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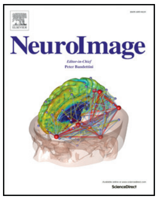

Orthographic processing deficits in developmental dyslexia: Beyond the ventral visual stream

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ABSTRACT

Fast effortless reading has been associated with the Visual Word Form Area (VWFA), a region in the ventral visual stream that specializes in the recognition of letter strings. Several neuroimaging studies of dyslexia revealed an underactivation of this region. However, most of these studies used reading tasks and/or were carried out on adults. Given that fluent reading is severely impaired in dyslexics, any underactivation might simply reflect a well-established reading deficit in impaired readers and could be the consequence rather than the cause of dyslexia. Here, we designed a task that does not rely on reading per se but that tapped early visual orthographic processing that forms the basis of reading. Dyslexic children aged 8–12 years and age-matched controls were asked to search for letters, digits, and symbols in 5-element strings (Experiment 1). This novel task was complemented by a classic task known to activate the VWFA, namely the passive viewing of pseudowords and falsefonts (Experiment 2). We found that in addition to significant group differences in the VWFA, dyslexic children showed a significant underactivation of the middle occipital gyrus (MOG) relative to the control group. Several areas in the MOG are known for their engagement in visuospatial processing, and it has been proposed that the MOG is necessary for ordering the symbols in unfamiliar strings. Our results suggest that the VWFA deficit might be secondary to an impairment of visuospatial processing in the MOG. We argue that efficient processing in MOG in the course of reading acquisition is critical for the development of effortless fast visual word recognition in the VWFA.

1. Introduction

Learning to read is one of the most important educational milestones in a child's development. Normally developing children typically achieve fluent reading between 2nd and 4th grades depending on the orthography of the language (Vaessen et al., 2010; Ziegler and Goswami, 2005). During this important period, children's reading ability undergoes a transition from rather serial letter-by-letter decoding to parallel processing of words as a whole. Critically, children with developmental dyslexia (~5–15% of children in primary school) fail to make this transition. As a consequence, many of them will never develop fast automatic word recognition and fluent reading despite normal intelligence, adequate educational opportunities and in the absence of any obvious neurological or sensory deficiencies (Shaywitz and Shaywitz, 2005; Snowling, 2001).

1.1. Orthographic processing deficits in dyslexia

There is a tremendous amount of research on the neural basis of phonological processing deficits and how such deficits affect phonological decoding and therefore reading development (for review, see Paulesu et al., 2014). However, much less is known about basic orthographic processing deficits in dyslexia. Yet, children with dyslexia exhibit deficits in processing letter strings in tasks with minimal phonological or lexical involvement, such as when being asked to search for a target letter in an unpronounceable string of consonants (Bosse et al., 2007; Collis et al., 2013; Hawelka et al., 2006; Ziegler et al., 2010). The first explanation that comes to mind is that these deficits are simply the consequences of the weaker reading experience of children with dyslexia. However, the same deficits can be found with digit strings (Collis et al., 2013; Hawelka et al., 2006; Ziegler et al., 2010), which

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Abbreviations: PPC, posterior parietal cortex; vOT, ventral occipitotemporal; VWFA, Visual Word Form Area; fMRI, functional magnetic resonance imaging; SPL, superior parietal lobule; RAN, rapid automatic naming; EPI, echo-planar imaging; MNI, Montreal Neurological Institute; DARTEL, Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra; FWE, familywise error; ROI, region of interest; BOLD, blood oxygenation level dependent; MOG, middle occipital gyrus; SVM, support vector machine; IPS, intraparietal sulcus; IPL, inferior parietal lobule; DMN, default mode network.

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undermines this explanation. Some authors have explained these deficits in terms of poor visual attentional processing (Dubois et al., 2010; Valdois et al., 2003; Vidyasagar and Pammer, 2010). Indeed, it has been shown that dyslexics who had the weakest performance in letter-in-string perception benefited the most from increased letter spacing, which has the effect of reducing the lateral masking of letters called crowding (Gori and Facoetti, 2015; Zorzi et al., 2012). Others have attributed poor letter-in-string perception to deficient letter position coding. Indeed, Collis et al. (2013) used a partial report task with letter, digit, and symbol strings. The response alternatives included other characters in the string, which made it possible to investigate position as well as intrusion errors. As in Ziegler et al. (2010), dyslexics performed significantly worse than age-matched controls with letter and digit strings but not with symbol strings. However, the dyslexics' deficits with letter string stimuli were limited to position errors, specifically at the string-interior positions 2 and 4. These results were taken to suggest that dyslexics have a deficit in processing a string of letters in parallel, probably due to difficulty in the coding of letter position.

The literature on letter-in-string processing can be placed in the more general context of deficits in visual search in dyslexia. Indeed, in classic visual search tasks using symbols, it has been shown that dyslexic children exhibited longer search times with an increasing number of distractors than age-matched controls (Casco et al., 1998; Vidyasagar and Pammer, 1999). Similarly, dyslexic children performed below their control peers in tasks where they had to report the number of elements belonging to a certain category in a string of symbols (Lobier et al., 2012b; Valdois et al., 2012). Moreover, serial visual search abilities in kindergarten were found to be predictive of future reading skills at first and second grades of primary school (Franceschini et al., 2012; Gori et al., 2015).

