# Atypical perceptual processing of faces in developmental dyslexia

Yafit Gabay, Eva Dundas, David Plaut and Marlene Behrmann

Department of Psychology, Carnegie Mellon University, Pittsburgh PA, USA

Number words: 9121

Number tables: 1

Number figures: 6

All correspondence should be directed to Yafit Gabay, Ph.D., Edmond J. Safra Brain Research Center for the Study of Learning Disabilities, Department of Learning Disabilities; Department of Communication Sciences and Disorders; Haifa University; Mount Carmel, Haifa, Israel 31905. Email: yafitvha@gmail.com

Acknowledgements: This research was supported by a grant from the National Science Foundation to MB (BCS-1354350) and by a Grant from the Temporal Dynamics of Learning Center, SBE0542013 (PI: G. Cottrell). We thank Dr Michael Tarr for the use of images from his database, Akshat Gupta for help in scheduling the participants and data analysis, and Dr Lori Holt for her support of this project. The face database in Experiment 2 was provided by the Max-Planck Institute for Biological Cybernetics in Tuebingen, Germany. The morphed face images in this study were created from facial images provided by Sharon Gilaie-Dotan, and are fully described in the paper: Gilaie-Dotan S., Malach R. Sub-exemplar shape tuning in human face-related areas. Cereb. Cortex. 2007; 17:325–338.

#### **Abstract**

Faces and words are commonly assumed to be processed by independent neural mechanisms located in the ventral visual cortex in the right (RH) and the left (LH) hemispheres, respectively. However, a recent theoretical account (Behrmann & Plaut, 2013; Plaut & Behrmann, 2011) proposes that specific constraints on neural and cognitive development cause these domains to become interdependent, both structurally and functionally. On this account, deficits in the development of word processing, such as in developmental dyslexia, should have direct and significant implications for the nature and organization of face processing. The current study explored the performance of dyslexic adults across a range of visual categories. Relative to matched controls, dyslexic individuals matched faces more slowly, showed disproportionate cost in performance, relative to typical readers, when target and distractor faces differed in viewpoint, and discriminated faces more poorly, particularly as the faces were morphed to be increasingly alike perceptually. Finally, the deficit with face and word processing was exaggerated relative to the visual processing of cars although dyslexics were slowed in their reaction time for all categories. Interestingly, similar hemispheric laterality profiles were observed for the dyslexic and control groups. Together, these results suggest that deficits in developmental dyslexia are not restricted to processing words, and affect face processing, as well, supporting an account in which word and face processing are not independent (Behrmann & Plaut, 2013; Plaut & Behrmann, 2011). Moreover, on this account, the finding of normal lateralization of face and word processing in developmental dyslexia suggests that the underlying abnormality in the dyslexia group may involve visual representations, and not solely deficits in language-related areas that interact with visual word representations.

Keywords: Developmental Dyslexia, Face Recognition, Hemispheric Specialization, Lateralization of Function, Word Recognition

#### 1. Introduction

Developmental dyslexia (DD), also known as 'specific reading disability', is a disorder in which children with normal intelligence and sensory abilities show substantial learning deficits for reading.

Although most of the research on DD has been conducted with children or adolescents, the reading difficulties can persist throughout the lifespan (Shaywitz et al., 1999), can continue to be evident in the eye movement patterns of well-educated adult DD individuals, and can adversely affect the work participation of such individuals (de Beer, Engels, Heerkens, & van der Klink, 2014).

Despite decades of research, the underlying psychological causes of DD continue to be debated (for a review see, Démonet, Taylor, & Chaix, 2004; Habib & Giraud, 2012). The commonly held view is that DD arises from deficient or impoverished phonological representations and, indeed, phonological impairments are one of the most common symptoms associated with DD (Vellutino, Fletcher, Snowling, & Scanlon, 2004). However, DD is also related to deficits in orthographic processing (Hasko, Groth, Bruder, Bartling, & Schulte-Körne, 2013; Pugh et al., 2000), non-linguistic deficits such as visual and auditory processing impairments (Clark et al., 2014; Farmer & Klein, 1995), attention deficits (Facoetti et al., 2006) and procedural learning difficulties (Lum, Ullman, & Conti-Ramsden, 2013) and, consistent with this multi-factorial origin, intervention along a host of different domains can result in improvement in DD (Hasko, Groth, Bruder, Bartling, & Schulte-Körne, 2014; Heim, Pape-Neumann, van Ermingen-Marbach, Brinkhaus, & Grande, 2014). The multi-faceted nature of DD has led researchers to search for a general explanatory framework that can account for the diversity of deficits in DD, although there is still no clear consensus on this topic (Hari & Kiesilä, 1996; R. I. Nicolson & Fawcett, 2011; Stein & Walsh, 1997; Vidyasagar & Pammer, 2010).

Just as with the cognitive profile, there is also substantial controversy regarding the underlying neural patterns associated with DD. For example, many recent studies have uncovered particular signatures of the disorder (compared with typical readers) including reduced BOLD signals in left

extrastriate cortex (Maisog, Einbinder, Flowers, Turkeltaub, & Eden, 2008; Pugh et al., 2000; Wandell, Rauschecker, & Yeatman, 2011), lower amplitude magnetoencephalography (MEG) signals in the vicinity of the left inferior occipitotemporal cortex (Salmelin, Service, Kiesila, Uutela, & Salonen, 1996), and changes in grey-white matter differences and in the integrity of white matter tracts in these same regions (see Richlan, Kronbichler, & Wimmer, 2012; Wandell et al., 2011). Others have argued that alterations in temporo-parietal cortex constitute the neural signature of DD although these alterations are often observed in conjunction with changes in occipitotemporal cortex (Raschle, Zuk, & Gaab, 2012)

The differences in left ventral occipitotemporal (VOT) cortex in DD, relative to controls, are consistent with a deficit in visual processing in some, if not all, individuals with DD. A key question is whether this visual recognition deficit is restricted to written words or extends to the processing of other types of visual stimuli as well (for a review see, Schulte-Körne & Bruder, 2010) and this controversy bears on the more general arguments about the domain-specificity of the visual word form area (Dehaene & Cohen, 2011; Price & Devlin, 2011; Roberts et al., 2012; Vogel, Petersen, & Schlaggar, 2014). A particularly informative contrast, and the focus of this paper, concerns the nature of the visual perceptual impairment in adults with DD and whether this impairment extends beyond the recognition of words to the recognition of faces.

#### 1.1. Interdependence of word and face processing

Words and faces constitute an interesting contrast because they are the two classes of visual stimuli for which literate individuals have the greatest perceptual expertise, and yet, as visual objects, they are entirely unrelated. Most researchers, therefore, assume that words and faces come to be recognized by independent mechanisms: words by the Visual Word Form Area (VWFA) in VOT in the left hemisphere (LH) (Petersen, Fox, Posner, Mintun, & Raichle, 1988), and faces by the Fusiform Face

Area (FFA) in an approximately homologous region in the right hemisphere (RH) (Kanwisher, McDermott, & Chun, 1997).

However, a recent theoretical proposal (Behrmann & Plaut, 2013; Plaut & Behrmann, 2011) postulates that specific constraints on neural and cognitive development cause these domains to become interdependent, both structurally and functionally (for related ideas, see Dehaene & Cohen, 2007; Dehaene et al., 2010). According to this proposal, both words and faces place extensive demands on high-acuity vision due to within-category exemplar homogeneity. As a consequence, words and faces compete for representational space in both hemispheres in the region of extrastriate cortex adjacent to higher-level retinotopic cortex that encodes central visual information (Levy, Hasson, Avidan, Hendler, & Malach, 2001), notably including both the VWFA and FFA. Because word representations are further pressured to be more closely connected to language/phonological information (to minimize connection length), which is left-lateralized in most individuals, the lefthemisphere visual area is increasingly tuned for the representation of orthographic inputs. And because the image statistics of words and faces, as classes differ so greatly, by virtue of competition, face representations gradually, although not exclusively, become more right-lateralized. As a result of these cooperative and competitive dynamics that ensue over the course of development, in the typical mature state, words are more strongly represented in the LH and faces are more strongly represented in the RH. However, both domains are processed bilaterally, such that the efficacy and degree of hemispheric lateralization of the two domains is causally linked and subject to a variety of factors that vary across individuals.

