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Atypical reliance on monocular visual pathway for face and word recognition in developmental dyslexia

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ABSTRACT

Studies with individuals with developmental dyslexia (DD) have documented impaired perception of words and faces, both of which are domains of visual expertise for human adults. In this study, we examined a possible mechanism that might be associated with the impaired acquisition of visual expertise for words and faces in DD, namely, the atypical engagement of the monocular visual pathway. Participants with DD and typical readers (TR) judged whether a pair of sequentially presented unfamiliar faces or nonwords were the same or different, and the pair of stimuli were displayed in an eye-specific fashion using a stereoscope. Based on evidence of greater reliance on subcortical structures early in development, we predicted differences between the groups in the engagement of lower (monocular) versus higher (binocular) regions of the visual pathways. Whereas the TR group showed a monocular advantage for both stimulus types, the DD participants evinced a monocular advantage for faces and words that was much greater than that measured in the TRs. These findings indicate that the DD individuals have enhanced subcortical engagement and that this might arise from the failure to fine-tune cortical correlates mediating the discrimination of homogeneous exemplars in domains of expertise.

1. Introduction

Developmental dyslexia (DD) is the most common childhood learning disorder, and, is defined, in the DSM5 manual, as a "specific language disorder" which impedes the acquisition of reading, writing, and spelling skills (American Psychiatric Association, 2013). The most common features of DD typically include phonological impairments, slowed lexical retrieval, and naming deficits (Vellutino et al., 2004). However, there is also evidence of additional, non-linguistic impairments in DD, including, but not limited to, procedural learning (Lum et al., 2013), statistical (Beach et al., 2022; Gabay et al., 2015) and motor learning (Stoodley et al., 2006) and temporal processing (Farmer & Klein, 1995; Gabay et al., 2019). A further domain in which deficits have been identified in DD is in the visual perception of word forms and this impairment is increasingly considered to significantly contribute to the reading difficulties of DD.

1.1. Deficits in face perception in DD

Given that the visual deficit in DD is considered to affect word reading primarily, perhaps surprisingly, individuals with DD appear to have difficulty in processing stimuli from another visual class with which humans have expertise, namely face recognition. Although some studies have reported intact face processing in individuals with DD (Brachacki et al., 1994; Holmes & McKeever, 1979; Rüsseler et al., 2003; Smith-Spark & Moore, 2009), many other, more recent findings, acquired over multiple different experimental paradigms, have documented deficient face perception in this population (Collins, Dundas, Gabay, Plaut, & Behrmann, 2017a; Gabay, Dundas, Plaut, & Behrmann, 2017; Sigurdardottir, Hjartarson, Gudmundsson, & Kristjánsson, 2019; Sigurdardottir, Ívarsson, Kristinsdóttir, & Kristjánsson, 2015). For example, DD individuals performed more poorly than controls in the recognition of faces (Tarkiainen et al., 2003) and, relative to controls, were disproportionately slowed in matching faces when the faces

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differed in viewpoint (Gabay et al., 2017), though they performed similarly to controls when matching upright target faces with inverted test faces (Gabay et al., 2017; Sigurdardottir et al., 2015). Also, Smith-Spark & Moore (2009) showed that typically developing readers (TR) were faster at naming famous faces which were learned earlier, rather than later, in life but that this was not so for the DD readers, suggesting that the differential impact of visual processing of faces on DD may have been present early in life perhaps even prior to the acquisition of literacy.

Faces, like words, are visual stimuli with which human adults have expertise, and individuals with DD appear to have deficits in both domains. In one experiment in which both face and word perception was assessed within the same participants, DD participants performed significantly more poorly in discriminating between words and between faces, relative to TR participants (Gabay et al., 2017). Notably, the DD group performed equivalently to the TR group in discriminating between cars which, for the majority of the population, is not a domain of expertise and, critically, this result indicates that the visual deficit in DD is not a failure in perception across-the-board. Moreover, recent investigations have indicated that there may be a relationship between word and face perception as the extent of the difficulty in matching faces can predict the presence of dyslexia and reading problems (Sigurdardottir et al., 2018; Sigurdardottir et al., 2021). The claim that individuals with DD experience visual deficits in, for example, visuomotor, visuospatial, and visual motion processing, has also been raised and appears to be increasingly supported by additional evidence (Eden et al.,

One possible account of the joint deficit in word and face recognition is that individuals with DD might not learn from their perceptual experience to the same extent as TD, and that this is exaggerated when within-class representations are homogeneous (Gabay & Holt, 2015; Nicolson & Fawcett, 2007, 2011; Sigurdardottir et al., 2018). This hypothesis is bolstered by evidence showing that, relative to matched TRs, individuals with DD experience difficulty learning a visual texture discrimination task and extracting regularities from related perceptual tasks (Ballan et al., 2022; Kligler & Gabay, 2023; Kligler et al., 2023; Lieder et al., 2019; Wang et al., 2014; Wang et al., 2019). Those with DD also show difficulties in learning complex multidimensional categories in which the rule for categorization is not explicitly stated (Gabay et al., 2023; Sperling et al., 2004) despite their having intact perceptual abilities (Gabay et al., 2023). Perceptual expertise, or the reduction thereof, has also been found to predict reading in dyslexic readers of Chinese, a non-alphabetical language (Wong et al., 2021). Together, these findings suggest that word and face processing deficits among participants with DD might reflect a more general difficulty in acquiring perceptual expertise.