1.2. The link between focused attention and reading

What is the link between visual search and reading? Clearly, during beginning reading, letters are recognized sequentially, with only a few letters being processed at a time. In current computational models of reading aloud (Perry et al., 2013, 2010, 2007,), this process has been implemented as an attentional window that moves across a letter string and provides the input to the phonological decoding network, which is necessary for orthographic learning (Ziegler et al., 2014). Focused spatial attention is needed for this operation. The visual guidance of attention is achieved through the dorsal stream, which receives its major input from the magnocellular system (see Vidyasagar and Pammer, 2010). The magnocellular dorsal pathway consists of large heavily myelinated neurons with fast conduction velocity, it passes dorsally to the visual motion-sensitive areas (MT/V5) situated at the occipitotemporal junction and from there onto the posterior parietal cortical (PPC) angular and supramarginal gyrus. Although it has been known for a long time that these areas are important for reading, it has recently been suggested that the angular and supramarginal gyri are involved in focusing visual attention very rapidly on the letters and their order in words rather than associating the visual form of a word with its sound and meaning (Stein, 2014). The visual part of this association is achieved by the ventral occipitotemporal cortex (vOT), which hosts the Visual Word Form Area (VWFA).

The VWFA is located in the fusiform gyrus. It receives its main input from the parvocellular system, and its main function is to detect the texture, form and colour of objects. The ventral route, which hosts the VWFA, can recognize letter strings but it cannot code their precise location, which of course is vital for reading development. Hypothetically, the rapid dorsal route provides feedback to V1 and the VWFA about where to attend in order to identify letters and specify their order in a word (Vidyasagar and Pammer, 2010). Thus, during reading development, the dorsal stream might allocate attention to appropriate areas of text, thus providing feedback to the ventral stream to allow fined-grained analyses of letters (Jones et al., 2008).

1.3. fMRI studies on dyslexia

There are an increasing number of neuroimaging studies on dyslexia (for reviews and meta-analyses, see Martin et al., 2015; Norton et al., 2015; Paulesu et al., 2014; Richlan et al., 2011, 2009). Almost all of them showed an underactivation of the vOT area in dyslexics (Blau et al., 2010; Brunswick et al., 1999; Horwitz et al., 1998; Kronbichler et al., 2004; Paulesu et al., 2001; Shaywitz et al., 2002, 1998; van der Mark et al., 2009). This is not really surprising because the vOT contains the Visual Word Form Area (VWFA), a region specifically tuned to process letter strings (Cohen et al., 2002; Dehaene and Cohen, 2011; Dehaene et al., 2002). Because activation in this region increases with reading skill, Shaywitz et al. (2002) referred to the left vOT as a “reading skill zone”. Because reading skills are impaired in dyslexia, it seems obvious to find an underactivation of the vOT in dyslexia (Sandak et al., 2004; Shaywitz and Shaywitz, 2005).

Some authors have suggested that the dysfunctional activation of the VWFA is secondary to a primary dysfunction of the temporoparietal reading system involved in controlled attention-demanding grapheme–phoneme processing and phonological decoding (McCandliss and Noble, 2003; Pugh et al., 2000). Several neuroimaging studies demonstrated underactivation of this left temporoparietal reading system, which includes the posterior superior temporal, supramarginal and angular gyri (Backes et al., 2002; Hoeft et al., 2006; Shaywitz et al., 2002; Temple et al., 2001). As suggested above, these regions might be involved in phonological decoding precisely because they make it possible to select graphemes, which are the input to the phonological decoding network.

In a recent meta-analysis of all neuroimaging studies on dyslexia published until September 2013, only three studies investigated letter-string processing with minimal lexical or phonological involvement (Peyrin et al., 2012; Reilhac et al., 2013; Temple et al., 2001). Studies from the Valdois group, including a recent fMRI study using adult dyslexics (Lobier et al., 2014), showed an underactivation of the bilateral superior parietal lobule (SPL) in processing letter or symbol strings. The activation of the posterior parietal cortex was found to be stronger for multiple-element than for single-element processing in skilled adult readers (Lobier et al., 2012a), which is supportive of its role in focusing attention. The study by Temple et al. (2001) showed reduced activation in extrastriate regions in letter matching, which included bilateral (left greater than right) middle/superior occipital gyrus and superior parietal lobe.

1.4. The present study

The goal of the present study was to investigate the interplay between the dorsal and ventral streams in basic orthographic processing, which involves processing of letter identities and letter position. Previous studies found a general underactivation of the VWFA in dyslexic readers. However, these studies are not very informative with respect to a causal deficit in orthographic processing because subjects were either asked to read out loud (Brunswick et al., 1999; Kronbichler et al., 2004; Paulesu et al., 2001), perform a rhyming task (Backes et al., 2002; Hoeft et al., 2006; Shaywitz et al., 1998) or make lexical or semantic decisions (Shaywitz et al., 2002, 1998; van der Mark et al., 2011, 2009) on words, pseudowords, irregular words or even sentences. Thus, underactivation can be expected because of the lack of reading experience. In particular, many of the studies scanned adult dyslexics, which leaves open possibility that the underactivations found in either the ventral stream (Brunswick et al., 1999; Paulesu et al., 2001; Shaywitz et al., 1998) or the parietal lobe (Lobier et al., 2014) are a consequence of long lasting deficits in reading fluency that occur earlier in development. In support of this interpretation, Richlan et al.'s (2009) meta-analysis showed that the underactivation in VWFA was mainly found in studies testing adult dyslexics (see also Martin et al., 2015).