The account makes specific predictions for typically developing readers: that word lateralization should precede face lateralization in development, and that the degree of face lateralization across individuals should depend on reading skill. Dundas, Plaut, and Behrmann (2013) reported findings that are consistent with these predictions. Using a sequential same/different

judgment task in which the first stimulus (word or face) was presented centrally and the second (of the same type) was presented briefly in the left or right visual field, they showed that adults, adolescents and children all showed the expected LH advantage for words, whereas only the adults showed a RH advantage for faces. Moreover, as predicted, the emergence of face lateralization was correlated with reading competence (as measured on an independent standardized test), even after regressing out age, quantitative reasoning scores, and face discrimination accuracy. The emergence of LH lateralization for words prior to the RH lateralization for faces was further confirmed in an ERP study in which children demonstrated a more negative N170 for words in the LH than RH but no difference in N170 amplitude for faces between the two hemispheres (Dundas, Plaut, & Behrmann, 2014a, 2014b). These findings support claims that the neural mechanisms for face and word recognition do not develop independently, and that earlier word lateralization drives later face lateralization.

## 1.2. Face processing in developmental dyslexia

If, as the Behrmann and Plaut (2013) account suggests, the development of word and face processing are causally linked, then deficits in the development of word processing should have direct and significant implications for the nature and organization of face processing. The specific predictions of the Behrmann and Plaut account, however, depend on the nature of the underlying abnormality that gives rise to the reading deficit<sup>1</sup>. An abnormality in left ventral occipitotemporal (VOT) cortex itself would be expected to most severely impair word processing but also face processing albeit to a lesser extent (see Behrmann & Plaut, 2012; Roberts et al., 2012 for supportive evidence form paitents with pure alexia due to left occipitotemporal brain damage). However, the pressure to left-lateralize word representations (from LH phonological areas) would be unchanged, and so the relative contribution of

-

<sup>&</sup>lt;sup>1</sup> We use the word "abnormality" here to refer to some unknown type of structural atypicality in connectivity, distribution or density of cell types, or other neurophysiological characteristic that prevents the area from being as effective in carrying out its function as it is in typically developing readers (Wandell et al., 2011).

the two hemispheres to word and face processing should be the same as in typically developing readers. On the other hand, if the underlying abnormality is elsewhere -- and a natural candidate would be in the LH regions supporting phonological representations -- then the pressure to left-lateralize word representations would be reduced, giving rise to more bilateral involvement for both word and face processing in DD compared to typically developing readers. Moreover, the reduced top-down influence of phonological representation on the development of visual word representations would not be expected to be relevant to face representations, and so, in this latter case, face processing performance would be expected to be normal in DD individuals. At the extreme, reduced competition from weakened word representations might even give rise to improved face processing compared to normal readers.

As a clear point of contrast, the traditional view that face and word processing are independent predicts that performance and hemispheric lateralization of face processing should be normal in developmental dyslexia. Although the existing literature on face processing in developmental dyslexia is not extensive, at first glance it might appear to support the traditional view. Brachacki, Fawcett, and Nicolson (1994) found no differences between dyslexic and non-dyslexic individuals in face recognition. Smith - Spark and Moore (2009) found that dyslexic and non-dyslexic university students did not differ in the speed or accuracy with which faces were named, although the non-dyslexic group was significantly faster to name early- than late-acquired faces of famous individuals. Also, several studies have demonstrated that DD individuals are unimpaired in recognition memory for unfamiliar faces (Rüsseler, Johannes, & Münte, 2003) and reveal normal performance when ordering unfamiliar faces in an old/new sequence (Holmes & McKeever, 1979).

Closer examination, however, suggests that the existing results are less than definitive. First, some studies (e.g, Brachacki et al., 1994) may have been insensitive to group differences because performance was at ceiling. Second, these studies focused more on mnemonic than perceptual aspects

of face perception, showing no group differences in recognition memory and/or naming when participants were able to encode the faces well (large size faces, long exposure duration etc.). These studies did not specifically tap into the perceptual aspect of face perception. Given the ambiguity of the existing empirical findings, the current study explored face processing skills in DD adults to determine whether, and to what extent, face perception and its lateralization is adversely affected in this population.

We start by documenting the reading deficit in a group of adult DD individuals. We then characterize their face perception performance in two different experiments, each of which is designed to elucidate, in fine-grained detail, the properties of any observed impairment. Finally, using a divided field paradigm, we examine the lateralization profile for word and face processing, and we explore the relationship between the hemispheric effects.

## 2. Word processing

To characterize the word recognition deficit of the dyslexic participants (see Table 1 for results of standardized tests), we report data from two experiments in which we parameterize certain variables (such as word length) known to differentially affect reading performance, and then examine the consequences of these manipulations on the DD adults and matched controls.

## 2.1 Methods

#### 2.1.1. Participants.

Twenty-four participants, twelve with DD (6M, 6F) and twelve matched controls (6M, 6F) participated in each experiment. All participants were university students in the area of Pittsburgh, were native English speakers with no reported signs of sensory or neurological deficits/attention deficit hyperactive disorder (according to the American Psychiatric Association, 2000) and came from families

with middle to high socioeconomic status. A well-documented history of dyslexia constituted the key inclusion criterion for the DD group: 1) each individual received a formal diagnosis of DD by a qualified psychologist prior to inclusion in this study; 2) each individual's diagnosis was verified by the diagnostic and therapeutic center at their university and they were receiving accommodations appropriate to their educational setting. In addition, as a group, individuals differed significantly from matched controls on all literacy measures. Diagnosis of a comorbid learning disability such as ADHD constituted an exclusion criteria for the DD group. The control group comprised individuals, age-matched with the DD participants, with no reported reading difficulty. The study was approved by the Institutional Review Board of Carnegie Mellon University, and written informed consent was obtained from all participants.

Participants completed a series of tests including verbal working memory (as measured by the forward and backward Digit Span from the Wechsler Adult Intelligence Scale, (Wechsler, 1997)), rapid naming (Wolf & Denckla, 2005) and phonological awareness (Spoonersim test adapted from Brunswick, McCrory, Price, Frith, & Frith, 1999). The Raven- Matrices test was used as a proxy of nonverbal intelligence (Raven, , 1992). It is fairly standard practice to use the Raven, which is independent of reading skills, as a proxy for intelligence as some of the tests in the WAIS involve vocabulary (which is known to be reduced in DD as they read less). They also completed untimed and timed (fluency) tests of Word Identification (WI) and Word Attack (WA) subtests from the Woodcock Reading Mastery Test-Revised, and the Sight Word Efficiency Forms A+B (i.e., rate of word identification) and Phonemic Decoding Efficiency, Forms A+B (i.e., rate of decoding pseudo words) subtests from the Test of Word Reading Efficiency (TOWRE-II; Torgesen, Wagner, & Rashotte, 1999).

2.1.2 Results - As expected, the two groups did not differ on the basis of age non-verbal intelligence, as measured by the Raven test (See Table 1, Section 2, 3). However, compared with the control group, the DD group showed a clear profile of reading disability (see Table 1), with significant group differences

on word reading and decoding skills, as evident on both rate and accuracy measures. In addition, compared with the control group, the DD group showed the characteristic deficits of reading difficulties, as manifest in phonological awareness (spoonerisms) and rapid naming (rapid automatized naming) tasks.

## 2.2.1 Naming latency

### 2.2.1.1 Stimuli

To assess speed and accuracy of word reading, in this experiment, a single word appeared centered over fixation for unlimited duration, and participants were required to read it aloud. Words were presented in uppercase Geneva 24-point bold font in black on a white background. To assess the effect of word length on RT and accuracy, 60 words, 20 each of 3, 5, and 7 letters, were included. Words subtended visual angles of ~0.5° vertically and ~1.5°, 2.4°, and 3.6° horizontally for the 3 word lengths, respectively. Word frequency was controlled, with an equal number of high- (>20 times per million) and low-frequency (<20 times per million) words per word length (Kucera & Francis, , 1967). The words had a mean word frequency of 52 (SD = 70), with half abstract and half concrete words.

## 2.2.1.2 Procedure

Subjects were instructed to read aloud each word as quickly and as accurately as possible. The words were shown individually, with word length randomly intermixed in the block of trials. On each trial, a fixation point appeared for 1000 ms after which the word appeared and remained visible until the subject responded verbally. An interval of 2 s occurred between trials. RT was recorded using a voice key and the experimenter noted any errors manually. Trials on which the microphone was mistriggered were removed from the analysis.

## 2.2.1.3 Results

Since accuracy rates were high (fewer than 2% errors), we focused our analysis on latencies. An analysis of variance (ANOVA) with length (three, five, and seven) as a within-subject factor and group (DD vs. controls) as a between-subject factor was conducted with RT as the dependent measure. For each individual, RTs more than 2 standard deviations from the mean of the cell were excluded from the analysis (3.5% for the DD and 0.5% for the controls). There was a main effect of group with the DD participants responding more slowly than controls, F(1, 22)=12.32, p<.05 (M=663.29ms, M=471.55ms for the DD and control group, respectively) (see Figure 1). There was also a main effect for length, F(2, 44)=3.23, p<.05, with faster RTs for 3 than 5 letter words, F(1, 22)=4.06, P<.05, or 7 letter words, F(1, 22)=5.57, P<.05, whereas RTs to 5- and 7- letter words did not differ from each other (P=n.s.). The interaction of group by length was not significant (P<1).

