Lateralization of word and face processing in developmental dyslexia and developmental prosopagnosia

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ABSTRACT

In right-handed adults, face processing is lateralized to the right hemisphere and visual word processing to the left hemisphere. According to the many-to-many account (MTMA) of functional cerebral organization this lateralization pattern is partly dependent on the acquisition of literacy. Hence, the MTMA predicts that: (i) processing of both words and faces should show no or at least less lateralization in individuals with developmental dyslexia compared with controls, and (ii) lateralization in word processing should be normal in individuals with developmental prosopagnosia whereas lateralization in face processing should be absent. To test these hypotheses, 21 right-handed adults with developmental dyslexia and 21 right-handed adults with developmental prosopagnosia performed a divided visual field paradigm with delayed matching of faces, words and cars. Contrary to the predictions, we find that lateralization effects in face processing are within the normal range for both developmental dyslexics and prosopagnosics. Moreover, the group with developmental dyslexia showed right hemisphere lateralization for word processing. We argue that these findings are incompatible with the specific predictions of the MTMA.

1. Introduction

In right-handed adults there is typically a right hemisphere dominance in face processing and a left hemisphere dominance in word processing (Dehaene and Cohen, 2011; Dien, 2009; Prete and Tommasi, 2018). It has been suggested that this lateralization pattern may reflect that some domains are particularly important for humans, leading to specialization of distinct brain areas for specific visual categories such as faces or words (Cohen and Dehaene, 2004; Kanwisher, 2010; McKone and Robbins, 2011). In support of this notion it has been found that an area lateralized to the right hemisphere is selectively activated during face processing (Kanwisher et al., 1997; McCarthy et al., 1997), and an area in the left hemisphere during visual word processing (Cohen et al., 2000, 2003). The assumed functional dedication and domain-specificity of these areas is reflected in the nomenclature provided for them; the fusiform face area (FFA) and the visual word form area (VWFA), respectively (Cohen et al., 2000; Kanwisher et al., 1997). Also, patients with apparently selective deficits for either face or word processing following brain injury (e.g., Barton et al., 2010; Gaillard et al., 2006; Susilo et al., 2015) represents a double dissociation that has been taken to support the existence of a domain-specific cerebral organization (for reviews see Farah, 2004; Robotham and Starrfelt, 2017).

1.1. Graded specialization and dependent development

In contrast to the idea that brain areas are dedicated to processing of specific visual categories of stimuli, others have argued for a more general or graded cerebral organization of higher visual functions (e.g., Behrmann and Plaut, 2013; McGugin et al., 2012; Price and Devlin, 2011). One such account is the many-to-many account (MTMA) according to which visual word and face processing are supported by bilateral, overlapping, but graded networks where face processing is more strongly represented in the right hemisphere and visual word processing more strongly represented in the left hemisphere (Behrmann and Plaut, 2013, 2015, 2020; Plaut and Behrmann, 2011). This partial asymmetry is thought to arise because of competition for cerebral...
resources and connection induced constraints. A key assumption is that it is the acquisition of reading ability that ignites the competition for cerebral resources, particularly in the left VWFA. Hence, prior to the acquisition of literacy, face recognition is thought to be mediated by bilateral structures. The notion that some functions—such as reading—become lateralized to the right hemisphere for a period hereafter (Lochy et al., 2019) just to become bilateral for a period hereafter (Lochy et al., 2019) just to become lateralized to the right hemisphere is damaged (Asperud et al., 2019; Gerlach et al., 2014; Dehaene et al., 2010). Evidence for a decrease in face responses in the left hemisphere with 1-month old infants (de Heering and Rossion, 2015), that it becomes more lateralized to the right hemisphere than the left hemisphere and vice versa for face processing (Behrmann and Plaut, 2013). Furthermore, it has been argued that the bilateral activation associated with both face and word processing is not an epiphenomenon of imaging methodology (Behrmann and Plaut, 2013, 2020). Rather, several studies have found both word and face recognition problems in patients with brain injury, independent of which hemisphere is damaged (Asperud et al., 2019; Gerlach et al., 2014; Roberts et al., 2015). Even some patients with apparently selective deficits for either faces (acquired prosopagnosia) or words (pure alexia) following brain injury, have been shown to have mild deficits in the other domain when sensitive testing is performed (Behrmann and Plaut, 2014).

1.2. Interdependency in word and face recognition development

The suggestion that reading acquisition induces a rightward shift in the cerebral areas supporting face recognition was initially based on comparison of illiterate and literate adults which indicated that improved reading skills were associated with decreased activation for faces in the left hemisphere but increased responses to faces in the right hemisphere (Dehaene et al., 2010) for a critical assessment of this claim see Rossion and Lochy (2021). However, the suggestion has also found more direct support in a later study where better reading skills were associated with increased activation during face processing in the right hemisphere in children learning to read (Dehaene-Lambertz et al., 2018). Likewise, increased activation for faces in the right hemisphere is associated with better reading skills in children (8-10-years-old) when dyslexic children are compared with typical readers (Monzalvo et al., 2012). Also, the development of left hemispheric lateralization for word processing seems to occur before the right hemispheric lateralization for faces (Dundas et al., 2013, 2014) and this interdependence may begin as soon as children learn to read letters in the Roman alphabet (Cantlon et al., 2011; Gentanni et al., 2018; Lochy et al., 2019). However, the evidence for interdependent development is not clear cut as there is evidence suggesting that face processing is right-lateralized in 4–6 month old infants (de Heering and Rossion, 2015), that it becomes bilateral for a period hereafter (Lochy et al., 2019) just to become right-lateralized again later. Also problematic is that a longitudinal single-case study of an illiterate man learning to read only found evidence for a decrease in face responses in the left hemisphere with improved reading skills, but no changes in the right hemisphere (Braga et al., 2017), and another longitudinal study with a group of children that did not find that activation of the VWFA was selective for faces prior to reading acquisition (Dehaene-Lambertz et al., 2018). Finally, a recent behavioral study found no evidence for a negative relationship between literacy acquisition and face recognition performance in children during the first year of school (Kühn et al., 2021). Such a relationship would be expected if reading and face recognition compete for the same cerebral resources. Hence, the evidence in favor of a reading acquisition induced rightward shift in face recognition is mixed, and according to a recent in-depth evaluation actually quite limited (Rossion and Lochy, 2021).