Here, we report results from a study, in which we used a visual search task with strings of letters, digits and symbols in children with dyslexia and age-matched controls. Performance was held constant around 80% by increasing exposure duration for each individual adaptively. Letter search in unpronounceable consonant strings is known to tap the Visual Word Form Area but the task does not rely on reading per se. The comparison between letter strings and digit strings allowed us to control for the fact that children with dyslexia might encounter letters less often due to their lack of reading experience but the same is not true for digits. The comparison between letter and symbol strings ($}#%\) allowed us to assess visual–attentional processes in the absence of alphanumeric information. Our attention-demanding visual search task on letters, digits and symbols is compared with a classic implicit reading task, in which subjects passively view pseudowords and falsefonts. This task is known to selectively activate the VWFA.

2. Materials and methods

2.1. Participants

Thirty three native French speaking children (mean age: 11.5 years, min: 8.3, max: 12.6) participated in the study, 15 of which were dyslexic. Their characteristics and test results are presented in Table 1. The dyslexic children were recruited through a national reference centre for the diagnosis of learning impairments (Centre de Reference des Troubles des Apprentissages) at the University Hospital La Timone in Marseille, France. Prior to the study, all children received a complete medical, psychological and neuropsychological assessment. Dyslexic children were included in the study if their reading age was at least 18 months below the age norm on a standardized reading test (Alouette; Lefavrais, 1967)[1] and if their nonverbal intelligence was above the 25th percentile on the Standardized Progressive Matrices (Raven, 1976). To make sure that potential deficits in digit processing were not due to the frequent comorbidity between dyslexia and dyscalculia, dyscalculia was used as an exclusion criterion. Most of our dyslexic children would have received standard speech and language therapy (once a week) but none of them was enrolled in a more extensive remediation programme. Control children were recruited from local schools and were selected to match dyslexic children in age and nonverbal IQ. They had no history of written or oral language impairment. All participants had normal or corrected to normal visual acuity. In addition to the standardized reading and nonverbal intelligence tests, all participants completed a standardized single word reading test taken from the ODEDYS neuropsychological battery (Jacquier-Roux et al., 2002) that contains 20 non-words, 20 regular words, and 20 irregular words, a standardized phoneme deletion and phoneme fusion test (Chevrie-Muller et al., 1997), and a rapid automatized naming test (Castel et al., 2008). The study was conducted with the understanding and consent of the participants and their parents. It was approved by the National Ethics Committee for Biomedical Research (RCB: 2011-A00172-39).

2.2. Stimuli and procedure

2.2.1. Experiment 1: Non-reading fMRI task

In this experiment, subjects had to detect a target character within a five element string (Fig. 1A). For each stimulus type, four characters were chosen as targets (G, F, S, T/2, 4, 6, 8/£, µ, <, ?). The position of each individual character within the string was randomized within one block, and the frequency of the positions for all the characters was controlled for. Stimuli were displayed in a 14-point Courier New font in dark grey (RGB: 150,150,150) on a light grey background (RGB: 192,192,192), and subtended 1.90° × 0.57° of the visual angle. Stimuli were presented in separate blocks (Fig. 1C). At the beginning of each block, a cue was presented, which indicated the target that had to be searched for in the strings. This was followed by 6 strings consecutively and the participants' task was to indicate with a mouse click whether or not the target was present in the string. The presentation of the cue lasted for 1000 ms followed by a 1500 ms blank screen. Each string was presented between 17 and 200 ms (adaptive procedure, see below), it was preceded by a 300 ms fixation and followed by a blank screen (1800–1983 ms) during which responses were collected. Every block contained three target-present trials (e.g.: 53271) and three target-absent trials (e.g.: 59317). The target appeared randomly at the first, middle or last position of the string. The sequence of trials within each block was randomized, with the constraint that target-present trials would never appear at the beginning or the end of the block.

The duration of a single string presentation was adjusted on-line at the level of a block by an adaptive procedure that kept the performance at 80%. Thus, when a child's performance dropped below 80%, the stimulus duration was increased by one step (17 ms), when it exceeded 80%, the presentation time decreased by one step, and when performance level was at 80%, it was unchanged. This calculation was performed separately for each stimulus category (i.e. letters, symbols and digits). After each block, a sound feedback (1000 ms) was given indicating the child's performance in a given block. We jittered the interval between the auditory feedback and the last trial between 2000 and 5000 ms to decorrelate the BOLD response to the feedback from the response in the block. The blocks were separated by a 4000–6000 ms fixation. An experimental run consisted of 12 blocks (5 min), 4 runs were presented altogether. Stimuli were presented using E-prime software (PST, Pittsburgh, PA).

2.2.2. Experiment 2: Reading fMRI task

We used a short 7 minute passive viewing task to identify the reading network and compare it with the results of the non-reading task (Fig. 1B). Three types of stimuli were flashed on the screen in 5 s blocks. A block contained either falsefonts, pseudowords or existing French words. All stimuli were six characters long. Falsefonts and pseudowords were presented visually for 200 ms without fixation between the strings. Real words were presented audiovisually for 600 ms, that is, the words were presented both visually and auditorily through MRI compatible ear-phones. There were 6 blocks of each stimulus type. Fixations between the blocks varied between 2200, 3400 or 4600 ms. Participants were instructed to attend carefully to the stimuli. All stimuli were presented in upper case, on a black screen with monospaced 14-point Courier New white fonts (1.90° × 0.57° of the visual angle). Since the main focus of the present article is on the reading network only the first two conditions are reported here. Stimuli were presented using E-prime software (PST, Pittsburgh, PA).