The behavioral differences between DD and TR groups are mirrored by alterations at the neural level, as reflected in reports of structural and functional dissimilarities in many cortical regions, including in visual cortex (for a discussion see Sigurdardottir et al., 2018; Sigurdardottir et al., 2021). For example, there is a delay in the development of structures mediating phonological representations, such as the bilateral superior temporal gyri, left middle temporal gyrus, right insula and right frontal cortex in children with a reading deficit relative to TR children (Chyl et al., 2019). Of particular relevance, altered connectivity between the left inferior parietal lobule and the visual word form area during print processing is evident in DD but not in age-matched or reading-level

matched TRs (Di Pietro et al., 2023). Also, in those with a family history of DD, there is atypical functional connectivity evident early in development between regions that are important for subsequent word form recognition (Yu et al., 2022; but see review by Ramus et al., 2018, on inconsistencies and methodological difficulties in some of the imaging studies). Rather few studies, however, have examined the behavior and neural correlates of both face and word recognition in the same DD individuals relative to their TR counterparts. In one such illustrative study, in addition to performing more poorly on tasks with both stimulus classes, relative to TR, the DD group evinced neither the normal ERP pattern of right hemisphere (RH) dominance for faces nor the normal ERP pattern of left hemisphere (LH) dominance for words, implicating widespread alteration of lateralized posterior neural circuitry in DD (Collins et al., 2017a). Last, MRI studies have also revealed altered activity and functional connectivity within a left fronto-temporo-parietal network in DD (e.g., Finn et al., 2014; Norton et al., 2015; Richlan, 2012; Richlan et al., 2011; Schurz et al., 2015; Shaywitz et al., 2002), along with structural abnormalities in the ventral visual pathway (Klingberg et al., 2000; Kristjansson & Sigurdardottir, 2023).

1.2. Potential subcortical mechanism in DD

The hypothesis we consider here is that, in DD, the difficulty in acquiring perceptual expertise, for example, for face and word processing might result from difficulty developing the necessary cortical underpinning and the undue reliance, then, on subcortical processing. One well-established claim is that, in babies and young children, subcortical structures, such as the superior colliculus, the pulvinar and the amygdala, process visual input primarily on the basis of low spatial frequency information, and gradually bootstrap cortex until the cortical computations are well consolidated (Johnson, 2005; Johnson et al., 2015). Mid- and high-spatial-frequencies such as those required for discriminating individual exemplars of faces and words are then primarily under the purview of the cortical computations. As recognition and categorization become efficient and expertise is gained, a large network of cortical regions is invoked (Fiez & Petersen, 1998). This same subcortical-cortical interactivity may continue to mature through adolescence (Cunningham et al., 2002), and may even continue to operate into adulthood for some processes such as computing coarse numerosity (see also Collins, Park, et al., 2017). A disturbance of the emergence of a cortical route from subcortical functions has already been proposed as an account for observed deficits in some developmental disorders, such as developmental prosopagnosia (Johnson, 2005), and this same account might extend to DD, as well.

Here, we evaluate whether, in adults with DD, there is an excessive reliance on subcortical processing of faces and words, and, thus, an atypical subcortical versus cortical profile. Because neuroimaging techniques are limited in their ability to measure data from subcortical structures, which are small and located deep in the brain (Liu et al., 2002; Mulert et al., 2004; Petersson et al., 1999), it has been difficult to examine the proposed subcortical-cortical dynamics and to characterize possible alterations of this subcortical-cortical coupling in DD. We have, therefore, adopted a behavioral paradigm that permits the dissociation between subcortical and cortical processing.

1.3. Our approach

To examine the contribution of subcortical versus cortical structures in DD versus matched TR controls, we examined the integrity of the monocular (subcortical and prestriate with some monocular neurons in V1; Bi et al., 2011) versus binocular (cortical) parts of the visual system. In the human visual system, as depicted in Fig. 1, there is monocular segregation of input until the signals reach binocular striate neurons (Menon et al., 1997). Thus, subcortical regions are eye-dependent while higher cortical regions are largely insensitive to the eye-of-origin of the visual information. By using a stereoscope that permits the presentation

¹ It may be surprising that DD individuals performed similarly to TR controls when matching upright target faces and inverted test faces when they appear to have a deficit in face perception more generally. One possible explanation is that, under these conditions, the matching is done in a featural rather than a holistic or configural fashion. This suggestion is also plausible given that inverted face matching is generally considered to be accomplished in a featural fashion (but see Tso et al., 2020, 2021; Sigurdardottir et al., 2021).

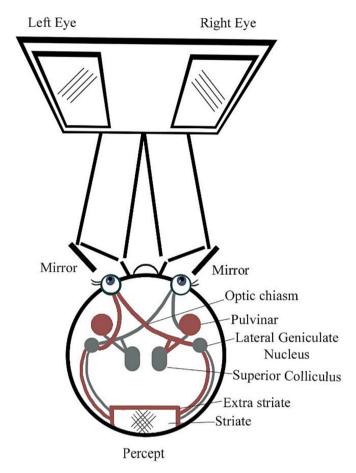


Fig. 1. Schematic diagram of stereoscope and stimulus presentation. Each screen presents visual information (reflected by a mirror) to a different eye. From the eye, the visual information passes through monocularly segregated subcortical regions, such as the Lateral Geniculate Nucleus and Pulvinar, and is subsequently propagated to binocular visual cortex neurons.

of visual input limited to a single eye (see Fig. 1), the involvement of monocular subcortical versus binocular cortical systems can be determined.

The logic of the approach is as follows: in a single trial, a stimulus, for example, a word or a face, is presented to one eye. Immediately thereafter, a second stimulus is presented either to the same eye or to the other eye. The participant perceives both the first and second stimuli as being presented in central vision. The participant is required to make same/different judgements across the two stimuli. If judgements are better when the second stimulus is presented to the same eye as the first stimulus, compared with when the second stimulus is presented to the other eye, one can infer that there is facilitation along the monocular visual pathway (both stimuli are present in same 'channel'). This procedure and approach have been used successfully to reveal monocular facilitation for face and object recognition in prior research (Gabay, Burlingham, et al., 2014; Leadner et al., 2022; Mozes & Gabay, 2022).

2. Methods

2.1. Participants

The participants were 40 college-age students, 20 individuals with DD (10 males and 10 females, mean age; 25.24), and 20 TR (10 males and 10 females, mean age; 25.05). This sample size is similar to that in prior studies that examine special populations (Bertoni et al., 2021; Gabay et al., 2017; Gabay et al., 2015; Meng et al., 2022). The sample size is also equivalent to that of prior research that examined the

manipulation of stereoscopic presentation on other cognitive processes (e.g., executive functions) in special populations (Peskin et al., 2020). Previous studies examining the manipulation of stereoscopic presentation on typical and special populations revealed medium to large effects sizes (i.e., $\eta p2 = 0.47/0.11$) (Gabay, Nestor, et al., 2014; Peskin et al., 2020). A post-hoc power analysis in G*power indicated that with a sample size of 40 participants, our omnibus ANOVA could detect moderate effect size (f = 0.33) with power = 0.98.