1.3. Developmental dyslexia and developmental prosopagnosia

For people with developmental dyslexia, obtaining word reading skills is a struggle that continues in adulthood (Shaywitz, 1996). According to the MTMA, this failure in reading acquisition will cause atypical cerebral organization for word and face processing. The argument is that “… if the acquisition of word recognition is impaired by, for example, a phonological deficit, as in DD (developmental dyslexia), the initial trigger for lateralization, namely, the optimizing of the LH [left hemisphere] to connect visual and language areas will not be present. The absence of this tuning for words in the LH will not result in the competition that drives the lateralization of faces.” (Behrmann and Plaut, 2020, p. 20). This hypothesis corresponds well with studies of developmental dyslexia that have found decreased activation of brain areas in the left hemisphere supporting visual word processing (the VWFA) (for a meta-analysis see Richlan et al., 2011). Importantly, according to the MTMA, the typical lateralization pattern—with word processing being more efficient in the left hemisphere and face processing being more efficient in the right hemisphere—should thus not be found in individuals with developmental dyslexia (Collins et al., 2017). The evidence in support of these predictions has been mixed, perhaps relating to the heterogeneity among developmental dyslexics. Neither Gabay et al. (2017) nor Collins et al. (2017) found a significantly altered lateralization pattern for word or face processing when comparing developmental dyslexics with controls, and Collins et al. (2017) even found that their developmental dyslexics showed the normal lateralization pattern for words. Consequently, the best supportive evidence reported by this group in favor of the MTMA concerns the finding of a significant interaction between visual field and stimulus type in controls—with better performance for words in the right visual field and for faces in the left visual field—but no similar significant interaction in the dyslexics (Collins et al., 2017; Gabay et al., 2017). However, in absence of any significant three-way interactions between visual field, stimulus type and group, indicating that the lateralization pattern differed significantly between controls and developmental dyslexics, these findings are more suggestive than affirmative.

With respect to developmental prosopagnosia—a condition where face recognition abilities do not develop to normal levels (Duchaine, 2011)—the prediction by the MTMA concerning lateralization effects is different, because reading ability seems to develop to a normal extent (Burns et al., 2017; Rubino et al., 2016; Starrfelt et al., 2018). Hence, for individuals with developmental prosopagnosia the MTMA predicts normal lateralization effects for words. In addition, the MTMA also predicts abnormal lateralization for face processing in DP (Collins et al., 2017). The evidence in support of this latter prediction is sparse. While Collins et al. (2017) did find altered lateralization effects for faces in parts of their ERP data (the N170 waveform) for a small group of developmental prosopagnosics (N = 7), the three-way interaction (group × stimulus type × visual field) was not significant and the developmental prosopagnosics even tended to show the normal left visual field advantage for faces behaviorally (p = .06).

Given the specificity of the hypotheses by the MTMA but the mixed results obtained thus far in rather small samples (range N = 7–15), we wanted to test these hypotheses in two somewhat larger datasets comprising individuals with developmental prosopagnosia (N = 21) or developmental dyslexia (N = 21) namely that: “… DDs [developmental dyslexics] will not show this [lateralization] advantage for either stimulus type [words/faces], while CPs [congenital prosopagnosics] will show that advantage for words, but not faces” (Collins et al., 2017, p. 419). We did this by means of a divided visual field paradigm similar to that previously used to examine lateralization for words and faces in children and adults (Dundas et al., 2013, 2014) and in adults with developmental dyslexia and developmental prosopagnosia (Collins et al., 2017; Gabay et al., 2017). If the predictions of the MTMA are borne out, we should...
find no – or at least reduced – right lateralization for face processing in developmental prosopagnosia and no – or at least reduced – lateralization for word and face processing in developmental dyslexia.

2. Method

Ethical approval was obtained by The Institutional Ethical Review Board, Department of Psychology, University of Copenhagen, (number IP-IRB/29102018).

2.1. Dataset comprising participants with developmental prosopagnosia and their control participants

This dataset comprised 21 right-handed individuals (5 males) with developmental prosopagnosia (age: $M = 38, SD = 11$), and a group of 21 typically developing controls, matched on age ($M = 38, SD = 10$), gender, and handedness. The developmental prosopagnosics were selected from a larger group of self-referred individuals that we have tested over period of several years. They were selected based on the criteria that they had completed the divided visual field task and were right-handed. The controls were also selected from a larger sample based on the same criteria, and in addition they had to match the developmental prosopagnosics on gender and handedness and as well as possible on age.