2.3. Acquisition details

Children were trained in a mock scanner prior to the actual experiment. They performed 2 runs from Experiment 1 as a training, during which the stimulus presentation time was continuously adapted as described above. At the end of the training, the final presentation time of the adaptive procedure was memorized for each stimulus type, separately, and entered as a starting value for the fMRI experiment. This ensured optimal presentation time for all children while performing the task in the scanner. Images were acquired on a 3-Tesla Medspec 30/80 Avance MRI whole body scanner (Bruker, Ettlingen, Germany), equipped with a circular polarized head coil. A foam padding and a rigid pillow were applied to restrict head movements in the head coil. The stimuli were projected centrally at the back of the magnet bore, which participants could see through a head coil mounted mirror. For

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[1] Although one control participant scored very low on the Alouette test (18 months below the age norm), we decided to include her in the control group based on her results in the rest of the tests as well as consultations on her progress at school, all of which suggested that her low Alouette score might be due to momentary lapses of attention rather than a reading impairment.

Table 1
Subject characteristics and performance (range) on the standardized IQ, reading, phonological awareness and rapid automatized naming tests.

	Control (N = 18)		Dyslexic (N = 15)		
	Mean	Range	Mean	Range	t
Age (months)	126	(100.86–144.93)	135	(104.56–152.3)	−1.76 (ns.)
RAVEN	33.78	(31–36)	33.33	(28–35)	0.76 (ns.)
Reading delay (months)	6.06	(−18–24)	−30.93	(−54–−15)	8.54***
RAN (s)	43.44	(32–56)	63.33	(41–146)	−3.13***
ODEDYS					
Irregular word reading score /20	18	(12–20)	10	(3–18)	7.11***
Irregular word reading time (s)	18	(11–29)	53	(22–97)	−6.04***
Regular word reading score /20	20	(18–20)	16	(11–20)	5.78***
Regular word reading time (s)	17	(10–30)	46	(19–95)	−5.84***
Nonword reading score /20	17	(14–20)	13	(7–18)	5.09***
Nonword reading time (s)	25	(12–35)	48	(25–70)	−5.94**
Phonological awareness					
Initial phoneme elision /12	12	(11–12)	12	(9–12)	1.54 (ns.)
Phoneme inversion /10	10	(10–10)	10	(6–10)	1.09 (ns.)
Phoneme addition /12	12	(11–12)	11	(9–12)	2.61**
Final phoneme elision /12	12	(12–12)	12	(11–12)	2.05**

Reading delay = difference between the subject's age and his/her results in the Alouette test (Lefavrais, 1967), RAN = rapid automatic naming.
(ns.) = non significant.
** p < .05.
*** p < .001.

functional data acquisition, 36 interleaved axial slices covering the whole brain without the cerebellum were obtained using a T2* weighted echo planar sequence with the following parameters: voxel size = 3 × 3 mm, slice thickness = 3 mm, slice gap = 0 mm, matrix size = 64 × 64, TR = 2,4 s, TE = 30 ms, flip angle = 81,6°. A fieldmap was acquired for geometric distortion correction of EPI images, which was used subsequently to create a voxel displacement map for data processing (Hutton et al., 2002). High resolution T1 weighted structural images