All participants were native speakers of Hebrew with no history of neurological disorders, psychiatric disorders, or attention deficits (according to the criteria of the American Psychiatric Association, 2013). In addition, all participants had normal or corrected-to normal vision. The DD group was recruited from the Yael Learning Disabilities Center at the University of Haifa, Israel. The inclusion criteria for the dyslexia group was (1) a formal diagnosis from a licensed clinician; (2) no formal diagnosis of attention deficit hyperactivity disorder (ADHD) or a developmental language disorder; (3) a score below a 1SD local norm cut-off for phonological decoding (Yael et al., 2015); (4) cognitive ability scores within the normal range, with a scaled score of 7 or above in Similarities and Block Design subtests from the Wechsler Adult Intelligence test (Wechsler, 1997).

The control group consisted of individuals with no reading problems (i.e., were above the local norm cut-off of phonological decoding) and the same level of cognitive ability (i.e., reaching a scaled score of 7 or above in Similarities and Block Design subtests from the Wechsler Adult Intelligence Scale; Wechsler, 1997). Participants were compensated for their role in the study by payment. Written informed consent was obtained from all participants. The study was approved by the faculty of education ethics committee at the University of Haifa.

2.2. Cognitive and literacy measures

As described below, all participants completed a battery of tests assessing language skills and overall cognitive status. This testing was conducted to confirm the status of the DD group as differing in reading and phonological skills from the TR group but not differing in attention or cognitive abilities (potentially alternative interpretations for any group differences that we might find; see Goswami & Bryant, 1989). We also correlated the scores from these standardized tests with performance on the key experimental variables to determine whether specific subtests such as Digit Span or Attentional function might predict performance on the exaggerated monocular advantage for face and/or word perception (see Results section).

Oral word letter decoding was examined by the One-Minute Test of Words (Shatil, 1997) and the One-Minute Test of Nonwords (Shatil, 1995), which assess the number of words and nonwords read aloud accurately within 1 min. The One-Minute Test of Words contains 168 nonvowelized Hebrew words of an equivalent level of difficulty, listed in columns, ranging from high to low lexical frequency. The One-Minute Test of Non-Words assesses participants' ability to read nonwords varying in complexity, with a maximum raw score of 45. Both accuracy and speed were examined.

Naming skills was assessed through the Rapid Naming Test (RAN; Breznitz, 2003) using colors, objects, numbers and letters. Participants were required to name aloud visually presented items as rapidly as possible. The exemplars are drawn from a constant category (RAN colors, RAN categories, RAN numerals, and RAN letters). This requires retrieval of a familiar phonological code for each stimulus and coordination of phonological and visual (color) or orthographic (letters) information.

Phonological processing was assessed by; (1) the Phoneme Deletion Test (Breznitz & Misra, 2003) which consists of 25 words. The experimenter reads a word and a phoneme aloud, and the participant reported the word after deletion of this phoneme, as fast and as accurately as possible. Accuracy and response speed were measured. (2) Phoneme segmentation test (Breznitz & Misra, 2003), which assesses the

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participant's ability to break a word into its component phonemes. For example, the syllable 'ko' has two phonemes /k//o/. (3) Spoonerism Task (modeled after Brunswick et al., 1999), in which participants were required to switch the first syllables of two word-pairs and then synthesize the segments to provide new words.

Verbal working memory was assessed by the Digit Span subtest from the Wechsler Adult Intelligence Scale (Wechsler, 1997). In this task, participants were required to recall the names of digits presented auditorily in the order of presentation. Task administration discontinued after a failure to recall two trials with a similar length of digits.

Intellectual ability was assessed by means of three subtests from the Wechsler Adult Intelligence Scale (Wechsler, 1997) and the Raven test. Verbal intelligence was assessed by the Similarities subtest. This test requires participants to indicate the semantic similarity of 19 pairs of words (e.g., dog/cat). Task administration is discontinued when a participant fails to provide the correct answer on four consecutive pairs.

Nonverbal intelligence was measured by; (1) the Block Design subtest, in which participants were required to rearrange blocks with different color patterns according to a stimulus presented to them on a card. (2) Raven's Progressive Matrices (RPM) (Raven & Court, 1998), in which participants were required to choose an item from the bottom of the figure that would complete the pattern at the top of an image.

Attentional functions measured by the Adult ADHD Self-Report Scale (ASRS) measure (Konfortes, 2010). The self-report contains an 18-item questionnaire based on the DSM-IV criterion for identifying ADHD in adults. The questions refer to the past 6 months. The ASRS measure is rated on a scale ranging from 0 to 4 (very often = 5 points, often = 4 points, sometimes = 3 points, rarely = 2 points, never = 1 point). A total score of over 51 points is used to identify ADHD.

The results of these tests, evaluated statistically using t-tests for independent samples (with Cohen's d), showed no difference between the groups on age, intelligence, or digit span. However, the DD group differed significantly from the TR control group on word reading and decoding skills, consistent with the symptomatology of DD (see Table 1).

Digit span and similarities subtests represent standardized scores with accuracy as the primary measure. Block design also reflects standardized scores, but performance is computed based on both accuracy and speed. All other tests represent raw scores.

2.3. Stimuli

Twenty-four male and 24 female face images, obtained from the Face-Place Database Project (Copyright 2008, Dr. M. Tarr, wiki.cnbc. cmu.edu/Face_Place), were used in the experiments. All images displayed frontal views of faces with neutral emotional expression. The faces were cropped to remove hair cues and were presented in grayscale against a black background. Face stimuli were 8° in height and 6° in width. The nonwords consisted of 48 four-letter strings in Hebrew (24 pairs) presented in white Times New Roman font against a black background, approximately 2° in height and 5.5° in width. The words, which served as a basis for creating the nonwords, were of high frequency and taken from Henik et al. (2005). Pseudowords were created by changing 1-2 letters of each word. For both words and faces, each pair was matched for brightness. Participants responded by pressing the "P" and "Q" buttons of a keyboard using the right and left index fingers for "same" and "different" trials. Faces and nonwords trials were presented in different blocks.