2.1.1. The group with developmental prosopagnosia

All participants with developmental prosopagnosia completed structured interviews regarding everyday difficulty with facial identity recognition and possible family history of developmental prosopagnosia. They all reported severe difficulties with face recognition in their everyday life, as evaluated by the first part of the Faces and Emotion Questionnaire (FEQ, 29-items) – (Freeman et al., 2015). The developmental prosopagnosia classification was ultimately based on abnormal scores on both the FEQ and the Cambridge Face Memory Test (CFMT) (Duchaine and Nakayama, 2006). This was established by comparing an individual’s performance with that of a Danish reference sample – compiled by us over a number of years – comprising 61 control participants. As it is less probable that a person will fall significantly below the mean on two measures (the FEQ and the CFMT) instead of only one of two, we calculated the conditional probability for a person to deviate significantly on both measures. This was done by taking into consideration the correlation between the FEQ and the CFMT in our reference sample, which was $r = 0.12$ (upper 95% CI [0.35] based on bias corrected and accelerated bootstrapping with 1000 samples), using the procedure by Crawford et al. (2007). Given the relatively small size of our reference sample the correlation estimate between the FEQ and the CFMT is not very accurate (cf. the upper 95% CI being 0.35). Hence, we applied a worst-case scenario in which the correlation between the measures was set at $r = 0.35$ (the higher the correlation between two measures ($X$ & $Y$) the more likely it will be to be impaired on measure $X$ if one is already impaired on measure $Y$). Based on these considerations, a participant had to obtain a performance point estimate corresponding to the 6.68% (- 1.5 SD) worst performing individuals in the normal population on both the FEQ and the CFMT in order to be classified as having developmental prosopagnosia. Less than 1.3% of the normal population will obtain scores as low as these on both measures if the person obtained a performance point estimate corresponding to the CFMT is not very accurate (cf. the upper 95% CI being 0.35). Hence, given the relatively small size of our reference sample the correlation estimate between the FEQ and the CFMT in order to be classified as having developmental prosopagnosia if that person obtained a score of 37 or above on the FEQ and a score of 46 or below on the CFMT (the scores on the FEQ and CFMT are available in the supplementary data file which can be found at https://osf.io/aqqc/).

All developmental prosopagnosics performed within the normal range (score of 32 or less) on The Autism-Spectrum Quotient (AQ) (Baron-Cohen et al., 2001). The developmental prosopagnosics did not receive remuneration for their participation.

2.1.2. The control group for the group with developmental prosopagnosia

Participants in the control group underwent the same test protocol as the prosopagnosic participants including the FEQ. All controls performed within the normal range (not below 2 SDs) on the Cambridge Face Perception Test (Duchaine et al., 2007) and the CFMT, evaluated by the age and gender adjusted norms provided in Bowles et al. (2009). They also performed within the normal range on the Autism-Spectrum Quotient. Controls received gift certificates of ~120 DKK (~20 USD) per hour for their participation.

2.2. Dataset comprising participants with developmental dyslexia and their control participants

All participants were high-school students (Danish: Højere forberedelsesseksamen). For all participants, the inclusion criteria were: a minimum age of 18-years, normal or corrected-to-normal vision, Danish as first language, no autism spectrum disorder, and no known brain damage based on self-report. Some control participants received a gift card of 150 DKK (~22 US Dollars) for their participation. The participants with developmental dyslexia and some controls did not receive remuneration due to school policies.

From a total dataset of 24 participants with developmental dyslexia and 24 controls, we only included the right-handed participants in the present study ($n = 21$ for both developmental dyslexics and controls), as the likelihood of left hemisphere dominance of language decreases for people with mixed- or left-handedness (Gerrits et al., 2019; Knecht et al., 2000). For additional details regarding the full dataset see Kühn et al. (2020).

2.2.1. The group with developmental dyslexia

All 21 right-handed participants (13 females; median age of 19, range 18–22) were from the same high school, enrolled in an educational program designed for people with developmental dyslexia. Presence of developmental dyslexia was officially verified as this was a requirement for attending the educational program. The diagnosis was informed by the official Danish test for dyslexia (Den Nationale Ord-blindtestest (Undervisningsministeriet, 2018) or based on psychological assessment (e.g., by school psychologists). As comorbidity is commonly seen in developmental dyslexia (e.g., Sexton et al., 2012; Willcutt and Pennington, 2000a, 2000b), we did not exclude participants in the developmental dyslexia group if they had other psychiatric diagnoses (other than those with autism). Six of the dyslexic participants reported a psychiatric diagnosis other than autism spectrum disorder. They were not asked to specify the diagnosis or provide more details due to data regulations and ethical protocol.

2.2.2. The control group for the group with developmental dyslexia

In total, 21 right-handed participants (16 females) with a median age of 19 years (range: 18–21), were included. Expanded exclusion criteria for the participants in the control group were developmental dyslexia and a psychiatric diagnosis; again, based on self-report.

2.3. General procedure

The participants with developmental prosopagnosia and their controls were tested individually over at least two test sessions, with the divided visual field task being performed on the second session. The participants with developmental dyslexia and their controls were tested in larger groups during 2018 and 2019. All testing took place in a classroom with two experimenters present. A short oral introduction was given by an experimenter prior to the experiment, and written
instructions were given on the screen as well as read out loud in headphones plugged in each laptop. All participants included here used their right hand for responding (for further information see Kühn et al., 2020).