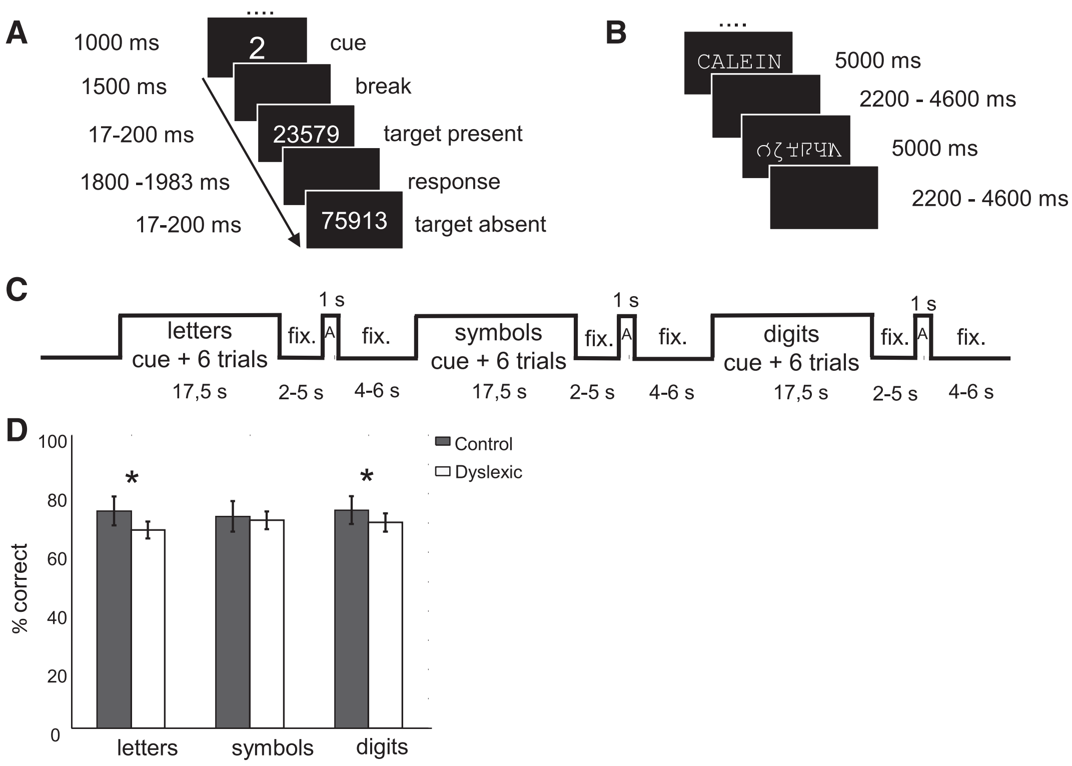

Fig. 1. Design and behavioural results. (A) Experimental procedure for Experiment 1: the non-reading fMRI task. Each stimulus block started with a visual cue indicating the target (e.g. "2"), followed by a 1500 ms blank screen. Then, subjects saw 6 strings of either letters, symbols or digits. The subjects' task was to indicate whether a target character (e.g. "2") was present or absent in the string. Each string was presented for 17–200 ms and was followed by a blank screen (1800–1983 ms) when the responses were collected. The duration of a single string presentation was adjusted by an adaptive procedure to keep the performance near 80%. Every block contained 3 strings with the target (e.g.: 23579) and three strings without the target (e.g.: 75913). The subjects were instructed to respond with their index finger when the target was present and with their third finger when the target was absent. (B) Illustration of Experiment 2: the reading fMRI task: strings of 6 characters were presented either in falsefonts or as pseudowords in a block design (3.6 s duration). (C) Overall flowchart of the experimental run in Experiment 1: stimulus types (letters, symbols, digits) were presented in separate blocks. To encourage the children's engagement in the task, a sound feedback (1000 ms) was presented after each block, indicating the subjects' performance (number of hits). A — sound (auditory) feedback, fix. — fixation cross. (D) Participants' performance in the non-reading fMRI experiment. Percentage of correct responses did not differ significantly between the control and dyslexic children in the symbol condition, but was significantly lower both in the letter and digit conditions.

covering the whole brain were acquired for anatomical data (3D sagittal volume using MPRAGE sequence).

2.4. Data processing

All fMRI data were pre-processed and analysed using the SPM8 software package (Wellcome Department of Imaging Neuroscience, University College London, UK). The first five scans of each run contained no stimulus information and were discarded to allow for signal stabilization. The remaining functional volumes were then corrected for EPI distortion and slice acquisition time, subsequently realigned using rigid body transformations to correct for head movements. The use of the art toolbox (http://www.nitrc.org/projects/artifact_detect/), the software for comprehensive analysis of artefact sources in time series data including spiking and motion led to the exclusion of one control participant from further analysis due to excessive head movements. Additional three dyslexic participants were excluded due to near chance level performance in Experiment 1 combined with excessive head movements. The spatial normalization of the functional data and the structural data into the MNI referential was performed as follows: T1-weighted scans were segmented into six tissue classes — grey matter, white matter, cerebrospinal fluid, skull and non-brain tissues using SPM12 (Ashburner and Friston, 2005; Ashburner, 2007). A study-specific template was then created using the Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL) algorithm and the transformation from this template to the MNI space was estimated. The structural and functional data of each subject were then spatially normalized to the MNI space, thanks to the convolution of both deformation fields (from native space to the DARTEL template and from this latter space to the MNI space). Functional data were finally smoothed with 8 mm (FWHM) Gaussian kernel.

Statistical parametric maps were generated using a linear combination of functions derived by convolving the standard SPM hemodynamic response function with the time series of the stimulus categories. In Experiment 1 we also modelled the auditory feedback and the cues as separate regressors. To control for confounds induced by head motion in the scanner movement parameters were entered in the design matrix as additional regressors of no interest. Individual contrast images were computed for each stimulus type (letters, symbols, digits in Experiment 1 and pseudowords, falsefonts in Experiment 2) minus baseline (fixation) for each session. Individual contrasts were then entered in an ANOVA for random effect group analysis. We used a threshold of $p < 0.001$, uncorrected for multiple comparisons at the voxel level, and a FWE-corrected threshold of $p < 0.05$ at the cluster level (Genovese et al., 2002), except for between-group comparisons where a threshold of $p < 0.001$, uncorrected for multiple comparisons ($k = 40$) was applied. For all analyses, brain regions were reported in accordance with the MNI brain atlas (xjview toolbox, http://www.alivelearn.net/xjview). The cortical maps from the SumsDB database (Dickson et al., 2001; Van Essen et al., 2003) were implemented in Caret 5 software (Van Essen, 2005).

Finally we carried out a region of interest (ROI) analyses for the between group results. To avoid circularity (Kriegeskorte et al., 2010, 2009), we defined the ROIs for the non-reading task based on activations in selected contrasts from the reading task and vice-versa. Thus each task served as a functional localizer for the other task. The search for activated voxels was constrained by a box, with boundaries large enough to encompass the reading activations in the localizer scan and similar activations in the corresponding region reported in the reading literature (see e.g. Szwed et al., 2014, 2011; Cohen and Dehaene, 2004 for the VWFA and Cohen et al., 2008; Monzalvo et al., 2012 for the middle occipital gyrus). Within such borders, ROIs were functionally defined independently for each participant, using the symbol vs. fixation contrast and the pseudowords vs. fixation contrast for the non-reading task and the reading task, respectively. For each subject we determined the 10 most activated voxels in the given localizer experiment. Then, from those voxels, we extracted the parameter estimates of activation for the other experiment, i.e. the experiment being analysed. For example: in the ROI analysis shown in Fig. 7A we determined the 10 voxels that were most activated within the VWFA in Experiment 2, and then we extracted, from those voxels, the parameter estimates for activations in Experiment 1. The activations were averaged first across voxels and then across subjects for each group and condition and entered in a repeated measures ANOVA. Stimulus category (letters, symbols, digits for Experiment 1 and pseudowords and falsefonts for Experiment 2) was selected as the within subject factor and group (controls and dyslexics) as between subject factor to identify significant differences in the selected ROIs (VWFA and middle occipital gyrus). Activation values reported in ROI plots are in arbitrary units proportional to BOLD activation percentage (beta: the regression coefficient estimates).