2.4. Procedure

In the experimental paradigm, participants were seated approximately 30 cm in front of a computer screen with a chin rest used to stabilize the head. The computer monitor was positioned 57 cm in front of a stereoscope (modeled ScreenScope LCD SA200LCD) so that the direct view of the monitor was blocked (see Fig. 1). Each eye could only view half of the screen. Before testing, in order to determine whether participants experienced a well-fused percept, a calibration process was administered. Initially, two rectangles were presented each to a different eve. Participants were asked whether they saw a single rectangle or two overlapping rectangles when looking through the stereoscope (note that two rectangles were presented throughout the task and all stimuli were presented inside those rectangles to ensure sustained calibration). If participants did not report seeing a single rectangle, the stereoscope was calibrated until this was so. Afterwards, participants were instructed to close one eye (this was done for each eye separately) and asked whether they saw a full rectangle (to make sure that the visual display was full for each eye separately). If participants reported seeing only a part of the

 Table 1

 Performance of the developmental dyslexia (DD) and typical readers (TR) on psychometric measures.

Measurement	TR	DD	T	P	Cohen's d
Age	24.57 (2.92)	25.15 (3.11)	-0.610	ns	0.19
Oral word letter decoding					
Oral words recognition speed	110.71 (29.98)	76.55 (25.45)	3.920	< 0.001	1.23
Oral words recognition accuracy	115.9 (16.99)	74.7 (20.75)	6.960	< 0.001	2.17
Oral non-words recognition speed	66.95 (10.59)	41.05 (13.69)	6.790	< 0.001	2.11
Oral non-words recognition accuracy	60.42 (10.56)	24.7 (9.52)	11.350	< 0.001	3.55
Rapid naming measures					
Naming letters speed	21.9 (2.49)	26.3 (3.89)	4.150	< 0.001	1.35
Naming numbers speed	17.6 (2.31)	22.0 (2.87)	5.26	< 0.001	1.68
Naming objects speed	33.15 (5.32)	40.35 (8.36)	3.160	< 0.05	5.3
Naming colors speed	29.28(5.82)	32.75 (5.59)	1.890	ns	0.61
Phonological processing					
Phoneme deletion accuracy	22.61 (3.85)	19.85 (4.19)	2.200	< 0.05	0.68
Phoneme deletion speed	102.45 (31.48)	177.6 (43.84)	6.070	< 0.001	1.96
Phoneme segmentation speed	70.25 (11.20)	134.3 (51.15)	5.330	< 0.001	1.73
Phoneme segmentation accuracy	15.15 (0.85)	11.2 (4.03)	4.170	< 0.001	1.36
Spoonerism speed	118.65 (29.08)	274.9(116.44)	6.000	< 0.001	1.84
Spoonerism accuracy	18.57(1.40)	15.6 (4.24)	3.460	< 0.05	0.94
Verbal working memory					
Digit span	11.47 (3.79)	10.35 (3.41)	1.650	ns	0.51
Intellectual ability					
Similarities (verbal intelligence)	12 (2.48)	11.85 (4.01)	0.440	ns	0.13
Block design (nonverbal intelligence)	12.95 (8.49)	12.9 (12.06)	0.610	ns	0.19
Raven	54.47(3.45)	53.57(4.21)	0.720	ns	0.23
Attentional functions					
ASRS	35.23(7.11)	31.75 (8.68)	1.370	ns	0.43

Note. ns indicates nonsignificant. Groups' standard deviation is the parenthesis.

rectangle at any of the eyes, the stereoscope was re-calibrated until the full rectangle was perceptible.

Under this arrangement, in a single trial, two stimuli could be presented in succession to the same side of the screen i.e., to the same eye (monocularly), or each of the two stimuli could be presented in different screen locations, i.e., to two different eyes (dichoptic/binocularly). A trial started with the appearance of a fixation cross (0.5°) for 1000 msec visible to both eyes. The first stimulus image appeared for 1000 msec followed by 1000 msec fixation and, thereafter, the second image appeared for 1000 msec (see Fig. 2).

The two sequential stimuli were either two unknown faces (front views, neutral expressions) or two unknown words (i.e., nonwords) (in Hebrew), and participants judged whether the two stimuli were the same or different (see Fig. 2B). Half the pairs were of identical images ("same" image match condition), whereas the remaining half were of different images ("different" image match condition). This same/ different image factor was orthogonally crossed with same/different eyes: on half the trials, both images were presented to the same eye, and on the other half, each image was presented to a different eve and these trial types were randomized in a block. For each visual category (faces, nonwords), participants completed two blocks of trials with each block comprising 96 trials (24 trials for same/differentresponse × same-/ different-eye presentation). The order of the blocks was counterbalanced across participants. Participants were instructed to respond after the presentation of the second image as quickly and as accurately as possible. Responses were made via two button presses, and accuracy and reaction time (RT) were measured. Each block began with 16 practice trials, and feedback was given: If no response was provided within 2500 msec or a wrong response was delivered, "incorrect response" appeared on the screen providing feedback for 1500 msec. If a correct response was given, "correct response" appeared. During the test phase, no feedback was provided.

3. Results

3.1. Statistical analysis

We employed RT as the dependent variable in the following analyses since accuracy rates were relatively high for both groups (averages: 93% among TR and 92% among DD). The perhaps surprisingly high accuracy of the DD group may have occurred as the words were both short and relatively common and that just a single item appeared on the screen at any one time. We specifically chose these experimental parameters to yield roughly equivalent accuracy across the two groups and to ensure roughly equivalent numbers of correct trials for RT analysis in both groups. Most studies adopting this paradigm have used RT as the dependent measure (or inverse efficiency which includes RT; Collins, Dundas, Gabay, Plaut, & Behrmann, 2017a; Gabay, Nestor, Dundas, & Behrmann, 2014). Only trials in which participants responded correctly were included in the RT analyses. Trials on which RT exceeded +/-2.5 standard deviations (per participant and experimental condition) from the subjects' mean RT were excluded from the analyses. This led to the removal of approximately 2.5 % of the data for each group.