## 2.2.2 Lexical decision

To characterize further the reading of the two groups and to do so without requiring an overt pronunciation (which may be more demanding in the DD than control group), we next examined performance in a lexical decision task.

#### 2.2.2.1 Stimuli

The words from the naming latency task above were combined with 60 nonwords, which were created by changing one or two letters of the real words. All nonwords were pronounceable and orthographically legal; for half the nonwords, the divergence from a real word occurred in the first half of the word whereas the converse was true for the other nonwords. This experiment was run in a separate session from the word-reading task.

## 2.2.2.2 Procedure

Following a fixation point that appeared for 1 s, a letter string was presented centrally and remained visible until response. Subjects decided whether or not the string was a real English word, and pressed one of two keys using two fingers of their dominant hand for a "yes" or "no" response. The keys were counterbalanced across subjects. The inter-trial interval was 1s. Subjects performed practice trials and were instructed to complete the task as quickly as possible without sacrificing accuracy.

Accuracy and RT were both analyzed.

## 2.2.2.3 Results

An analysis of variance (ANOVA) with length (three, five, and seven) and string type (non-words vs. real words) as within-subject factors and group (DD vs. controls) as a between-subjects factor was conducted first with accuracy as the dependent measure and then with RT.

In the analysis of accuracy, there was a significant main effect for group as DD participants made overall more errors compared with controls, F(1, 22)=10.44, p<.01, (M=93%, M=96%, for the DD and control groups respectively). This group difference was qualified in an interaction with string type, F(1, 22)=3.55, p=.07: whereas the DD made more errors than the control group for non-words, (M=92.9%, M=96.9%) for the DD and control group respectively), there was no significant difference in accuracy between the groups for words (p=.118, M=94.6%, M=96%) for the DD and control groups respectively), mirroring the result from the naming latency experiment. There was also a main effect of length (F2,2)=10.5, p<.001), with more errors as length increased and an interaction of length with string type (F(2,44)=5.2, p<.005), with more errors as length increased for nonwords compared with words.

In the analysis of RT, as with accuracy, there as a significant effect of length, (F2,2)=10.9, p<.001), which was qualified by an interaction with string type, (F(2,44)=7.6, p=.001), as well as a significant main effect of string type, (F(1,22)=8.9,p<.005). As shown in Figure 2, there was a main effect for group, F(1, 22)=20.127, p<.01, with DD participants performing significantly more slowly than the controls. The interaction of group by length was significant, F(2, 44)=8.418, p<.01, as evident by the significant linear trend of length for the DD group, F(1, 22)=20.19, p<.01, but not for the control group, F<1. There was also an interaction of group x string type, (F1,22)=4.7, p<.05), with the DD group responding significantly more slowly to nonwords than to words, compared with the control group. The marginally significant triple interaction of group, stimulus type and length, F(2, 44)=3.05, p=.057, indicates that, in the DD group, the increase in RT as a function of length was more pronounced for nonwords compared with words, F(1, 22)=10.85, p<.01, whereas no such difference was evident in the control group (F<1). Unsurprisingly, given the three-way interaction, the interaction of group by string type was also significant, F(1, 22)=4.68, p<.05, such that DD participants were slower for nonwords compared with words, F(1, 22)=13.31, p<.01, (M=1269.54 msec, M=956.99 msec for nonwords and words respectively), while there was a numerical but not reliable difference for the control group, F<1 (M=687.25, M=636.9, for nonwords and words respectively). We calculated the slope for words and nonwords across string length separately for each of the control and DD participants, and an ANOVA using the slope of RT revealed a significant difference between the two groups for both words, F(1, 22)=8.37, p<.01, and nonwords, F(1, 22)=6.66, p<.05.

Together, the findings from the naming latency and lexical decision experiments confirm a significant difference in word processing between the control and DD group. The differences are predominantly in RT rather than in accuracy, which is unsurprising given the unlimited exposure duration. The DD group was disproportionately slowed relative to the controls as a function of word

length and, unsurprisingly given the existing literature, this was so to a greater degree in nonword than word reading (Nergård-Nilssen & Hulme, 2014).

## 3. Face processing

Having characterized the reading deficit of the DD using both standardized clinical measures (Table 1) and experimental-based measures, we now assess the face perception skills of the DD group and employ manipulations that are known to induce signature patterns of performance in typical observers. For example, we compare performance for upright and inverted faces to examine whether the DD individuals exhibit the standard decrement for the latter over former trials, the so-called 'face inversion' effect (Bruce, Valentine, & Baddeley, 1987). We also explore the effect of viewpoint, or depth rotation to determine whether the DDs show the expected cost in matching faces shown over different viewpoints. These manipulations provide fine-grained methods for uncovering the strengths and weaknesses of face perception in DD.

#### 3.1. Inversion and Depth Rotation in Face Matching

## 3.1.1.Participants

Participants who completed the reading studies reported above also participated in these face recognition experiments.

## 3.1.2. *Stimuli*

The stimuli consisted of color pictures of male and female faces from the Max-Planck Face Database (Troje & Bülthoff, 1996). This database consists of a series of 3D models of real faces (no hair) in 3 rotations in depth around the vertical axis—full-frontal face (0°), right three-quarter (45°), and right profile (90°) (see Fig. 3a–c, examples of the 3 degrees of rotation). Each face was positioned on a black square background (7.5 × 7.5 cm). A total of 97 different faces were used for the experimental trials.

### 3.1.3.Procedure

On each trial, three stimuli appeared on a gray background: a target face (centered over fixation, 5.5 cm from the top of the screen) and two choice faces, to the left (9.5 cm from left, 16 cm from top) and right side of the fixation point (22.5 cm from left, 16 cm from top) (see Fig. 3). Each trial began with a fixation cross appearing for 250 ms, followed by the 3 stimuli, which remained on the screen until response. In the first part of the study, only upright faces, varying within and across rotation, were shown (see example in Fig. 3). The target could appear in one of three possible rotations — frontal (F), three-quarters (T) or profile (P) — and this was true of the choices too, resulting in nine possible target face × choice faces rotation combinations. Note that, on any one trial, the two choice faces were always rotated to the same angle within a trial, for example, both might be 45°, as shown in Figure 3. The nine conditions were randomly mixed within each block of trials, with 30 trials per cell for a total of 270 trials. Trials were divided into two blocks with a short break between them. Participants pressed a left or right key to indicate the side of the match to target.

Following this, participants completed an additional block of trials, in which the target was always upright, and on half the trials, the choices were both upright, whereas on the other half, the choices were both inverted (See Figure 3e). The target and choice faces were only ever shown in the frontal view (see Fig. 3e). Again, there were 40 trials per cell (inverted/upright) for a total of 80 trials.

## 3.1.4. Results

We start by considering the face inversion effect and then examine the effect of depth rotation on face perception performance.

Inverted vs. upright. The comparison of the DD and control groups with orientation (upright vs. inverted) as a within subject factor and accuracy as the dependent measure revealed a significant main effect of orientation, F(1, 22)=10.6, p<.005, with more errors to inverted faces than to upright faces. There was neither a main effect of group nor an interaction of group x orientation, (F<1). The same analysis but with RT revealed that the DD group was significantly slower overall than the control group, F(1, 20) = 12.99, p<.01, (M=1496.9ms M=1188.9ms for the DD and control groups respectively), and the inverted faces produced slower responses than upright faces, F(1,22)=25.3, p<.000). There was no significant interaction of group x stimulus orientation (F<1).

Matching across depth rotation. An analysis of variance (ANOVA) with target (F, T, P) and choice/distractor (F, T, P) as within subject factors and group (DD vs. controls) as a between-subjects factor, and mean accuracy (or, separately thereafter, RT of correct responses only) as the dependent variable was conducted.

With accuracy as the dependent measure, there were no main effects or interactions with group and this may not be surprising given the prolonged exposure duration of the stimulus (i.e., the paradigm is not data-limited). There was, however, an interaction of target orientation x distractor orientation, confirming the expected result that when the target and the choices share orientation accuracy is higher than when matching is required across viewpoint; accuracy is highest when the target and distractor share orientation (FFF .99; PPP .98 and TTT .98) compared with crossing orientation (for example, FPP .88 or PFF .86). The cost associated with matching viewpoint is well documented in the literature, including within this paradigm (Marotta, McKeeff, & Behrmann, 2002) .