Table 2
Behavioural measurements for Experiment 1 (the non-reading fMRI task). Presentation time and reaction time reported in milliseconds, performance in percentage of correct trials. Standard deviations are shown in brackets.

	Control (N = 18)	Dyslexic (N = 15)	
	Mean (SD)	Mean (SD)	t
Performance (% correct)	79.26 (11.09)	68.47 (11.49)	*F = 8.94******
Letters	80.32 (10.24)	66.39 (11.17)	3.73***
Symbols	77.49 (13.99)	69.93 (11.52)	1.67 (ns.)
Digits	79.98 (9.06)	69.1 (11.78)	2.99**
Presentation time (ms)	126.72 (48.40)	176.39 (24.90)	*F = 15.19****
Letters	131.88 (52.28)	174.36 (26.49)	−2.85**
Symbols	131.19 (51.64)	182.30 (17.10)	−3.66***
Digits	117.07 (41.28)	172.49 (31.12)	−4.27***
Reaction time (ms)	736.21 (93.70)	703.99 (102.50)	*F = 1.13* (ns.)
Letters	744.26 (104.52)	701.43 (104.44)	1.17 (ns.)
Symbols	733.91 (89.14)	685.16 (104.93)	1.44 (ns.)
Digits	738.52 (98.26)	722.81 (100.07)	.45 (ns.)

(ns.) = non significant.
** p < .05.
*** p < .001.

3. Results

3.1. Behavioural results

Reaction time, accuracy, and duration thresholds (i.e., average stimulus presentation time in the adaptive procedure used in Experiment 1) in the non-reading task are shown in Table 2. Three dyslexic subjects were excluded from the behavioural analysis since they performed at chance level (see also Data processing). For the remaining subjects, three separate 2 × 3 ANOVAs were carried out using reaction times,[2] thresholds, and accuracy as dependent variables. The group (control vs. dyslexic) was used as a between-subject factor and stimulus type (letters, symbols and digits) as a within-subject factor. A significant difference on accuracy was found between the groups ($F(1,31) = 8.94$, $p < .001$), reflecting the fact that controls were generally more accurate than dyslexics (79% vs. 68%, respectively). Post-hoc t-tests revealed that there was no significant group difference in the symbol condition ($t(31) = 1.67$, ns) (Fig. 1D). Controls performed significantly better than dyslexics in the letter and digit conditions ($t(31) = 3.73$, $p < .001$ and $t(31) = 2.99$, $p < .001$, respectively) (Fig. 1D). No significant interaction between group and stimulus type ($F(2,62) = 2.40$, ns) was found. The main effect of stimulus type for RT scores was marginally significant ($F(2,62) = 2.97$, $p = .058$), while group differences ($F(1,31) = 1.13$, ns) and the interaction of group with stimulus type ($F(2,62) = 2.02$, ns) did not reach significance. Stimulus duration (threshold) yielded a marginally significant main effect of stimulus type ($F(2,62) = 3.08$, $p = .053$) and a significant

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[2] Reaction times that were longer than 2 SD calculated from the individual subjects' mean were excluded from further analysis. Only correct trials were analysed.

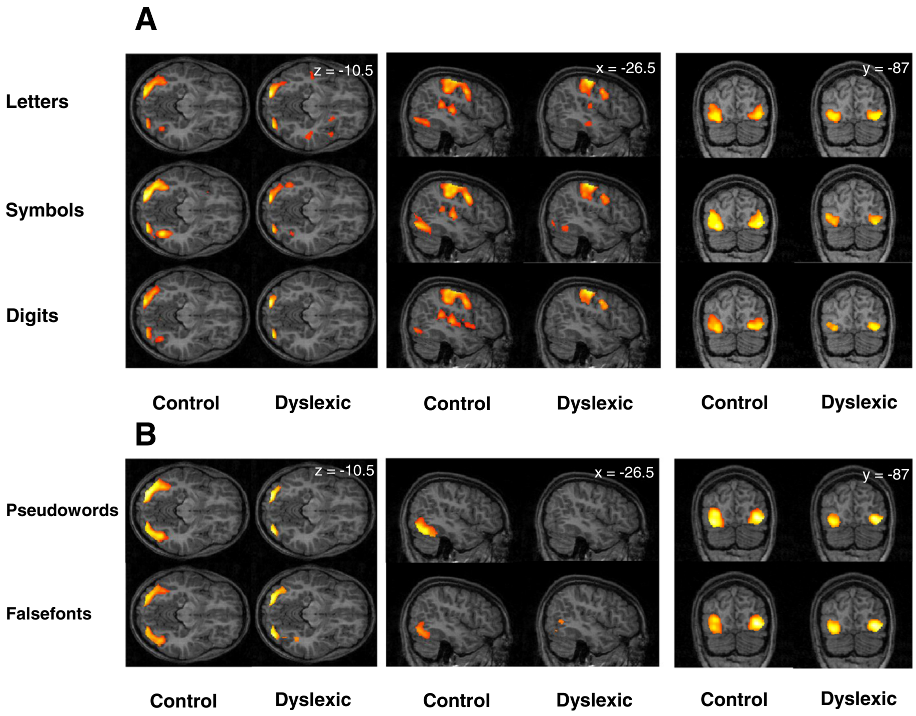

Fig. 2. Whole-brain activations by conditions and groups in the two experiments. (A) Experiment 1 — the non-reading task: responses in the ventral visual stream, the dorsal stream and in the temporal language and motor systems for letters (first row), symbols (second row) and digits (third row) in the control (first column) and dyslexic (second column) groups. (B) Experiment 2 — the reading task: responses in the ventral visual stream and in the dorsal stream for pseudowords (top row) and falsefonts (bottom row) in the control (first column) and dyslexic (second column) groups. BOLD activations are overlaid on a single subject brain normalized to MNI template. Thresholds: $p < 0.001$, uncorrected for multiple comparisons at the voxel level, and a FWE-corrected threshold of $p < 0.05$ at the cluster level.