2.4. The divided visual field task

The divided visual field task was modeled over the divided visual field task developed by (Dundas et al., 2013). This paradigm capitalizes on the lateralization of the visual system where input from the right visual field (RVF) is initially processed by the left hemisphere (LH) and input to the left visual field (LVF) is initially processed by the right hemisphere (RH). When participants fixate their eyes centrally on the screen, a measure of lateralization can be obtained by means of brief exposure durations (below 200 ms) of stimuli in either the right or left side of the visual field, which prevents eye movements to the presented stimuli and thus exposure to the contralateral visual field (Gazzaniga et al., 2015).

Participants were seated centrally in front of the screen and instructed to fixate the cross each time it appeared. Participants were instructed to decide if two succeeding stimuli were the same or different by pressing “1” to indicate “same” or “2” to indicate “different”. The experimental setup was the same for all stimulus types (cars, faces, cropped faces, words). On each trial, a central fixation cross appeared for 2000 ms, followed by a target stimulus shown centrally for 1000 ms. Then a central fixation cross appeared for 300 ms, followed by the second stimulus presented for 150 ms shown randomly to the left or the right side of the central fixation cross. The center of the second stimulus was presented approximately 3.3 degrees of visual angle off screen center and subtended between 3.1 and 6.1 degrees of visual angle in width and 1.9–6.3 degrees of visual angle in height depending on the stimulus category. The participants had 4000 ms to respond but were instructed to respond as quickly and accurately as possible (see Fig. 1). Failure to respond resulted in an invalid trial. There were eight experimental blocks of 40 trials, that is, a total of 320 trials with an equal number of same (40 trials) and different trials (40 trials) for each of the four categories with half presented in each visual field. Stimuli from the different categories were mixed within blocks with small breaks between blocks. Prior to testing, a practice block of 32 trials, with eight items from each category, were run. Stimuli in the practice block were not used during actual testing. Accuracy feedback was given after each trial during the practice session, but no feedback was given during data collection. Both accuracy and reaction time (RT) were measured. For each category in each visual field, the maximum total correct responses was 40. Testing took approximately 30 min.

2.4.1. Stimuli

Four different categories of stimuli were presented: words, full faces, cropped faces and cars. There were 20 different stimuli in each category presented on a white screen. All stimuli were selected in pairs to ensure a high degree of similarity between the two stimuli in each pair, thus 10 stimulus-pairs with high similarity were selected for each category (see examples in Fig. 2). The words consisted of four-letter, regular Danish nouns, where the two words in each word-pair only differed in one of the two central letters (Dundas et al., 2013). Both full faces and cropped faces were black-and-white photographs of male or female faces in a frontal view under the same light settings. Each face in a pair was of the same gender with a high degree of similarity. For full faces both hair and some clothing were visible. To produce the cropped faces, a vertical elliptic crop was imposed on photos of faces to remove hair, ears and chin, and consequently only the internal features of the face were presented. For the last category, cars, black-and-white photographs of real cars were shown, and in each pair the cars were photographed from the same angle.

2.5. Statistical analyses

Invalid trials were not counted in the total score. A trial was considered invalid if a participant failed to respond within a time window of 201–4000 ms following target onset. The mean percentage of invalid responses was 0.8 in the developmental dyslexia group, and 0.4 in its control group. For the developmental prosopagnosic group it was 0.1, and 0.9 in its control group. As stimulus exposure duration was limited in this experiment, we decided a priori to give most weight to results based on accuracy, here d-prime ($d'$), which was calculated for each condition for each participant. $d'$ is a bias-free measure of discrimination sensitivity expressed as a standardized effect size with a high score indicating better sensitivity (e.g., Wickens, 2002). However, in order to present the full picture, analyses were also performed on trimmed latency data. Trimming was done to obtain more stable measures of RT (Ratcliff, 1993) and was based on valid and correct responses only. It was performed by removal of responses that deviated more than 2.5 SD from the mean of a specific participant in a specific condition (e.g., words, left visual field, same response). This resulted in an average of 3.2 percent (range: 0.9–5) removed trials in the developmental prosopagnosic group and 2.9 (range: 0–4.3) in its control group. For the

![Fig. 1. Illustration of the trial structure; here with faces as stimuli. The size proportions of the stimuli relative to the frame are not representative of the actual experiment.](image-url)
developmental dyslexia group the average percent removed trials was 3.2 (range: 1.7–4.7) and 2.7 percent (range: 1.5–3.7) in its control group. Statistical analyses were performed in SPSS version 26. To reduce the impact of outliers and deviation from normality we used t-tests, and 95% CIs, based on bias-corrected bootstrap analyses with 1000 samples. All t-tests were two-sided, and an alpha-level of 0.05 was applied.

In our analyses we did not use the results from the full faces but only those from cropped faces because the studies we will compare our results with used only cropped faces (Collins et al., 2017; Dundas et al., 2013, 2014; Gabay et al., 2017). We also note that of the two face conditions, the condition with cropped faces was judged the most sensitive test of face perception because $d'$ was higher for full faces compared to cropped faces for all four groups (all ps < .001), and because there were more outliers present for full faces than for cropped faces. However, data from the full faces are available in the supplementary material accompanying this paper (https://osf.io/axqgc/).

Fig. 2. Examples of matched stimulus pairs for the divided visual field task for: (a) cars, (b) cropped faces, (c) non-cropped faces, and (d) words.

With respect to the category cars, this was only included because the reference studies included it. Thus, we had no specific hypotheses regarding this category but include the results from it here for completeness.