With RT as the dependent measure (see Figure 4), there were both significant main effects of target, F(2, 44)=12.4, p<.000 and of distractor, F(2,44)=27.1, p<.000. There was also an interaction between the target x distractor orientation, F(4, 88)=111.4, p<.000, reflecting the same result as for

accuracy, with slower RTs when targets and choice did not match in orientation (for example, FPP 2683ms; PFF 2543.9ms) compared to when they did match (FFF 1208.5 ms; PPP 1215.7 and TTT 1256.3ms). There was also a main effect for group, such that DD participants were significantly slower than the control group across the board, F(1, 22)=20.6, p<.01 (controls mean 1584.8ms; DD 2149.1ms) and a three-way interaction of group x target x choice/distractor, F(4, 88)=4.5, p<.005. Further analysis revealed that every pairwise condition was significantly different between DD and the controls but that, when the target and distractor shared the same orientation and matching was not across viewpoint (e.g. FFF, PPP, TTT), the difference between controls and DD was smaller compared to the other conditions, [FF versus average FPP and FTT: F(1, 22)=15.58, p<.01; PPP versus average PFF and PTT F(1, 22)=13.93, p<.01; TTT versus average TFF and TPP F(1, 22)=5.04, p<.05]. This finding indicates that the DD showed the expected cost in RT as the target and distractor viewpoint differed but that the cost in matching across orientation was even greater in DD than that observed in the controls.

One potential concern is that the group differences we observe might stem from a deficit in attention (although a frank diagnosis of ADHD is exclusionary) or from some other generalized difficulty, such as the slowing in RT in DD, which may be exacerbated across the duration of the experiment. To evaluate this, we performed additional analyses to examine the stability of group differences along each experiment. If group differences emerge gradually along the course of the experiment, it would suggest that they are driven perhaps by fatigue or difficulty in sustaining attention. We divided the trials of the face rotation experiment into four bins (N=270; approx. equal number trials per bin) along the sequence of trials and repeated the same ANOVA with Target (F, T, P) and choice/distractor (F, T, P) and bin (1-4) as within subject factors and group (DD vs. controls) as a between-subjects factor a between-subjects factor. No interaction of group with bin was found (all F < 1.7). This result suggests that, although DD are slow across the board, this is not a result of performance falling off over time and indicates that it is unlikely that a factor such as fatigue or

attention can account for the findings. Furthermore, the presence of specific interactions in the data (such as the three way interaction of group x target x choice/distractor) is unlikely to be explained by a generalized group difference. Last, we recognize that these analyses (incorporating bin as a factor) may not be perfectly controlled: along the sequence of the experiment, trials were randomized from each condition so it is potentially possible that the bins had differing distributions of trials from the different conditions. This is not surprising as the experiment was not originally designed to control the sampling of trials over time. Nevertheless, the absence of any interaction with bin and the presence of the three way interaction noted above suggest that the group differences are not a product of a generalized effect in the DD group.

In summary, this simultaneous matching study revealed significantly slower performance in the DDs than controls and that, further, there was disproportionate slowing for DDs as faces were matched across rather than within the same viewpoint.

## 3.2. Simultaneous face discrimination

The following experiment further examines face processing in the DD and control groups, under conditions in which we manipulate perceptual complexity.

### 3.2.1 Stimuli

Participants viewed two faces presented side-by-side on a computer screen for same/different discrimination (see Figure 5a). The faces could be either the same (25% of trials; N=60) or different (75%; N=180). The different trials were drawn equally from Easy, Medium or Difficult conditions (N=60 in each of these levels of difficulty). The Easy condition consisted of a picture of two different faces (say Face A and Face B). For the medium and difficult trials, the two faces were morphed together using the

MorphMan 4.0 software. For the medium condition, Face A was presented with a morph that comprised 33% of Face A and 66% of Face B, while in the difficult condition, Face A was presented with a morph that comprised 66% of Face A and 33% of Face B. Each stimulus was roughly 2 x 3 inches. The midpoint of each stimulus was located 5.2 inches from the fixation point and subjects viewed the display at approximately 50 cm. These stimuli have been used in a previous study to capture behavioral differences across the age span in face perception (Thomas et al., 2008).

#### 3. 2. 2. Procedure

Participants were informed that, on each trial, two faces would appear simultaneously on either side of a red fixation dot in the center of the screen. Participants were to maintain fixation and decide whether the two faces were the same or different. Responses were made using two keys on the keyboard and participants were told to respond as quickly and as accurately as possible. The order of the trials was randomized within a block.

#### 3.2.3 Results

We conducted an analysis of variance (ANOVA) with level (easy, medium, and difficult) as a within-subject factor and group (DD vs. controls) as a between-subjects factor using accuracy and then using RT as the dependent variable (see Figure 5b).

With accuracy, there was a main effect of group such that DD participants made significantly more errors compared with controls, F(1, 22) = 5.7, p < .05, (M = 60.5% M = 70.5% for DD) and controls respectively). There was also a significant main effect of level of complexity, F(2, 44) = 275.1, p < .01, with accuracy decreasing as visual complexity proceeded from easy to difficult. No other main effects or interactions reached significance. Although there was no interaction between group x complexity level, additional analysis revealed that DD participants did not differ from controls on easy trials F(1, 22) = 2.04, p = .164, whereas significant group differences were observed on both the medium and difficult trials F(1, 22) = 5.7, p < .05.

With RT, there was a significant effect of level of visual complexity, F(2,44) = 6.47, p < .01, with RTs significantly slower between easy and medium trials, F(1, 22) = 12.02, p < .01 and marginally significant between medium and difficult trials, F(1, 22) = 3.19, p = .08. No other main effects or interactions reached significance.

As above, as a means of checking whether performance drops off differentially across groups across the duration of the experiment, we further examined the accuracy of the DD and control groups on the simultaneous face discrimination task over the time course of the experiment. To do so, we divided the trials into four bins (N=240; 60 trials per bin) along the sequence of the experiment and repeated the same ANOVA with level (easy, medium, and difficult) and bin (1-4) as within-subject factors and group (DD vs. controls) as a between-subjects factor. No interaction of group with Bin was found (all F < 1), suggesting that generalized fatigue or differential effects of attention over the course of the experiment cannot account for the reported findings. As with the previous study, this experiment was also not designed to ensure equal representation of all conditions over the course of the experiment and thus the sampling by bin may be inadvertently unequal in terms of the trial types. The absence of any effects of bin, however, indicates that generalized factors are unlikely to explain the observed group differences.

The findings from this study show that DD were less accurate in discriminating faces compared with typical readers and confirm the findings from the previous face matching experiment, attesting to the fact that face perception is not normal in DD.

## 4. Hemispheric organization for word and faces

The findings thus far reveal that the individuals with DD perform significantly more poorly than controls not only on word recognition but on face recognition as well. The final experiment evaluates the theoretical account in which hemispheric organization of word and face perception are linked and

in which, given the atypical face and word perception in DD, understanding the profile of hemispheric organization, relative to controls, might shed some light on the nature of the interdependence between face and word laterality. This study examines performance for visual stimuli presented in the left and right half-fields. For ease of understanding, we will refer to the results in terms of the hemisphere (LH or RH) rather than to the visual field to which the stimulus was projected (RVF or LVF).

#### 4.1 Participants

Twenty-two participants, eleven with DD (5F, 6M) and eleven matched control individuals (5F, 6M) participated in this experiment. Nine DD participants and six controls participated in the word and face experiments reported earlier, and the new DD (2) and control (5) participants were assessed using the same standardized measures used previously. The group of DD and control participants did not differ on the basis of age or intelligence (See Table 1, Section 4). As expected, compared with the control group, the DD group showed a clear profile of impairment: they differed significantly from the control group on word reading and decoding skills in both rate and accuracy measures and showed the characteristic deficits in the three major phonological domains: phonological awareness (spoonerisms), verbal short-term memory (digit span) and rapid naming (rapid automatized naming).

#### 4.2 Stimuli

Thirty male and thirty female face images obtained from the Face-Place Database Project (Copyright 2008, Dr M. Tarr) were used in this experiment. All faces were forward facing with neutral expression (see example in Figure 6a). The faces were cropped to remove hair cues and presented in grayscale against a black background. Stimuli were 1.5 inches in height and 1 inch in width, yielding visual angles of 4.8 and 3.2 degrees, respectively. On each trial, the pair of faces matched on gender.

The word stimuli consisted of 60 four- letter words (30 pairs), taken from a study by Dundas et al. (2013) and presented in gray, Arial, 18-point font against a black background. Stimuli were

approximately a ½ inch in height and 1 inch in width, yielding visual angles of 1.6 and 3.2 degrees, respectively. Pairs were matched so that the words differed by one of their interior letters, with 15 of the pairs having a different 2<sup>nd</sup> letter and 15 having a different 3<sup>rd</sup> letter (see example pair in Figure 6a). The mean word frequency in English was 53.89 per million [range 0.118-578.5] and the mean bigram frequency was 778.633 per million [range 83.48-2000.66] (Marcus, Marcinkiewicz, & Santorini, 1993). Note that the faces and words used in this study were previously used by Dundas et al. (2013) and successfully elicited a left visual (LVF) and a right visual field (RVF) advantage for faces and words, respectively, as one might have predicted.