difference between the two groups ($F(1,31) = 15.19$, $p < .001$) indicating that presentation times were on average 50 ms longer for dyslexics than controls. There was no significant interaction of the group with condition in the case of stimulus duration ($F(2,62) = .88$, ns).

3.2. fMRI results

3.2.1. Whole brain analysis — Basic results

Fig. 2A displays the BOLD signal in each condition (letters, symbols and digits) against fixation in Experiment 1 (the non-reading task). All three string types engaged brain areas typically active in reading tasks. In both subject groups, these included bilaterally: the ventral and dorsal visual areas, the language network and a parietal attentional network. A list of activated brain regions with their coordinates is presented in Supplementary Tables 1–8. Brain areas responding to non-pronounceable symbols were slightly more extended than for pronounceable letters or digits. Overall, the activations in both groups comprised comparable regions. The contrasts of the pseudoword and falsefont conditions against fixation baseline (Experiment 2: reading task) are shown in Fig. 2B. Both conditions elicited strong activations extending to the most anterior parts of the ventral visual stream. However, in both conditions, activations in the dyslexic group were smaller in extent than that of controls and clustered around the posterior part of the VWFA.

3.2.2. Whole brain analysis — Between-condition comparisons

Given the strong overlap of activations across the different conditions in Experiment 1 with only the symbol condition showing a slightly more extended pattern of activations, we present only the comparisons between the symbols and the other two conditions. As shown in Fig. 3A, the symbols > letters contrast resulted in significant clusters in the right superior parietal lobule and right fusiform and middle temporal gyri. The symbols > numbers contrast showed a similar but bilateral pattern. In the reverse contrast the only significant clusters were found in the right cuneus and the left inferior frontal gyrus. In Experiment 2, only

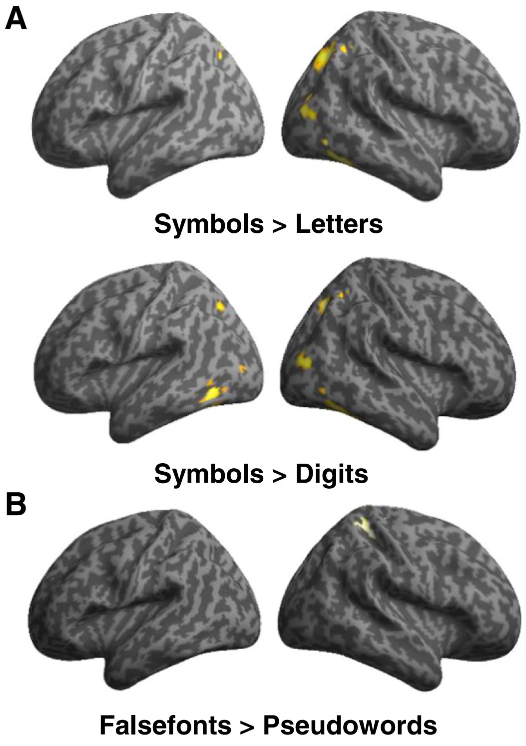

Fig. 3. Stimulus effects across groups. (A) Areas activated more by symbols than letters (top row) or digits (middle row) in Experiment 1 — the non-reading task. (B) Areas activated more by falsefonts than pseudowords in Experiment 2 — the reading task. BOLD activations are rendered on an inflated canonical SPM brain. Thresholds: $p < 0.001$, uncorrected for multiple comparisons at the voxel level, and a FWE-corrected threshold of $p < 0.05$ at the cluster level.

the falsefonts > pseudowords contrast yielded significant results with a cluster of activated voxels in the parietal cortex (see Fig. 3B).

3.2.3. Whole brain analysis — Between-group comparisons

Direct group comparisons for the letter condition against baseline for the Control > Dyslexic contrast revealed stronger activations for control children in language related regions and the dorsal visual stream, i.e. a cluster in the right superior temporal gyrus and bilaterally in the middle occipital gyrus respectively (Fig. 4A, top row). The opposite comparison (Dyslexic > Control) for letters showed differences in various nodes of the default mode network (DMN) in the parietal, temporal and frontal lobes. At every suprathreshold maxima of the Dyslexic > Control comparison (Fig. 5), the dyslexic population showed positive or near-baseline activations for all stimuli. Activations in the control population were markedly negative. This pattern suggests that dyslexic subjects failed to disengage the default mode network (DMN) during task performance (see Discussion).