To test if the lateralization pattern was significantly different between groups for words, cropped faces or cars, we first computed two laterality measures based on difference scores: (i) one based on $d'$ (LVF $d'$ score minus RVF $d'$ score), and (ii) one based on RT (LVF RT minus RVF RT). This was done for each participant and for each category. A value of 0 on these measures will indicate no visual field difference/laterality effect whereas higher values will indicate greater effects of laterality. We then examined whether the two groups – either developmental prosopagnosics vs. controls or developmental dyslexics vs. controls – differed on these laterality measures by means of independent sample t-tests. These analyses amount to testing for the presence of interactions between visual field and group: Only if the lateralization pattern for a given stimulus category differs significantly between groups will the difference be significant. These comparisons are clearly the most important in the present context because it is only interactions that can provide positive evidence regarding lateralization differences across developmental prosopagnosics, developmental dyslexics and controls, cf. section 1.3. For regular mixed factorial ANOVAs with Group (developmental prosopagnosics vs. controls/developmental dyslexics vs. controls) and Visual field (LVF vs. RVF) on data for words and cropped faces, which yield the same results as the analyses presented below, please see the appendix.

The first analyses presented below are thus targeted at between-group differences in the lateralization pattern (interactions). These analyses are supplemented with: (i) analyses of the absolute lateralization patterns within each group, and (ii) between-group differences across visual fields. The interaction analysis is directly relevant for main hypothesis tested, but the supplementary within-group comparisons qualify the interpretation of potential interactions: If the paradigm cannot reproduce the expected visual field effects in the control groups, lateralization differences between groups will be harder to interpret. To anticipate some of the results, such a concern did arise for the stimulus category words, which did not yield the expected RVF advantage in the control groups. We will discuss this anomaly at length in section 4.0.

3. Results

3.1. Developmental prosopagnosia

We found no significant positive correlations (ρ) between RT and $d'$ for any of the stimulus types, computed in each visual field for each of the groups (all $p$’s > 0.05), suggesting no significant trade-offs between latency and discrimination sensitivity. Summarized results for $d'$ and RT for words, cropped faces, and cars in each visual field are presented in Table 1.

3.1.1. Lateralization differences between groups (interaction effects)

The analyses examining whether the individuals with developmental prosopagnosia differed from their controls in lateralization pattern revealed no significant difference for words based on $d'$ (Mean difference = 0.03, 95% CI = [-0.38, 0.36], $p = .89$), but a significant difference for RT (Mean difference = 61, 95% CI = [23, 101], $p = .02$). The RT difference reflected that responses to words were faster in the LVF/LH than in the LVF/RH for the developmental prosopagnosics but the reverse for the control group. There were no significant differences between the two groups for cropped faces on $d'$ (Mean difference = 0.20, 95% CI = [-0.13, 0.55], $p = .24$), or RT (Mean difference = 42, 95% CI = [-15, 101], $p = .21$), or for cars on $d'$ (Mean difference = -0.06, 95% CI = [-0.41, 0.27], $p = .72$), or RT (Mean difference = -35, 95% CI = [-83, 16], $p = .15$). Hence, except for the finding that the group with
developmental prosopagnosia revealed a pattern more towards the expected lateralization pattern for words, no differences were found between the groups in lateralization effects neither in sensitivity nor latency.

3.1.2. Lateralization effects within each group

The results of the within-group supplementary analyses are summarized in Table 2. In the control group, the only significant difference found was for cropped faces in RT, with faster responses to cropped faces presented in the LVF/RH. In the developmental prosopagnosic group, the only significant difference found was also for cropped faces but in terms of \( \Delta t \), with higher discrimination sensitivity to faces presented in the LVF/RH. Thus, each group exhibited the expected lateralization pattern for faces but not for words albeit reflected in different measures. See also Fig. 3 for an illustration of the main results across both developmental prosopagnosics, developmental dyslexics and controls for faces and words.

### Table 1

Results for \( \Delta t \) and reaction time (RT) in ms for each stimulus type in each visual field for individuals with developmental prosopagnosia and their controls.

| Developmental Prosopagnosics | Controls |
|------------------------------|----------|
| **Words LVF** | **Words LVF** |
| \( \Delta t \) | 2.91 | 3.01 |
| RT | 856 | 816 |
| **Words RFV** | **Words RFV** |
| \( \Delta t \) | 3.11 | 3.24 |
| RT | 816 | 837 |
| **Cropped faces LVF** | **Cropped faces LVF** |
| \( \Delta t \) | 1.58 | 1.96 |
| RT | 836 | 825 |
| **Cropped faces RFV** | **Cropped faces RFV** |
| \( \Delta t \) | 1.29 | 1.88 |
| RT | 880 | 911 |
| **Cars LVF** | **Cars LVF** |
| \( \Delta t \) | 1.97 | 2.02 |
| RT | 771 | 841 |
| **Cars RFV** | **Cars RFV** |
| \( \Delta t \) | 2.20 | 2.18 |
| RT | 803 | 838 |

Note. The mean and standard deviation (SD) with bootstrapped bias corrected and accelerated (BCa) 95% CIs listed for \( \Delta t \) and reaction time (RT) for left visual field (LVF) and right visual field (RFV).