In addition to faces and words, we included a third category, that of cars, to serve two purposes. The inclusion of this additional class not only provides measures of visual discrimination of a further set of visual stimuli in DD relative to controls but also offers a control benchmark of hemispheric specialization as these car stimuli do not yield an advantage in either hemisphere (Dundas et al., 2013). The 60-car stimuli were presented in gray scale at a three-quarter left-front facing view. Stimuli were approximately 1.75 in. in width and 1 in. in height, yielding visual angles of 5.57° and 3.2°, respectively (see Figure 6a).

## 4.3 Procedure

The experiment was run on a laptop computer using E-prime software (Schneider, Eschman, Zuccolotto, & Guide, 2002). Participants sat approximately 18 inches from the screen. Words, cars and faces were presented in separate blocks of trials. Participants viewed a central fixation cross whose duration ranged between 1500 and 2500 msec. Following the offset of the fixation cross, a centrally presented stimulus (word, face, or car) appeared for 750 msec and was followed immediately by a second stimulus of the same type (word, face, or car) presented for 150 msec in either the left or right visual field with the center of the stimuli being 5.3 degrees from fixation. Participants were instructed to keep their gaze fixated centrally throughout the experiment and to respond by pressing one of two

buttons to indicate whether the second stimulus was identical to the first or not (same/different judgment). The fixation cross appeared following the button press and indicated the start of the next trial. The presentation of stimuli in the left and right visual field was randomized per subject with equiprobable presentation in each field within a block. For all classes of stimuli, there were 96 trials, which were split into three blocks to give participants a rest between blocks. The presentation order of word blocks versus faces blocks was counterbalanced across participants. In addition to the instruction to maintain fixation, the brief exposure duration of the 'probe' in the half-field ensured that a saccade away from fixation was highly unlikely. Therefore, this design allowed us to explore the relative contribution of the LH and RH to the processing of different visual stimuli.

#### 4.4 Results

An analysis of variance (ANOVA) was conducted with stimulus type (words, faces, or cars) and hemisphere (LH, RH) as within-subject factors and group (DD vs. controls) as a between-subjects factor using accuracy as the dependent variable. The same analysis was then repeated with RT as the dependent measure.

With accuracy, there was neither a main effect of group, F(1, 20)=2.67, p=.11, nor of stimulus type, F(2, 40)=.328, p=.72 (see Figure 6b). As expected, there was an interaction of stimulus x hemisphere, F(2,40)=8.03, p<.01, with higher accuracy for words presented to the LH than to the RH, F(1, 20)=5.69, p<.01 (.86 versus .91) and higher accuracy for faces presented to the RH than the LH, F(1, 20)=4.88, p<.05 (.90 versus .86), and no modulation by hemisphere for car stimuli, F(1, 20)=2.69, p=.11, (right versus left .89 versus .87). There was also an interaction of stimulus type by group, F(2, 40)=3.833, p<.05: whereas the controls and DDs performed equally well on cars (.89 for both groups), the controls performed significantly better than the DDs on both stimulus types but to an even greater degree on matching faces (controls vs DD: .91 versus .84, p<.04) than on matching words (controls versus DD: .90 versus .87, p<.05). Furthermore, DD participants were less accurate in matching faces and words

compared with cars, F(1, 20)=4.06, p=.057, with equivalent performance matching faces and matching words, F(1, 20)=2.25, p=.14. The control group exhibited similar accuracy across all stimulus types (minimum p=.19). There was no significant three-way interaction, suggesting that the lateralization of the three stimulus types was equivalent across the two groups, [F<1].

We further examined the accuracy performance of the DD and control groups on the hemi-field task throughout the course of the experiment. To do so, we divided the trials into four bins along the sequence of the experiment (N=96, N=24 per bin for each block separately) and repeated the above ANOVA with stimulus type (words, faces, or cars), hemisphere (LH, RH) and bin (1-4) as within-subject factors and group (DD vs. controls) as a between-subjects factor. No interaction of group with bin was found (all F < 1.75), once again excluding generalized factors as key to the observed group differences. Note that in this experiment because the stimuli were blocked by type (cars, faces and words), the only inequality in sampling per bin might arise from the difference in the number of left or right visual field trials per bin. As with the previous studies, no effect of bin is observed and so the potential slight inequality that might result from the sampling is unlikely to be spuriously driving the group differences.

With RT as the dependent measure, the main effect of group was marginally significant, F(1, 20)=3.57, p=.07, with slower responses for the DD than the control group. There was also a significant main effect of stimulus type, (F(2,40)=11.5, p<.001), with words requiring significantly longer responses times than the other two classes. No other main effects or interactions were significant.

We further examined the RT performance of the DD and control groups on the hemi-field task throughout each block of the experiment. To do so, we divided the trials of a single block into four bins along the sequence of the experiment (N=96 per block, N=24 per bin) and repeated the above ANOVA with stimulus type (words, faces, or cars), hemisphere (LH, RH) and bin (1-4) as within-subject factors and group (DD vs. controls) as a between-subjects factor. There were no interactions with bin and any other factor nor any higher-order interactions with bin (all F < 1.44). As above, the same point holds

with respect to potentially uneven sampling of trials from different conditions within a bin. The clear absence of an effect of bin or any interaction with bin here and in all the other analyses largely excludes explanations concerned with general differences across groups in their performance over the time of the experiment.

The findings thus far accord with those from the previous experiment in that the DD individuals perform more poorly than the controls for faces and for words (in accuracy) and marginally so for all stimuli in RT. Because slowing of performance is a well-known feature of DD (Marcus et al., 1993), it is difficult to know whether the slowing for cars indicates altered performance across all visual domains in DD or is a function of this more generalized slowing. Thus, we will focus on the accuracy difference in which there was a clear and significant decrement in performance in DD for words and faces over cars.

#### 6. Discussion

The purpose of the current research was twofold. The first goal was to inform the ongoing debate regarding the selectivity of the behavioral deficit in developmental dyslexia (DD), by examining whether the disorder is restricted to the processing of written words or affects the recognition of other visual stimuli, such as faces, as well. The second, related goal was to test the predictions of a recent theoretical proposal (Behrmann & Plaut, 2013; Plaut & Behrmann, 2011) that the mechanisms of word and face recognition are not independent, as traditional theories assume, but become interdependent over the course of development because they compete for proximity to the same neural resources (high-acuity visual information in bilateral ventral occipitotemporal cortex). Word representations further compete for proximity to phonological information, which is typically left-lateralized. As a result, initially, bilateral face representations become increasingly somewhat more right-lateralized over the course of reading acquisition in response to greater competition from word representations in the LH.

Thus, on this account, deficits in word recognition should have direct implications for the overall level of

performance and hemispheric organization of face processing. In particular (and as discussed in the Introduction), an abnormality in left VOT per se should impair faces well, albeit to a lesser extent than words, but should leave their relative hemispheric organization unaffected (as the pressure to left-lateralized word representations would be unchanged). On the other hand, an abnormality of LH phonological processing outside of left VOT should reduce the LH advantage for words and give rise to more bilateral organization but leave faces unaffected.

### 6.1 DD recognition of stimuli other that words

Our initial experiments with a group of adult individuals with DD confirmed the deficit in word recognition, as reflected in performance both on standardized tests and on more experimental-based measures. Individuals with DD performed significantly more slowly than matched controls when required to name words aloud and they made more errors and responded more slowly in a word/nonword lexical decision task. DD individuals, relative to controls, also exhibited a disproportionate increase in RT as a function of length for non-words compared with words.

Importantly, impaired processing in DD was not limited to words but was also evident for faces. First, although individuals with DD showed the normal face inversion effect (poorer performance on inverted vs. upright faces), as is also the case with individuals with pure alexia following left VOT damage (Behrmann & Plaut, 2013), they matched faces more slowly than controls. DDs also showed an exaggerated cost, relative to controls, when target and distractor differed in viewpoint. Moreover, DD participants were significantly poorer than controls at discriminating between faces morphed to be more or less similar to one another (especially as the different faces were increasingly alike perceptually). These findings provide clear evidence for an impairment in face perception in DD on several different tasks. Although one might argue that our sample size was relatively small and that the group differences (and interactions with experimental variables) might have been even more evident

with a larger sample, we note that the findings are stable over the various experiments i.e. a deficit in face processing was observed over multiple, different experimental paradigms.