For full evaluation of all the data, a four-way repeated measures

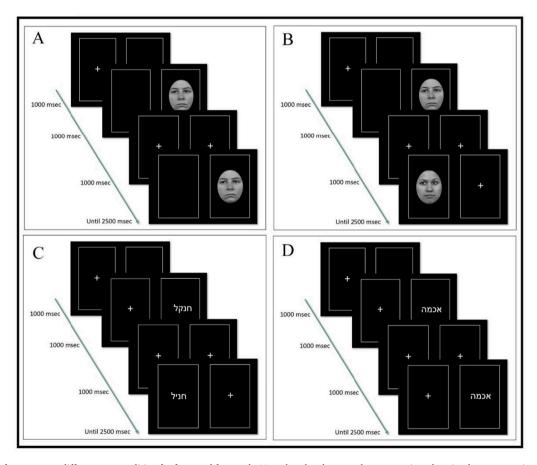


Fig. 2. Examples of same versus different eye condition for faces and for words. Note that the observer always perceives the stimulus as appearing in the center of the screen. A. Example of the same eye condition (two faces in same monocular pathway), and same image condition (the same faces were presented one after the other). B. Example of the different eye condition (different faces are presented to two, different monocular pathways, and different image condition. C. Example of the same eye condition (same monocular neural channels are exposed to the non-word), and same ID condition (the same non-word was presented one after the other). D. Example of the different eye condition (different monocular neural channels are exposed to the non-word), and different ID condition (different non-words were presented one after the other).

omnibus ANOVA was conducted with Group (TR/DD) as the between-subjects variable, and Stimulus (faces/words), Eye (same/different eye), and Image Match (IM: same/different stimuli), as within-subject factors using RT as the dependent variable. A main effect of Stimulus was found [$F(1,38)=13.1, p=.001, \eta p^2=.26$] with faster RTs for words than faces. There was also a significant main effect of Eye [$F(1,38)=26.9, p=.00, \eta_p 2=0.46$] with faster RTs when the two stimuli were shown to the same versus different eye condition. This monocular advantage is consistent with the engagement of the monocular portion of the visual stream, attesting to the viability of the current paradigm with these groups of individuals and replicating previous findings with typical readers (Gabay, Burlingham, et al., 2014; Gabay, Nestor, et al., 2014). The main effect of IM was also significant with faster responses when the same images were displayed compared with when two different images were displayed [$F(1,38)=21.1, p=.000, \eta_p^2=0.36$].

There was a significant interaction of Eye and Group $[F(1,38) = 7.6, p=.000, \eta_p^2 = 0.21]$ which we discuss further below, and the three-way interaction between Stimulus, Eye and IM was also significant $[F(1,38) = 7.06, p=.011, \eta_p 2=0.15]$. As shown in Fig. 3, collapsed across Group, for faces, the interaction between Eye and IM was significant $[F(1,38) = 21.6, =.000, \eta_p^2 = 0.39]$: for the same IM condition, RTs were 60 ms faster for the same eye over different eyes $[F(1,38) = 31.11, p=.000, \eta_p 2=0.45]$ (double facilitation from same stimulus and same eye) but this comparison was not significant for the different IM condition [F < 1]. For words, the interaction between same/different eye and same/different IM was not significant $[F(1,38) = 2.49, p=.122, \eta_p 2 = 0.04]$.

More relevant for the present study are interactions involving the variable of Group. The three-way interaction between Group, Eye and IM was also significant [F (1,38)=4.38, p=.043, η_p 2=0.1. As evident from Fig. 4, there was no interaction between Group and Eye for the different IM condition [F (1,38)=0.24, p=.62, η_p 2=0.01]. In contrast, there was a significant two-way interaction between Group and Eye [F (1,38)=7.6, p=.008, η_p 2 = 0.16]. For the same IM condition: there was a greater advantage for same versus different eyes (monocular benefit) for DD compared to TR (mirroring the result above with facilitation from same vs different eye and same versus different image) although both groups showed a significant monocular advantage collapsed over stimulus [F (1,38)=5.44, p=.024, η_p 2=0.0; F (1, 38)=47.24, P=.00, η_p 2=

0.59; for the TR and DD groups respectively].

The four-way interaction was not statistically significant $[F(1,38)=0.25,\,p=.623,\,\eta_p^{\,2}=0.0]$ (for full ANOVA results and graph, see Supplementary materials). Because performance differed as a function of whether the two images were matched or not (this distinction was also observed previously e.g., Gabay et al., 2014), we broke down the fourway interaction into two separate analyses, one for the same IM and one for the different IM trials. We were specifically interested in comparing the groups as a function of Eye given the a priori interest in whether TR and DD individuals differ across the monocular/binocular factor.

For each of the two trial types, a separate ANOVA was conducted with Stimulus x Eye as repeated measures and Group as the between subjects variable. For trials where the images matched, in addition to the main effect of Stimulus, $F(1,38)=11.7, p<.001, \eta_p^2=0.24]$ and of Eye, $F(1,38)=42.9, p<.001, \eta_p^2=0.53]$. there was also a significant interaction of Eye x Group, $F(1,38)=10.3, p<.003, \eta_p = 0.21]$. No other interactions were significant, p>.05. For trials on which the images did not match, there was only a main effect of Stimulus, $F(1,38)=12.3, p<.001, \eta_p = 0.25]$. No other main effects or interactions were significant, p>.05. There were no main effects of Group for either analysis. The Stimulus factor did not interact with Eye or Group or their combination, indicating that the Group differences were equivalent for words and faces.

As revealed in Fig. 5, when the two images did not match, there were no differences for either group as a function of whether the images were presented to the same versus different eyes. The absence of any difference may be due to the overall slowing in RT for each group, akin to a floor effect (Pike & Ryder, 1973) and often associated with 'no' responses (Nickerson, 1965). When the images did match, however, both TR and DD showed a significant advantage for the same eye versus different eye condition; RT for the difference score of (different minus same) eye was 30.4 ms for the TR and, at least numerically (although not necessarily statistically) almost three times that for the DD 89.6 ms. As evident, then, the monocular advantage was evident for both groups but to a much greater extent for DD than for TR and, interestingly, this applied equivalently for both words and faces, as revealed by the lack of an interaction with Stimulus type.