### Table 2

Results from the analyses examining within-group lateralization effects for words, cropped faces and cars.

| Mean diff. | S.E. | 95% CI | \( p \) | Mean diff. | S.E. | 95% CI | \( p \) |
|-----------|------|--------|------|-----------|------|--------|------|
| **Developmental prosopagnosics** | | | | **Developmental prosopagnosics** | | | |
| **Words LVF** | | | | **Words LVF** | | | |
| \( \Delta t \) | .2 | .17 | -54.14 | .26 | -23 | .14 | .51 | .06 |
| RT | 39 | 16 | -13.66 | .11 | -21 | 14 | 53 | 8 |
| **Cropped faces LVF** | | | | **Cropped faces LVF** | | | |
| \( \Delta t \) | .28 | .09 | -08.47 | .008 | .08 | .14 | .18 | .34 |
| RT | -43 | 25 | -91.9 | .09 | -86 | 18 | 121 | 49 |
| **Cars LVF** | | | | **Cars LVF** | | | |
| \( \Delta t \) | .23 | .13 | -50.4 | .09 | -16 | .13 | .38 | .05 |
| RT | -32 | 15 | -67.1 | .07 | 3 | 18 | 34 | 39 |

**Developmental dyslexics**

| Mean diff. | S.E. | 95% CI | \( p \) | Mean diff. | S.E. | 95% CI | \( p \) |
|-----------|------|--------|------|-----------|------|--------|------|
| **Words LVF** | | | | **Words LVF** | | | |
| \( \Delta t \) | .01 | .12 | -25.22 | .92 | .11 | .12 | .34 | .14 |
| RT | -40 | 15 | -72.14 | .046 | 4 | 7 | 10 | 18 |
| **Cropped faces LVF** | | | | **Cropped faces LVF** | | | |
| \( \Delta t \) | .32 | .17 | -01.65 | .076 | .40 | .17 | .06 | .72 |
| RT | -70 | 15 | -100.42 | .006 | -37 | 11 | 56 | 19 |
| **Cars LVF** | | | | **Cars LVF** | | | |
| \( \Delta t \) | .37 | .13 | -62.12 | .01 | -16 | .14 | .49 | .14 |
| RT | -10 | 15 | -42.17 | .50 | -12 | 8 | 28 | 5 |

3.1.3. Between-group differences in average performance across visual fields

The results from the supplementary analyses are summarized in Table 3. There were no significant RT differences between the groups for any of the stimulus categories. For \( \Delta t \), there was an effect of group for cropped faces with discrimination sensitivity being lower for the group with developmental prosopagnosia. Hence, as could be expected, the individuals with developmental prosopagnosia performed worse than the controls with faces but not with the other stimulus types.

3.2. Developmental dyslexia

We found no significant positive correlations (\( p \)) between RT and \( \Delta t \) for any of the stimulus types, computed in each visual field for each of the groups (all \( p's > .05 \)), suggesting no significant trade-offs between latency and discrimination sensitivity. Summarized results for \( \Delta t \) and RT for words, cropped faces, and cars for each visual field are presented in
3.2.1. Lateralization differences between groups (interaction effects)

The analyses examining whether the individuals with developmental dyslexia differed from their controls in lateralization pattern revealed no significant difference for words based on $d'$ (Mean difference = 0.10, 95% CI = [-0.23, 0.44], $p = .57$), but a significant difference for RT (Mean difference = -43, 95% CI = [-81, -12], $p = .03$). The RT difference indicated reverse lateralization effects for the two groups with the developmental dyslexics showing an unexpected pattern with faster RT to words presented in the LVF/RH and the controls slightly faster responses to words presented in the RVF/LH. There were no significant differences for cropped faces on $d'$ (Mean difference = -0.08, 95% CI = [-0.56, 0.36], $p = .72$), or RT (Mean difference = -33, 95% CI = [-72, 4], $p = .1$), or for cars on $d'$ (Mean difference = -0.21, 95% CI = [-0.56, 0.18], $p = .3$), or RT (Mean difference = 2, 95% CI = [-40, 36], $p = .92$). Hence, the group with developmental dyslexia revealed an altered pattern of lateralization for words compared with controls, but not for the other stimulus types.

3.2.2. Lateralization effects within groups

The results of the within-group supplementary analyses are summarized in Table 2 and Fig. 3. In the control group, the only significant differences found were for cropped faces for both $d'$ and RT. The results were in the same direction with more efficient processing of faces in LVF/RH than in the RVF/LH.

In the developmental dyslexia group, RTs for cropped faces were significantly faster in the LVF/RH compared to the RVF/LH, and though it did not reach significance ($p = .08$), the difference in $d'$ also indicated better performance in the LVF/RH. For words, a significant difference was found for RT, with faster responses to words presented in the LVF/RH. For cars a significant difference was found for $d'$, indicating that the sensitivity score was higher for cars presented in the RVF/LH than cars presented in the LVF/RH, but RT did not indicate any significant difference.

In sum, both the developmental dyslexics and the controls showed the expected lateralization pattern for faces with more efficient processing in LVF/RH than in the RVF/LH. For words, however, neither group showed the expected RVF/LH advantage. In fact, the
induces a rightward shift in the cerebral areas supporting face recognition (Dundas et al., 2013), and more specifically that acquisition of literacy demand they place on cerebral resources (Behrmann and Plaut, 2020; Collins et al., 2017). This raises the question of whether developmental disorders like developmental prosopagnosia and developmental dyslexia give rise to altered patterns of cerebral organization (Behrmann and Plaut, 2020).

### 4. Discussion

It has been suggested that the degree of lateralization observed in face processing may be a product of competition between abilities in the demand they place on cerebral resources (Behrmann and Plaut, 2020; Dundas et al., 2013), and more specifically that acquisition of literacy induces a rightward shift in the cerebral areas supporting face recognition (Dehaene et al., 2010; Dundas et al., 2013). This raises the question of whether developmental disorders like developmental prosopagnosia and developmental dyslexia give rise to altered patterns of lateralization? According to the many-to-many account (MTMA) of cerebral organization (Behrmann and Plaut, 2020) – which suggests that reading acquisition is a key determinant in lateralization of face processing – the answer is ‘yes’. According to this account we should find no – or at least reduced – right lateralization for face processing in developmental prosopagnosia and no – or at least reduced – lateralization for word and face processing in developmental dyslexia (Behrmann and Plaut, 2020; Collins et al., 2017).

