watson, Smith, Young, & Andrews, 2016; Watson, Hartley, & Andrews, 2014). For example, category-selective patterns of response are still evident when images have been scrambled in a way that preserves some of their visual properties, but removes their semantic properties (Coggan, Baker, & Andrews, 2016; Coggan, Liu, Baker & Andrews, 2016; Long, Yu, & Konkle, 2018; Watson, Hartley, & Andrews, 2017). Similarly, objects from different categories but with similar image properties give rise to similar patterns of response (Coggan et al., 2019). The behavioural findings in this study using pareidolic objects provide strong converging evidence for the importance of image properties in the representation and recognition of objects and provide insights into the way that domain-general processing might occur (Andrews, Watson, Rice, & Hartley, 2015b; Behrmann & Plaut, 2013).

In conclusion, we show that faces and pareidolic objects with similar image properties to faces are significantly affected in individuals with DP. However, we did not find any effects for pareidolic objects that did not have similar image properties to faces. This difference between pareidolic objects could not be explained by how face-like they were perceived. These results provide new insights into object recognition deficits in DP. Further evidence for the role of image properties is shown by the covariation between faces and pareidolic objects with similar image properties in the neurotypical population. Together, our results support the idea of an underlying domain-general representation in visual cortex that is based on the image statistics of objects.

Data accessibility

Experimental stimuli, code and anonymised data are publicly available at https://osf.io/c7esz/

Legal copyright restrictions prevent public archiving of the additional tests used in this study, which can be obtained from the copyright holders in the cited references (see 'Additional tests').

Preregistration

No part of the study was pre-registered prior to the research being conducted.

Author contributions

G.E. and T.A. designed the study. G.E. conducted the experiments and analysed the data; R. C. contacted DP participants. All authors contributed to the writing of the manuscript.

Open practices

The study in this article earned an Open Data badge for transparent practices. Materials and data for the study are available at https://osf.io/c7esz/.

Acknowledgments

We would like to thank Ash Yakunina for assistance with testing. Special thanks to all DP and control participants for their continuous contribution to our research. We would like to thank two anonymous reviewers for their helpful comments. This works was supported by an ESRC doctoral studentship to G.E.

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2022.04.011.

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