The few previous investigations that have targeted more perceptual aspects of face perception have also revealed differences in the behavioral and neural profiles of DD and control participants. For example, in one earlier MEG study that characterized both behavioral and electrophysiological responses, DD individuals were both less accurate in a facial recognition task and were slower in judging the similarity of faces (Tarkiainen, Helenius, & Salmelin, 2003). Additionally, these same DD individuals showed reduced activation of the right parietotemporal cortex at about 250 ms after stimulus onset.

Also, a relatively recent meta-analysis of fMRI studies identified a different neural pattern in DD compared with controls, but in this case, the study revealed that the most consistent hypo-activation was found in the left occipitotemporal region. This finding is also congruent with experiments suggesting an early failure to engage this system in children with dyslexia (Maurer et al., 2007) and in kindergartners bearing a genetic predisposition for the disorder (Raschle et al., 2012).

It is also important to consider how the current findings can be reconciled with some previous studies that have yielded apparently contradictory results. Specifically, whereas some studies have also found impairments in face processing by individuals with DD (Tarkiainen et al., 2003), a number of other studies have not (Brachacki et al., 1994; Smith-Spark & Moore, 2009). One factor that may have contributed to discrepancies in the literature concerns task difficulty. In our task with morphed faces, there was no difference between the DD and control groups in the easy discrimination condition; the difference was evident only in the more perceptually taxing conditions. We note too that Gregory et al. (1994) reported no difference between the DD and control groups but acknowledged that a ceiling effect in their face processing task may have precluded observing any differences. Other studies that also failed to reveal differences in face processing in DD and controls (Rüsseler et al., 2003) did not tap into perceptual processing per se but rather tested memory or naming of faces under unlimited exposure. The

pattern of the current results suggests that more perceptual demanding conditions are important for revealing face processing deficits in those with DD (Nicolson & Fawcett, 1990).

The current data are consistent with an accumulating body of evidence establishing a close relationship between face and word processing, and distributed rather than domain-specific networks for word and face processing. For example, patients with prosopagnosia and pure alexia exhibited processing impairments that were not restricted to the domain of expected impairment (Behrmann & Plaut, 2012); thus, individuals with pure alexia following a unilateral LH lesion also showed a deficit for face recognition, albeit not as great as in individuals with prosopagnosia following a unilateral RH lesion, and prosopagnosics exhibited an impairment in word recognition, although, again, not as severe as in the pure alexics. Also consistent with the interdependence of these domains, Moore, Brendel, and Fiez (2014) demonstrated that a patient with pure alexia was much poorer than controls at learning an artificial writing system in which faces (instead of letters) corresponded to phonemes. Lastly, and perhaps not surprisingly in light of the behavioral co-occurrences describe here, in a recent neuroimaging study, 10-year-olds with DD showed reduced activation to words in the left VWFA and to faces in the right FFA compared to controls (Monzalvo, Fluss, Billard, Dehaene, & Dehaene-Lambertz, 2012). Furthermore, the BOLD response for face stimuli was significantly more right lateralized among typical readers compared with DD participants, whereas both groups showed similar right-lateralization for other categories such as chalkboards and houses using whole brain asymmetry analyses.

# 6.2 Hemispheric organization of visual representations in DD

To address the second goal of the study, we used lateralized visual presentation to examine the hemispheric organization of word and face processing (relative to cars) in DD and matched control participants. The DD individuals performed significantly less accurately than the controls on both faces and words (and to an even greater degree on faces). Performance on cars was equally accurate across

the groups. Also, within-group comparisons showed that controls performed equivalently across all stimulus categories in accuracy, but that the DD participants were less accurate in matching faces and words than cars and that their performance in matching faces and words did not differ. Thus, both face and word processing were affected in DD and there was slowing in response for all visual categories. We interpret this last finding with caution given the well-known generalized slowing in RT in DD. As expected given the well-established hemispheric specialization literature, we observed higher accuracy for words presented to the LH than RH, and higher accuracy for faces presented to the RH than LH, but this held equally across the two groups.

These results provide additional support for the co-occurrence of word and face processing deficits in DD but, interestingly, do not indicate an atypical pattern of lateralization in DD. The findings support the Behrmann and Plaut (2013) theoretical proposal under the assumption that DD individuals have an abnormality within VOT itself that impairs both word and face processing. The finding of normal laterality of face and word processing in DD suggests that the underlying abnormality involves visual representation per se, and not solely deficits in language-related areas that interact with visual word representations.

## 6.3 Word and face recognition: consideration of heterogeneity

Finally, it is important to address how our findings and account can be reconciled with the substantial documented heterogeneity of symptoms (and presumed causes) of DD. A prominent hypothesis is that DD arises from a primary deficit in access to, and manipulation of, phonological representations (Snowling, 2000) and, indeed, phonological deficits are among the most common symptoms associated with DD (Vellutino et al., 2004). However, DD also includes symptoms that are not directly phonological, such as sensory and attention deficits (Farmer & Klein, 1995; Valdois, Bosse, & Tainturier, 2004). Moreover, other findings seem to implicate a procedural learning deficit (Gabay, Schiff,

& Vakil, 2012a, 2012b; R. Nicolson & Fawcett, 1990; R. I. Nicolson & Fawcett, 2011), such that individuals with DD have difficulty automatizing skills and must rely on conscious strategies to compensate.

That our findings of impaired face processing in DD held at a group level despite the presumed heterogeneity of our DD population speaks to the pervasiveness of the effects. This result notwithstanding, future research might attempt to determine whether particular subtypes of DD exhibit greater impairment in face processing compared to others. At first glance, it might seem obvious that those with more directly visual problems would have the greatest problems with face processing. However, it is important to keep in mind that visual word representations develop not only under the influence of bottom-up visual information but also on the basis of interacting with top-down language/phonological information (Price & Devlin, 2011). In this way, a deficit in phonological processing (or perhaps even one in procedural learning) might indirectly cause abnormalities in visual word representations which, due to partial sharing of neural resources, subsequently compromise face representations. Additionally, our study includes a group of high-achieving young adults with dyslexia. It may be suggested that our results are all the stronger for being clearly evident in a group of high-achieving young adults with dyslexia. Nevertheless, caution is warranted in extending these results broadly; further evidence will be necessarily to determine whether these impairments extend to samples of dyslexics who are not university students.

In summary, detailed behavioral testing of individuals with developmental dyslexia (DD) revealed concurrent deficits in face and word processing. The particular association of word and face processing deficits is surprising under the standard view that these domains are processed by independent mechanisms, but follows directly from a theoretical proposal in which word and face representations compete during development to be near high-acuity visual information (Behrmann & Plaut, 2013; Plaut & Behrmann, 2011). In addition, our finding of normal laterality of face and word

processing in DD suggests that the underlying abnormality involves visual representation per se, and not solely deficits in language-related areas that interact with visual word representations.

#### 7. References

- Behrmann, M., & Plaut, D. C. (2012). Bilateral hemispheric processing of words and faces: evidence from word impairments in prosopagnosia and face impairments in pure alexia. *Cerebral Cortex*, bhs390.
- Behrmann, M., & Plaut, D. C. (2013). Distributed circuits, not circumscribed centers, mediate visual recognition. *Trends in Cognitive Sciences*, *17*(5), 210-219.
- Brachacki, G. W., Fawcett, A. J., & Nicolson, R. I. (1994). Adults with dyslexia have a deficit in voice recognition. *Perceptual and Motor Skills*, 78(1), 304-306.
- Bruce, V., Valentine, T., & Baddeley, A. (1987). The basis of the 3/4 view advantage in face recognition. *Applied Cognitive Psychology*, 1(2), 109-120.
- Brunswick, N., McCrory, E., Price, C., Frith, C., & Frith, U. (1999). Explicit and implicit processing of words and pseudowords by adult developmental dyslexics A search for Wernicke's Wortschatz? *Brain*, *122*(10), 1901-1917.
- Clark, K. A., Helland, T., Specht, K., Narr, K. L., Manis, F. R., Toga, A. W., & Hugdahl, K. (2014).

  Neuroanatomical precursors of dyslexia identified from pre-reading through to age 11. *Brain*, awu229.
- de Beer, J., Engels, J., Heerkens, Y., & van der Klink, J. (2014). Factors influencing work participation of adults with developmental dyslexia: a systematic review. *BMC Public Health*, 14, 77. doi: 10.1186/1471-2458-14-77
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, 56(2), 384-398.
- Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences*, 15(6), 254-262.
- Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Nunes Filho, G., Jobert, A., . . . Cohen, L. (2010). How learning to read changes the cortical networks for vision and language. *Science*, *330*(6009), 1359-1364.
- Démonet, J.-F., Taylor, M. J., & Chaix, Y. (2004). Developmental dyslexia. *The Lancet, 363*(9419), 1451-1460.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2013). The joint development of hemispheric lateralization for words and faces. *Journal of Experimental Psychology: General, 142*(2), 348.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2014a). An ERP investigation of the codevelopment of hemispheric lateralization of face and word recognition. *Neuropsychologia, 61,* 315-323.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2014b). Variable Left-hemisphere Language and Orthographic Lateralization Reduces Right-hemisphere Face Lateralization.