In the present study we tested these rather specific hypotheses in individuals with either developmental prosopagnosia or developmental dyslexia. In the group with developmental prosopagnosia we found no evidence of an altered pattern of lateralization for faces. In fact, both the developmental prosopagnosics and their controls showed the expected left visual field (LVF)/right hemisphere (RH) advantage for face processing, and the magnitude of this difference did not differ between the groups (i.e., there was no significant interaction between VF and group). This replicates, and does so in a positive manner, the finding by Collins et al. (2017) who ‘merely’ found a trend towards a LVF/RH advantage for faces in their group of developmental prosopagnosics. The finding of a LVF/RH advantage for faces within the normal range in developmental prosopagnosia is rather interesting because acquired prosopagnosia is typically associated with RH damage (Rossion, 2014, 2015); presumably because of the RH dominance in face processing in normal subjects. Consequently, if developmental prosopagnosia also primarily reflected a RH anomaly one would expect the normal LVF/RH for face processing to be abolished in developmental prosopagnosia. Given that we do find a LVF/RH advantage in developmental prosopagnosia this could therefore

### Table 3

Results from the between-group differences (developmental prosopagnosics vs. controls & developmental dyslexics vs. controls) in average performance across visual fields for each stimulus type measured by d’ and reaction time (RT) in ms

| Developmental prosopagnosics | Developmental dyslexics |
|------------------------------|-------------------------|
|                              | Mean diff. | S.E. | 95% CI   | p    | Mean diff. | S.E. | 95% CI   | p    |
| Words                        |            |     |          |      |            |     |          |      |
| d’                           | -.22       | .21 | -.62 : -.21 | .32 | -.38       | .20 | -.77 : .01 | .07 |
| RT                           | 9          | 46  | -.71 : 107 | .84 | 115        | 38  | 44 : 187 | .008 |
| Cropped faces                |            |     |          |      |            |     |          |      |
| d’                           | -.52       | .18 | -.85 : .16 | .008 | -.28       | .20 | -.64 : .17 | .16 |
| RT                           | -9         | 49  | -.101 : .88 | .86 | -.68       | .36 | -.4 : 138 | .06 |
| Cars                         |            |     |          |      |            |     |          |      |
| d’                           | .04        | .18 | -.35 : .36 | .84 | -.14       | .19 | -.51 : .21 | .45 |
| RT                           | -53        | 43  | -.137 : .35 | .24 | 73         | 38  | -.5 : 145 | .06 |

Note. The mean difference (Mean diff.), standard error (S.E.), bootstrapped bias corrected and accelerated (BCa) 95% CIs, and p-value (p) for the two-tailed bootstrapped paired t-test. Significant effects (p < .05) are given in bold.

### Table 4

Results for d’ and reaction time (RT) in ms for each stimulus type in each visual field for the individuals with developmental dyslexia and their controls

| Developmental dyslexics | Controls |
|-------------------------|----------|
|                         | Mean     | BCa 95% CI | SD | BCa 95% CI | Mean | BCa 95% CI | SD | BCa 95% CI |
| Words LVF               |          |            |    |            |      |            |    |            |
| d’                      | 2.58     | 2.27 : 2.92 | 0.75 | 0.57 : 0.86 | 2.90 | 2.63 : 3.12 | 0.62 | 0.42 : 0.77 |
| RT                      | 7.30     | 674 : 792 | 134 | 85 : 175 | 637 | 602 : 673 | 85 | 62 : 102 |
| Words RVF               |          |            |    |            |      |            |    |            |
| d’                      | 2.60     | 2.38 : 2.83 | 0.53 | 0.39 : 0.62 | 3.01 | 2.75 : 3.25 | 0.64 | 0.44 : 0.78 |
| RT                      | 7.69     | 696 : 853 | 176 | 98 : 243 | 634 | 603 : 668 | 78 | 66 : 85 |
| Cropped faces LVF       |          |            |    |            |      |            |    |            |
| d’                      | 2.05     | 1.79 : 2.36 | 0.72 | 0.53 : 0.86 | 2.39 | 2.11 : 2.68 | 0.73 | 0.56 : 0.84 |
| RT                      | 6.96     | 655 : 740 | 109 | 66 : 140 | 644 | 602 : 688 | 117 | 59 : 156 |
| Cropped faces RVF       |          |            |    |            |      |            |    |            |
| d’                      | 1.73     | 1.37 : 2.11 | 0.84 | 0.66 : 0.97 | 1.99 | 1.78 : 2.19 | 0.54 | 0.42 : 0.63 |
| RT                      | 7.66     | 714 : 825 | 145 | 91 : 184 | 681 | 642 : 720 | 104 | 73 : 123 |
| Cars LVF                |          |            |    |            |      |            |    |            |
| d’                      | 1.96     | 1.67 : 2.25 | 0.64 | 0.46 : 0.80 | 2.18 | 1.93 : 2.44 | 0.58 | 0.44 : 0.67 |
| RT                      | 7.10     | 662 : 761 | 116 | 78 : 145 | 636 | 588 : 687 | 119 | 82 : 144 |
| Cars RVF                |          |            |    |            |      |            |    |            |
| d’                      | 2.32     | 2.07 : 2.60 | 0.60 | 0.43 : 0.71 | 2.34 | 2.03 : 2.71 | 0.70 | 0.45 : 0.86 |
| RT                      | 7.19     | 670 : 773 | 130 | 71 : 165 | 647 | 604 : 694 | 115 | 71 : 144 |