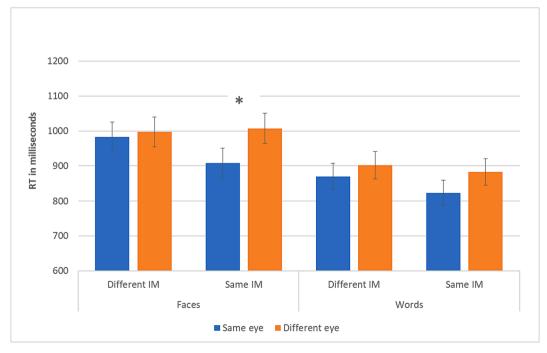


Fig. 3. RT for faces and words as a function of Stimulus and Eye. Error bars represent one standard error of the mean.

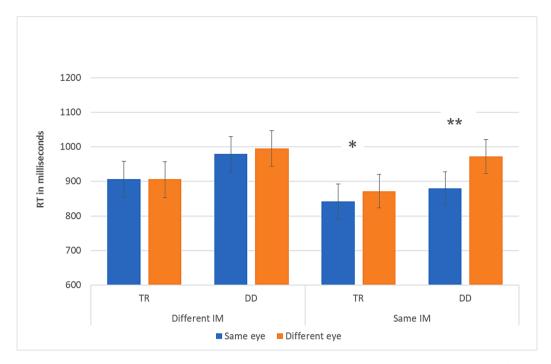


Fig. 4. RT for same versus different judgements as a function of eye (same, different) condition for TR and DD groups. in milliseconds. Error bars represent one standard error.

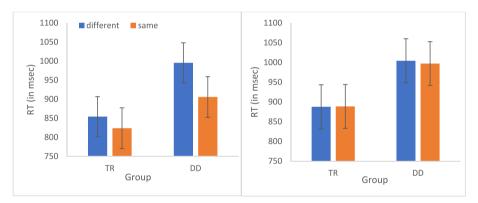


Fig. 5. Mean RT (+1SE) for same and different eyes plotted separately for TR and DD participants. Left figure: Image match trials; Right figure: Image non-match trials.

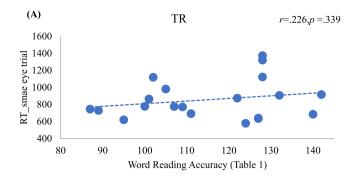
3.1.1. Relationship of monocular advantage and other variables

Because we hypothesized that the reading deficit in DD may emerge from the atypical contribution of the monocular subcortical channel, using Pearson correlation (two-tailed), we correlated the RT of trials on which the two items appeared in the same eye and, separately, trials on which the two items appeared in different eyes, separately for the TR or DD groups with measures of their reading ability. This latter metric was the independently established accuracy (number of correct words read per minute) and RT (number of words read per minute) in reading the 168 non-vowelized Hebrew words (see Table 1 Shatil test, Oral word letter decoding). Neither the same eye nor different eye RTs were correlated with either single word accuracy or RT for the TR individuals. There was, however, a significant negative correlation between the same eye RT and the accuracy of single word reading for the DD individuals, r =-0.453, p < .05 (see Fig. 6). This correlation reveals that the faster the RT for the same-eye trials, the higher the word reading accuracy. No RT word reading correlations were present in the DD group nor did the correlation hold for the different eye (n.s.), suggesting that the correlation was not simply the result of overall poorer performance for the DD group. Instead, the correlation indicates that the more accurate the

reader, the faster the discrimination of the words in the monocular channel (same-eye RT). No significant correlations between RT for the same-eye trials and other cognitive variables were observed.

4. Discussion

DD has long been considered an outcome of a deficit in language, more generally, and in phonological processing, in particular. Surprisingly, however, there is a growing literature revealing that individuals with DD also exhibit deficits in face processing (Åsberg Johnels, Hadjikhani, Sundqvist, & Galazka, 2022; Collins, Dundas, Gabay, Plaut, & Behrmann, 2017a; Gabay, Dundas, Plaut, & Behrmann, 2017; Monzalvo, Fluss, Billard, Dehaene, & Dehaene-Lambertz, 2012; Sigurdardottir, Hjartarson, Gudmundsson, & Kristjánsson, 2019; Sigurdardottir, Ívarsson, Kristinsdóttir, & Kristjánsson, 2015; Sigurdardottir, Ólafsdóttir, & Devillez, 2021). Although there are documented alterations in high-level visual cortex and other associated cortical regions in DD in response to the presentation of words, as revealed on MRI studies (Cross et al., 2023; Di Pietro et al., 2023), here, we specifically examine a possible explanation for the deficit in both word and face perception



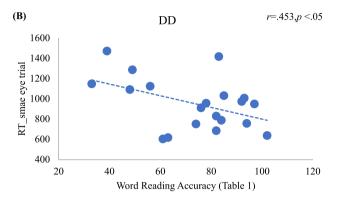


Fig. 6. Pearson correlation in (A) TR and (B) DD of the RT from same eye trials (collapsed across faces and words) and accuracy of word reading (number of words per minute) on standardized reading measure.

between DD and matched typical reading (TR) controls and one that could even underlie the atypical cortical neural profile. Specifically, we focus on the differential reliance on subcortical structures in DD versus TR. Over the course of development, these subcortical structures are assumed to bootstrap cortical regions which have more fine-grained representations for discriminating homogeneous exemplars in classes such as faces and words.

As has been postulated, early in development, there is greater reliance on subcortical than cortical systems (Johnson, 2005), and, over maturation, these subcortical systems aid the wiring of cortical involvement thereby supporting the development of perceptual expertise (Waldschmidt & Ashby, 2011). If this subcortical-cortical connectivity is perturbed, however, then we might observe atypical reliance on or greater engagement of subcortical visual mechanisms in those with DD than in TR readers in the domains of face and word perception and this may also explain the observed difference in neural cortical profile in DD than TR readers. Because it is difficult to evaluate subcortical engagement directly in humans as the structures are small and deep and their activation not easily quantified by neuroimaging, we adopted an alternative approach which permits inferences about processing via monocular versus binocular visual pathways. Using a stereoscope for eye-specific stimulus presentation, we measured whether performance is facilitated when two consecutive stimuli are presented to the same eye (subcortical monocular channel) as compared to two different eyes (cortical and intraocular).