- Facoetti, A., Zorzi, M., Cestnick, L., Lorusso, M. L., Molteni, M., Paganoni, P., . . . Mascetti, G. G. (2006). The relationship between visuo-spatial attention and nonword reading in developmental dyslexia. *Cognitive Neuropsychology*, 23(6), 841-855.
- Farmer, M. E., & Klein, R. M. (1995). The evidence for a temporal processing deficit linked to dyslexia: A review. *Psychonomic Bulletin & Review*, *2*(4), 460-493.
- Gabay, Y., Schiff, R., & Vakil, E. (2012a). Attentional requirements during acquisition and consolidation of a skill in normal readers and developmental dyslexics. *Neuropsychology*, 26(6), 744.
- Gabay, Y., Schiff, R., & Vakil, E. (2012b). Dissociation between the Procedural Learning of Letter Names and Motor Sequences in Developmental Dyslexia. *Neuropsychologia*, *50*(10), 2435-2441.
- Habib, M., & Giraud, K. (2012). Dyslexia. Handbook of clinical neurology, 111, 229-235.
- Hari, R., & Kiesilä, P. (1996). Deficit of temporal auditory processing in dyslexic adults. *Neuroscience Letters*, 205(2), 138-140.
- Hasko, S., Groth, K., Bruder, J., Bartling, J., & Schulte-Körne, G. (2013). The time course of reading processes in children with and without dyslexia: an ERP study. *Frontiers in Human Neuroscience*, 7.
- Hasko, S., Groth, K., Bruder, J., Bartling, J., & Schulte-Körne, G. (2014). What does the brain of children with developmental dyslexia tell us about reading improvement? ERP evidence from an intervention study. *Name: Frontiers in Human Neuroscience*, 8, 441.
- Heim, S., Pape-Neumann, J., van Ermingen-Marbach, M., Brinkhaus, M., & Grande, M. (2014). Shared vs. specific brain activation changes in dyslexia after training of phonology, attention, or reading. *Brain Structure and Function*, 1-17.
- Holmes, D. R., & McKeever, W. F. (1979). Material specific serial memory deficit in adolescent dyslexics. *Cortex*, *15*(1), 51-62.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17(11), 4302-4311.
- Kucera, H., & Francis, W. Computational analysis of present-day American English, 1967. *Brown, Providence*.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center–periphery organization of human object areas. *Nature Neuroscience*, *4*(5), 533-539.
- Lum, J. A., Ullman, M. T., & Conti-Ramsden, G. (2013). Procedural learning is impaired in dyslexia: Evidence from a meta-analysis of serial reaction time studies. *Research in Developmental Disabilities*, 34(10), 3460-3476.
- Maisog, J. M., Einbinder, E. R., Flowers, D. L., Turkeltaub, P. E., & Eden, G. F. (2008). A Meta-analysis of Functional Neuroimaging Studies of Dyslexia. *Annals of the New York Academy of Sciences*, 1145(1), 237-259.
- Marcus, M. P., Marcinkiewicz, M. A., & Santorini, B. (1993). Building a large annotated corpus of English: The Penn Treebank. *Computational Linguistics*, 19(2), 313-330.
- Marotta, J. J., McKeeff, T. J., & Behrmann, M. (2002). The effects of rotation and inversion on face processing in prosopagnosia. *Cognitive Neuropsychology*, 19(1), 31-47.

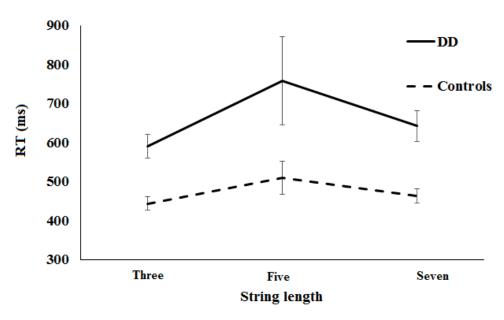
- Maurer, U., Brem, S., Bucher, K., Kranz, F., Benz, R., Steinhausen, H.-C., & Brandeis, D. (2007). Impaired tuning of a fast occipito-temporal response for print in dyslexic children learning to read. *Brain*, 130(12), 3200-3210.
- Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., & Dehaene-Lambertz, G. (2012). Cortical networks for vision and language in dyslexic and normal children of variable socioeconomic status. *Neuroimage*, 61(1), 258-274.
- Moore, M. W., Brendel, P. C., & Fiez, J. A. (2014). Reading faces: Investigating the use of a novel face-based orthography in acquired alexia. *Brain and Language*, 129, 7-13.
- Nergård-Nilssen, T., & Hulme, C. (2014). Developmental Dyslexia in Adults: Behavioural Manifestations and Cognitive Correlates. *Dyslexia*.
- Nicolson, R., & Fawcett, A. (1990). Automaticity: A new framework for dyslexia research? *Cognition*, *35*(2), 159-182.
- Nicolson, R. I., & Fawcett, A. J. (2011). Dyslexia, dysgraphia, procedural learning and the cerebellum. *Cortex, 47*(1), 117-127.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature*, 331(6157), 585-589.
- Plaut, D. C., & Behrmann, M. (2011). Complementary neural representations for faces and words: A computational exploration. *Cognitive Neuropsychology*, 28(3-4), 251-275.
- Price, C. J., & Devlin, J. T. (2011). The interactive account of ventral occipitotemporal contributions to reading. *Trends in Cognitive Sciences*, *15*(6), 246-253.
- Pugh, K. R., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., . . . Shaywitz, B. A. (2000). Functional neuroimaging studies of reading and reading disability(developmental dyslexia). *Mental Retardation and Developmental Disabilities Research Reviews, 6*(3), 207-213.
- Raschle, N. M., Zuk, J., & Gaab, N. (2012). Functional characteristics of developmental dyslexia in left-hemispheric posterior brain regions predate reading onset. *Proceedings of the National Academy of Sciences*, 109(6), 2156-2161.
- Raven, J. Court, JH, & Raven, J.(1992). Standard progressive matrices. *Manual for Raven's Progressive Matrices and Vocabulary Scales*.
- Richlan, F., Kronbichler, M., & Wimmer, H. (2012). Structural abnormalities in the dyslexic brain: A meta-analysis of voxel-based morphometry studies. *Human Brain Mapping*. doi: 10.1002/hbm.22127
- Roberts, D. J., Woollams, A. M., Kim, E., Beeson, P. M., Rapcsak, S. Z., & Ralph, M. A. L. (2012). Efficient visual object and word recognition relies on high spatial frequency coding in the left posterior fusiform gyrus: evidence from a case-series of patients with ventral occipito-temporal cortex damage. *Cerebral Cortex*, bhs224.
- Rüsseler, J., Johannes, S., & Münte, T. F. (2003). Recognition memory for unfamiliar faces does not differ for adult normal and dyslexic readers: an event-related brain potential study. *Clinical Neurophysiology*, 114(7), 1285-1291.
- Salmelin, R., Service, E., Kiesila, P., Uutela, K., & Salonen, O. (1996). Impaired visual word processing in dyslexia revealed with magnetoencephalography. [Comparative Study]. *Ann Neurol*, 40(2), 157-162. doi: 10.1002/ana.410400206