Note. The mean and standard deviation (SD) with bootstrapped bias corrected and accelerated (BCa) 95% CIs listed for d’ and reaction time (RT) for left visual field (LVF) and right visual field (RVF).
indicate LH anomalies in developmental prosopagnosia. This is supported by a recent functional imaging study that indicated greater left than right hemisphere abnormalities in developmental prosopagnosia (Gerlach et al., 2019). It must be noted that this piece of converging evidence needs qualification given that some of the developmental prosopagnosics examined in the present study also participated in the functional imaging study. However, when these nine individuals are removed from the present analysis, we still find a reliable LVF/RH advantage in the remaining 12 individuals (Mean d’ LVF-RVF difference = 0.4, 95% CI = [0.13, 0.65]). Consequently, the effect is not driven by the subset of developmental prosopagnosics who also participated in the imaging experiment. With respect to the group with developmental dyslexia, we did not find an altered lateralization for faces, contrary to the prediction of the MTMA. Just like the developmental prosopagnosics, the developmental dyslexics also showed a significant LVF/RH advantage for faces, and of a magnitude within the normal range (for a similar finding in dyslexic children see Pirozzolo and Rayner (1979)). It is important to note that this is not merely a null finding. Both the dyslexics and the controls showed a LVF/RH advantage for faces, and this advantage was numerically larger for the developmental dyslexics than for the controls (in terms of RT). This suggests that the LVF/RH advantage in face processing is not contingent on reading related functional restructuring of the LH.

Finally – and again in contrast to the predictions of the MTMA – we did not find equally (in)efficient processing of words if the LVF and RVF in the group with developmental dyslexia. Rather, the developmental dyslexics showed more lateralization than the controls in word processing, but in the opposite direction where word processing was more efficient in the LVF/RH than in the right visual field (RVF)/left hemisphere (LH). We note, however, that this finding was not based on our primary measure d’ but rather on latency (RT), and it departs from previous findings of a normal RVF advantage (Collins et al., 2017) or no visual field differences for words in the developmental dyslexia (Gabay et al., 2017). Moreover, we failed to find the normal RVF/LH advantage for words in the control group, which we will discuss further below. For these reasons, the present finding of a significant LVF/RH advantage for words in developmental dyslexia should be treated carefully. Despite these reservations the finding does seem compatible with a meta-analysis showing decreased activation in left hemisphere regions supporting visual word recognition in developmental dyslexia (Richlan et al., 2011).

Our failure to find a significant RVF/LH advantage for words in the two independent groups of controls contrasts with the earlier studies using the same paradigm (Collins et al., 2017; Dundas et al., 2013, 2014; Gabay et al., 2017). Only when the data from our two control groups are pooled do we find a marginally significant difference in the expected direction for discrimination sensitivity (d’) (Mean difference = –.17, 95% CI = [–.35, 0.01], p = .065) but not for RT (Mean difference = –9, 95% CI = [–26, 9], p = .32). One aspect that differs between the present and previous studies is that the previous studies (Collins et al., 2017; Dundas et al., 2013, 2014; Gabay et al., 2017) presented the stimuli at greater eccentricity (5.3° from fixation) than the present study (3.3° from fixation). It is not the case, however, that the word stimuli in the present study were presented partly in foveal vision as they subtended 3.1° of visual angle and did not differ in the first and last letter position. In fact, only the car stimuli extended somewhat into foveal vision (1.5°). However, lack of a RVF/LH advantage for words does not reflect that the stimuli in general were presented too near central vision to produce effects of lateralization per se. Indeed, we obtained clear and expected lateral effects for the face stimuli. We do think, however, that the lower eccentricity of the present study may have caused discrimination to be easier here than it was in the previous studies (Collins et al., 2017; Dundas et al., 2013, 2014; Gabay et al., 2017). In the previous studies, that did report the expected RVF/LH advantage for words, the accuracy was in the range of 82–88% correct responses. In comparison, the range was 92–93% for our groups except for the developmental dyslexics whose accuracy was on average 88% correct. Consequently, the word condition may have been too easy for the control participants to reveal an effect of visual field. As an example, the magnitude of the RVF/LH for word processing increases with word length (Chiarello, 1988) and the present words were only four letters. It must be noted, however, that even if it is true that the present word condition was too easy to reveal the normal RVF/LH advantage this has no direct bearing on the positive findings we report; the LVF/RH advantage for words in the group with developmental dyslexia. This might have become more pronounced with a more sensitive design that could have picked up the expected RVF/LH advantage for words in the control participants.

In conclusion, the findings from the present study of lateralization effects in developmental prosopagnosia and developmental prosopagnosia do not support the part of the MTMA that assumes that lateralization of face processing is induced by acquisition of literacy. Nor do we find evidence for the proposition that developmental prosopagnosia is associated with altered lateralization of face processing. These findings are in keeping with a recent in-depth study which suggests that there is little evidence in favor of an interdependency between the acquisition of reading skills and lateralization of face recognition (Ross and Lochy, 2021).

Credit author statement

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Declaration of competing interest

None.

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Appendix A. Supplementary data

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