4.1. Greater subcortical facilitation for faces and for words in DD compared to TR

First and foremost, we replicated previous findings of a monocular advantage in RT (better judgements when both face stimuli were presented to the same than different eyes) for face perception implicating a subcortical contribution to face recognition in the TR group (Gabay, Burlingham, et al., 2014; Gabay, Nestor, et al., 2014). Interestingly, the

monocular advantage for faces held only when the two images were same, and not when the images were different, as has also been documented previously (Gabay, Burlingham, et al., 2014). That the effect is observed only for same images implicates either facilitation from the repeat of an identical image or interference (stimulus–response incompatibility) when two different images (requiring a 'different' response) were presented to the same eye (perhaps favoring a 'same' response).

Having established our ability to replicate previous results, we then compared the DD group against a matched TR group after verifying the differences in these two groups on standardized reading and neuropsychological measures. The major result was the presence of a significant two-way interaction of Eye x Group, without modulation by Stimulus (face or word) (especially evident for the same image matched trials, see Fig. 5). Also, the monocular advantage in DD appears to apply equivalently across both face and word Stimulus types. Moreover, and strikingly, the same eye advantage is close to three times larger in DD than TR (different eye- same eye RT: TR 30.4 ms, DD 89.6 ms). This group difference offers strong support for the greater reliance on the monocular channel relative to the binocular channel for the DD than for the TR. We also established a significant relationship between the accuracy of the monocular trials and general reading skill, reflected by a significant correlation between the same-eye RT and accuracy of single word reading, documented independently as part of the inclusion neuropsychological testing. This correlation indicates that the faster the RT for the same, but not different eye, trials, the higher the word reading accuracy and provides evidence for the greater reliance on the subcortical pathway in DD compared with TR. Taken together, these findings are consistent with prior research indicating altered face and word processing in those with DD (Åsberg Johnels, Hadjikhani, Sundqvist, & Galazka, 2022; Collins, Dundas, Gabay, Plaut, & Behrmann, 2017a; Gabay, Dundas, Plaut, & Behrmann, 2017; Monzalvo, Fluss, Billard, Dehaene, & Dehaene-Lambertz, 2012; Sigurdardottir, Hjartarson, Gudmundsson, & Kristjánsson, 2019; Sigurdardottir, Ívarsson, Kristinsdóttir, & Kristjánsson, 2015; Sigurdardottir, Ólafsdóttir, & Devillez, 2021). The findings go beyond these previous results by offering a mechanistic account of why there might be atypical visual competence in DD versus TR and why this occurs in the processing of faces and words. Together with the current results, these findings indicate that those with DD appear to rely on subcortical regions for both word and face recognition to a greater degree than typical readers. Specifically, the account offered is that, over the course of development, the more rudimentary, low spatial frequency and coarse subcortical visual representations are insufficient especially in differentiating homogeneous exemplars in categories such as words and faces. To acquire expertise, then, subcortical activation is thought to bootstrap cortical visual representations which are more precise and sensitive to high spatial frequency input. In the event of a failure to bootstrap cortex, face and word perception rely disproportionately on subcortical computations which are inadequate and deficits for both visual classes ensue.

4.2. Subcortical involvement in bootstrapping cortex

What remains to be addressed is a more detailed account of the over-reliance on subcortical systems in those with DD. Three main possibilities might be proposed although these may not be mutually exclusive: a problem in overactivity in subcortical structures, a fundamental problem in cortex itself, independent of subcortical integrity, and last, a problem in bootstrapping cortex from subcortical structures. The first explanation of the deficit arising in subcortical regions does not seem viable. Given that these regions are implicated to a greater not lesser degree in DD and that the better the same eye RT, the better the single word reading in DD indicates that subcortical regions are probably contributing more, not less, than they should be doing.

A second interpretation is that there is a fundamental problem with visual cortex function per se in DD. The consequence of this cortical atypicality is that cortical structures themselves cannot be fine-tuned, resulting in greater reliance on subcortical visual structures. This idea of a fundamental problem in cortex does not seem a likely explanation as the DD participants do not experience difficulty in all domains of perception and, as noted, the recognition of cars by DD is not different from that of TR (Gabay et al., 2017).

Last, the greater monocular advantage in DD than in TR might result from the failure to bootstrap cortex over the course of development in the DD group, and we have already alluded to this possibility. We also note that, as suggested by others, the fine-tuning of cortex might be especially relevant for the development of perceptual expertise (Waldschmidt & Ashby, 2011), which is crucial for classes of stimuli in which exemplars are highly similar. We have suggested that this has not happened in DD - the increased reliance on the monocular channel might explain the differences between DD and TR, and the findings from the correlation and regression analyses, consistently, indicate that the greater the facilitation in the same-eye channel, the better the word reading accuracy. The failure, on this account, is that cortex cannot be optimized by subcortical bootstrapping.

Although further converging evidence is needed, we suggest speculatively, then, that the greater subcortical involvement in DD during face and word recognition arises from a failure in bootstrapping of cortex from subcortical regions and it is this fine-tuning that may permit the derivation of precise representations of faces and of words. It is this failure that specifically results in greater reliance on and subcortical engagement of visual stimuli that, typically, are in domains of expertise such as word and face recognition. Although we did not test another visual category which is typically not a domain of expertise, previous findings have demonstrated no monocular advantage for the sequential discrimination of cars (Gabay et al., 2014) and, indeed, there are no differences in car perception for DD and TR (Gabay et al., 2017). Face and word processing both require the development of expertise, in which DD participants have a difficulty (Collins, Dundas, Gabay, Plaut, & Behrmann, 2017a; Gabay, Dundas, Plaut, & Behrmann, 2017; Sigurdardottir, Hjartarson, Gudmundsson, & Kristjánsson, 2019; Sigurdardottir, Ívarsson, Kristinsdóttir, & Kristjánsson, 2015).