- Schneider, W., Eschman, A., Zuccolotto, A., & Guide, E.-P. U. s. (2002). Psychology Software Tools Inc. *Pittsburgh*, *USA*.
- Schulte-Körne, G., & Bruder, J. (2010). Clinical neurophysiology of visual and auditory processing in dyslexia: A review. *Clinical Neurophysiology*, *121*(11), 1794-1809.
- Shaywitz, S. E., Fletcher, J. M., Holahan, J. M., Shneider, A. E., Marchione, K. E., Stuebing, K. K., . . . Shaywitz, B. A. (1999). Persistence of dyslexia: the Connecticut Longitudinal Study at adolescence. [Comparative Study
- Research Support, U.S. Gov't, P.H.S.]. *Pediatrics*, 104(6), 1351-1359.
- Smith-Spark, J. H., & Moore, V. (2009). The representation and processing of familiar faces in dyslexia: Differences in age of acquisition effects. *Dyslexia*, *15*(2), 129-146.
- Snowling, M. J. (2000). Dyslexia: Blackwell Publishing.
- Stein, J., & Walsh, V. (1997). To see but not to read; the magnocellular theory of dyslexia. *Trends in Neurosciences, 20*(4), 147-152.
- Tarkiainen, A., Helenius, P., & Salmelin, R. (2003). Category-specific occipitotemporal activation during face perception in dyslexic individuals: an MEG study. *Neuroimage*, 19(3), 1194-1204.
- Thomas, C., Moya, L., Avidan, G., Humphreys, K., Jung, K. J., Peterson, M. A., & Behrmann, M. (2008). Reduction in white matter connectivity, revealed by diffusion tensor imaging, may account for age-related changes in face perception. *Journal of Cognitive Neuroscience*, 20(2), 268-284.
- Torgesen, J. K., Wagner, R., & Rashotte, C. (1999). TOWRE–2 Test of Word Reading Efffciency.
- Troje, N. F., & Bülthoff, H. H. (1996). Face recognition under varying poses: The role of texture and shape. *Vision Research*, *36*(12), 1761-1771.
- Valdois, S., Bosse, M. L., & Tainturier, M. J. (2004). The cognitive deficits responsible for developmental dyslexia: Review of evidence for a selective visual attentional disorder. *Dyslexia*, *10*(4), 339-363.
- Vellutino, F. R., Fletcher, J. M., Snowling, M. J., & Scanlon, D. M. (2004). Specific reading disability (dyslexia): What have we learned in the past four decades? *Journal of Child Psychology and Psychiatry*, 45(1), 2-40.
- Vidyasagar, T. R., & Pammer, K. (2010). Dyslexia: a deficit in visuo-spatial attention, not in phonological processing. *Trends in Cognitive Sciences*, *14*(2), 57.
- Vogel, A. C., Petersen, S. E., & Schlaggar, B. L. (2014). The VWFA: it's not just for words anymore. *Frontiers in Human Neuroscience*, 8.
- Wandell, B. A., Rauschecker, A. M., & Yeatman, J. D. (2011). Learning to see words. *Annual Review of Psychology*, 63, 31-53.
- Wolf, M., & Denckla, M. B. (2005). *RAN/RAS: Rapid automatized naming and rapid alternating stimulus tests*: Pro-ed.

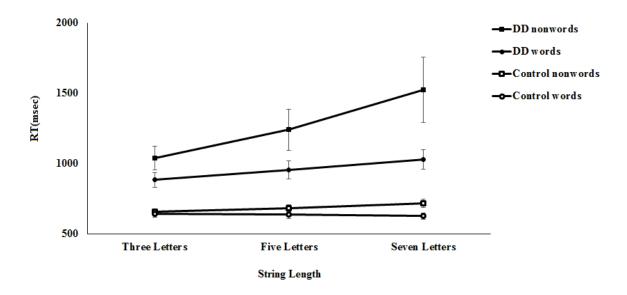
Table 1- Demographic and Psychometric data of DD and control groups

Measure	Group			
	DD	Controls	р	Section
Age (in years)	21.41	22.91	n.s.	2, 3
	21.54	22.63	n.s.	4
Raven	56.5	57.91	n.s.	2, 3
	56.45	58.18	n.s.	4
Digit span <sup>a</sup>	11.08	13	n.s.	2, 3
	10.9	13.5	<.05*	4
RAN objects <sup>a</sup>	101.5	114	=.07	2, 3
	103.45	117.45	<.05*	4
RAN colorsª	96.66	110.58	<.01**	2, 3
	100.09	110.45	<.05*	4
RAN numbersª	105.5	112.33	<.01**	2, 3
	106.90	114.18	<.01**	4
RAN letters <sup>a</sup>	102.16	109.75	<.01**	2, 3
	103.54	112.27	<.01**	4
WRMT-R WIª	97.41	113.08	<.01**	2, 3
	99.81	113.72	<.01**	4
WRMT-R WAª	94.83	115.33	<.01**	2, 3
	98.72	115.63	<.01**	4
Towre SA (A+B) ª	95.66	113.16	<.01**	2, 3
	100.09	113.81	<.01**	4
Towre PD (A+B) <sup>a</sup>	88.08	115.08	<.01**	2, 3
	91.36	115.45	<.01**	4
Spoonerism time	139.166	98.25	<.05*	2, 3
	132.09	95.81	<.05*	4
Spoonerism accuracy	8.25	11.33	<.01*	2, 3
	8.45	11.27	<.05*	4

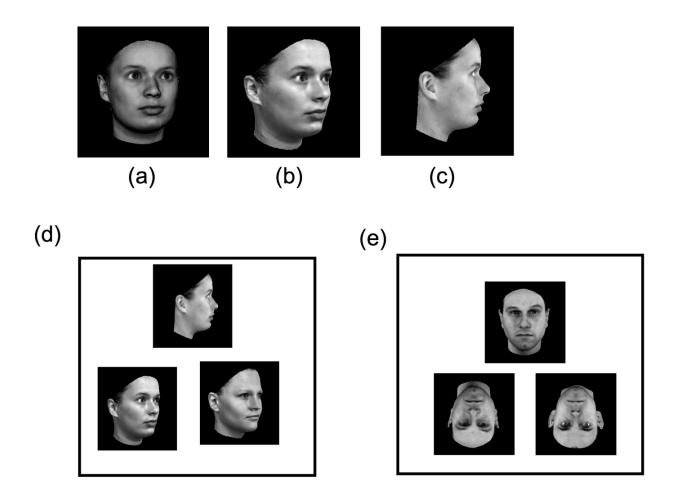
<sup>\*</sup> p < .05, \*\* p < .01.  $^{a}$ Standard scores, other raw scores. Numbers represent means. Section 2, 3 relate to data from the word and face processing experiments, whereas section 4 relates to data of the hemispheric lateralization experiment.



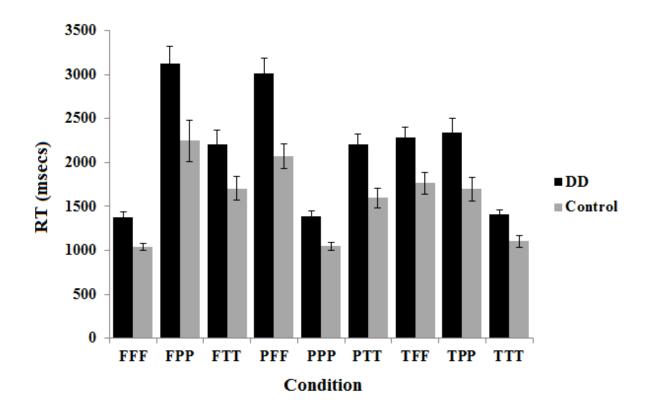
**Figure 1:** Mean RT (and +/-1 SE) as a function of word length for the DD and the control group during naming latency.



**Figure 2:** Mean RT (and +/-1 SE) for the DD and control groups as a function of length in the lexical decision task.

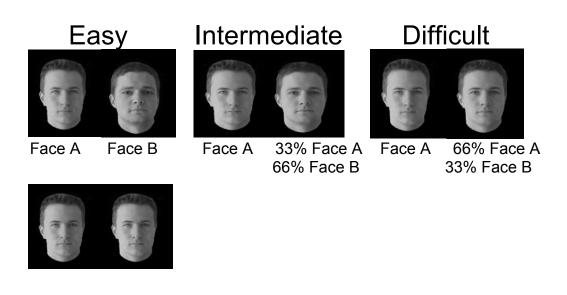


**Figure 3:** Examples of stimuli and display from viewpoint manipulation face experiment. Examples of (a) Frontal (b) three-quarter and (c) profile view of a single face. (d) Display of upright target on top and two upright choices for left/right decision below and (e) Display of upright target on top and two inverted choices for left/right decision below.



**Figure 4:** Mean RT (and +/- 1 SE) of the control and the DD groups as a function of condition during face matching task. F=Frontal, T=three-quarters, p=profile.

(a)



(b)

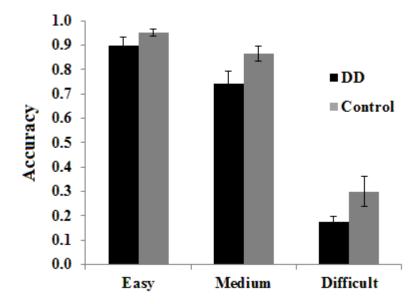
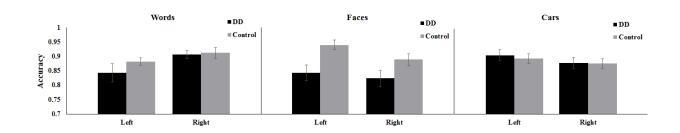


Figure 5: (a) Example trials: face discrimination. Top row: Different trials, from left to right (i) an easy discrimination pair, (ii) an intermediate discrimination pair and (4) a difficult discrimination pair; Bottom row: Example same trial. (b) Mean accuracy as a function of level for the DD and control groups during face discrimination

(a)



(b)



**Figure 6: (a)** Example of a pair of faces, words and cars used in the half-field lateralization study **(b)** Mean accuracy for DD and control groups as a function of stimulus type and hemi-field.