This last explanation is also consistent with the delayed neural commitment hypothesis of DD according to which DD difficulties are manifest not only in deficits in skill learning but also in the creation of the neural circuits that underpin reading readiness (Fawcett & Nicolson, 2019; Nicolson & Fawcett, 2018). According to this framework, delayed neural commitment leads to delays in the acquisition of the reading subskills, resulting in the prolongation of prior habits that interfere with new learning and, concomitantly, a delay in the creation of the neural circuits needed for efficient processing. Thus, those with DD may not be as successful as TR readers in establishing the cortical correlates for the fine-grained discrimination of complex visual patterns resulting in deficits in both face and word perception (Johnson, 2005; Johnson et al., 2015). Evidence from, for example, functional MRI conducted at high spatial resolution such as 7 T to permit identification of subcortical structures and their response profile or from a very large sample at 3 T with sufficient power to detect small signal changes is crucial to verify this account. These more refined neuroimaging approaches may, with close scrutiny, adjudicate between the three possible accounts we have provided above.

4.3. Further and future considerations

We have proposed that a possible account for the pattern of results obtained here is one in which subcortical functions do not bootstrap more sophisticated and advanced computations supported by cortical functions. One of these more advanced computations might be configural processing, a well-known signature of perceptual expertise and visual cortex is assumed to achieve fine-grained exemplar differentiation using configural or holistic face processing (Palmeri et al., 2004; Schiltz & Rossion, 2006). However, Sigurdardottir et al. (2021) reported that

DD participants had poorer featural processing than the controls and no difference in global form face perception. In fact, the explanation offered in this paper is that word and face perception are associated under conditions when featural processing is required and the perception of both stimulus classes suffers. The featural deficit account by Sigurdardottir et al. (2021) need not necessarily be at odds with the one proposed here. We have not explored the distinction between featural versus configural processing here—on our account, the apparent impairment in featural processing may be the overt manifestation of a more severe deficit in which even featural information is not adequately relayed to cortex. Potentially, those with more severe DD might bootstrap neither featural nor configural information whereas those who are affected less might fail to bootstrap cortex specifically for configural information.

The exact relationship between holistic and featural processing in DD versus TR is not yet resolved. For example, like in Sigurdardottir et al. (2021), holistic processing for faces in DD has been replicated but, surprisingly, there was an even greater reliance on holistic processing for words in DD compared to TD (Brady et al., 2021). Consistently, Chinese adults with DD also showed a stronger holistic processing effect than TR controls along with featural deficits for the components of characters (Tso et al., 2021; see also Tso et al., 2020 for discussion of right versus left hemisphere differences in DD than in TRs). There is a clear need for further research to disentangle all these factors: severity of DD, configural versus featural processing, differences in hemispheric lateralization (Collins, Dundas et al., 2017), and potential differences in the manifestation of these factors as a function of orthography (for example, English versus Chinese). In addition to further behavioral testing, we advocate the adoption of advanced neuroimaging of both cortical and subcortical activation profiles in DD versus TR controls (and potentially, too, MEG to elucidate the temporal relay between subcortical and cortical structures) and such studies may better adjudicate the differential featural/configural aspects for face and word perception in

In this study, we adopted a well-established approach to differentiate eye-specific effects and distinguish between monocular versus binocular effects, using the Wheatstone stereoscope method. This is just one approach and many different directions can be pursued to elucidate the altered underlying mechanism/s in DD. For example, we do not know whether these results generalize to another sample of individuals with DD; although we determined that we have sufficient statistical power to observe group differences (see Methods), as always, testing a larger sample would further reinforce these findings. Of course, we do not know whether the results uncovered here are specific to this paradigm or are more general and replicated using other paradigms and approaches. A further direction to pursue might be to replicate the same paradigm but to shorten the duration of stimulus exposure. We adopted long exposure times (1000 ms for the first stimulus and 2500 for the second to permit responses to be made). We selected these parameters to ensure that the DD individuals would be, at least, reasonably accurate and that we would have sufficient trials for analyzing RT which is the standard analytic approach for this kind of stereoscopic study. We predict that the discrepancy between DD and TR would be further exaggerated in a paradigm with limited exposure duration.

Further, in the present study, we focused on individuals with confirmed phonological deficits, but other subtypes of dyslexia also exist in English as well as in Chinese. One study of dyslexia among Chinese readers, for example, indicated that orthographic skills was a better predictor of both Chinese exception character and pseudo-character reading than was phonological skills (Ho et al., 2007). Additional exploration of the relationship between phonological and visual deficits (and other deficits too perhaps) in DD is clearly warranted. The observed correlation between visual processing and word reading accuracy indicates that a similar pattern could be observed in surface dyslexia and future studies should examine this question in other subtypes of dyslexia while also using additional face/word processing tasks. Finally future studies could also examine these questions while using manipulations

that can facilitate the involvement of subcortical structures such as employing different image spatial frequencies (Gabay, Nestor, et al., 2014) and shorter presentation times.

4.4. Conclusions

The current study supports the notion of atypical reliance on subcortical brain mechanisms during face and word processing among participants with DD, which manifests in longer RTs in a forced-alternative discrimination task. While a visual processing deficit, in and of itself, may not be solely causal in DD, there are likely to be concurrent deficits in language and phonological processing, as well.

Last, the current findings may have important theoretical and clinical implications. Not only do they provide insight into the basic processes affecting deficits among DD participants, but if replicated and characterized further, these findings have translational potential for the early identification and intervention in those with DD. For example, incrementally training individuals to differentiate stimuli that differ in high spatial frequency components, may recruit the necessary cortical computations. Another possibility might be to piggyback face and word recognition on the typical car recognition abilities, gradually making the cars increasingly more face-like, for example. A modification of the approach proposed by Moore et al., 2014 (albeit in the context of acquired dyslexia) using Facefont orthography, in which faces rather than typical letter-like units are used to represent phonemes, may be viable although a different 'carrier' stimulus (not faces) would need to be used. Funding declaration

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Declarations Ethics approval and consent to participate.

The Institutional Review Board of the University of Haifa approved the study, which was conducted in accordance with the Declaration of Helsinki, with written informed consent provided by all participants.

Consent for publication

All authors consent for publication of the manuscript in its present form.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandc.2023.106106.

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