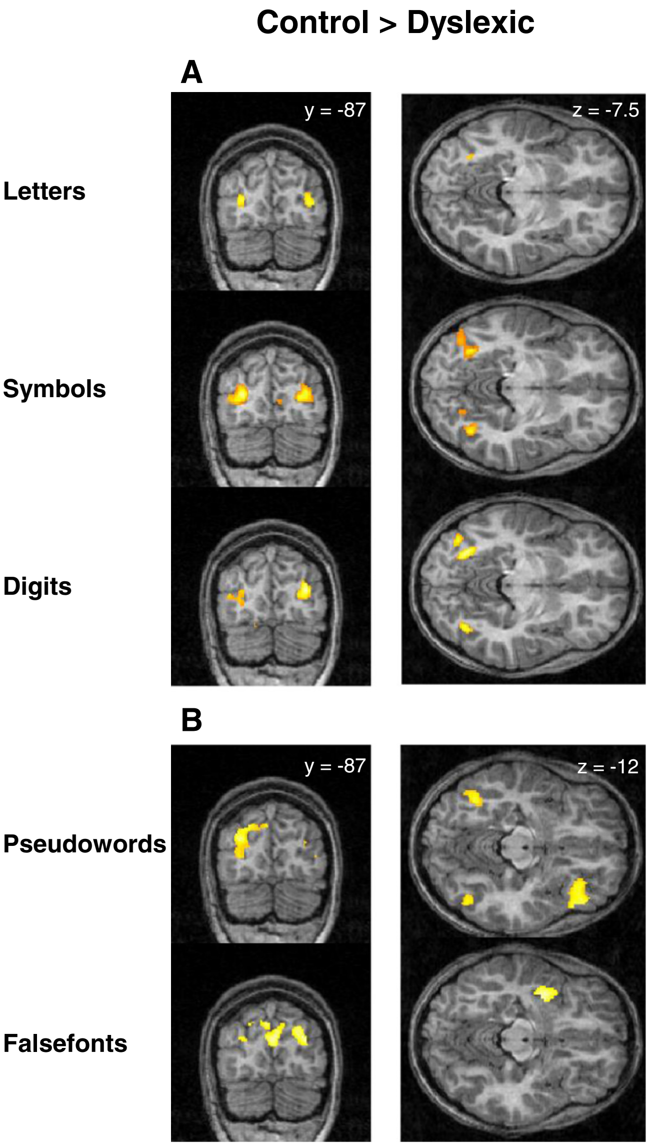

Fig. 4. Activation differences between dyslexic and control groups. (A) Experiment 1 — the non-reading task: stronger responses induced activation in the bilateral middle occipital gyri (first column) and bilateral VWFA (second column) in the control group relative to the dyslexic group for the letter, symbol and digit conditions (first, second and third rows, respectively). (B) Experiment 2 — the reading task: stronger responses induced in the left middle occipital gyrus, bilateral VWFA and right inferior frontal gyrus for the pseudoword condition (upper row) and stronger activations in the bilateral middle occipital gyri, cuneus and left superior temporal gyrus for the falsefont condition (bottom row) in the control group as opposed to the dyslexic group. BOLD activations are overlaid on a single subject brain normalized to MNI template. Thresholds: $p < 0.001$, uncorrected for multiple comparisons ($k = 40$).

When comparing the two groups in the symbol condition (symbols against baseline), controls engaged more strongly the left ventral visual stream comprising the middle temporal gyrus, the dorsal visual stream bilaterally with clusters in middle occipital gyri, and language areas with a cluster in the left superior temporal gyrus and an anterior cluster in the left inferior frontal gyrus (Fig. 4A, middle row). In the reverse comparison, dyslexic children showed stronger activations in the DMN similar to the letter condition (results not shown). For control children, the digits elicited stronger activations bilaterally in the fusiform gyri, the middle occipital gyri and the superior temporal gyri as well as in the left inferior temporal gyrus (Fig. 4A, bottom row). Dyslexic children had stronger activations in the parietal and frontal nodes of the DMN (results not shown). The group comparisons for contrasts between conditions did not reveal any significant clusters.

Finally, we analysed the between-group effects in Experiment 2. Direct group comparisons showed that in the case of the pseudoword > baseline contrast, control children activated more strongly both ventral and dorsal posterior regions such as the left inferior and middle temporal gyri, and the middle and superior occipital gyri bilaterally (Fig. 4B, top row). There were no voxels that were more active in dyslexic children than in control children. For falsefonts (falsefonts > baseline), the between-group contrast (Control > Dyslexics) revealed stronger activations for control children than dyslexics in voxels of the middle occipital and temporal gyri bilaterally and the left superior temporal gyrus (Fig. 4B, bottom row), but no voxels showed stronger activations in dyslexic than control children. We also found no significant between-group differences for the pseudowords vs. falsefonts contrast.

To explore the functional role of the above-described middle occipital gyrus (MOG) activations and their relative position in the occipital cortex, we plotted the activation peaks of the between-group MOG differences from Experiments 1 and 2 onto a map of visuotopic areas (Fig. 6). To this aim, we used the SumsDB database (Dickson et al., 2001; Van Essen et al., 2003). While precise localization would require subject-level retinotopic mapping, nonetheless, this comparison allows us to roughly assess the potential role of the areas showing the main between-group effect (see Discussion).

3.2.4. ROI analysis

In the following ROI analysis, we focused on two brain areas that consistently showed significant activations in both experiments: the left VWFA and the left middle occipital gyrus. To avoid circularity, we defined the ROI for the analysis of Experiment 1 based on contrasts from Experiment 2, and vice-versa. In the left VWFA in Experiment 1 (Fig. 7A), we found a significant activation difference between groups ($F(1,30) = 7.37$, $p < .05$), regardless of stimulus type (no interaction with condition). A main effect of condition across groups indicated that the VWFA was activated most strongly by symbols ($F(2,60) = 10.18$, $p < .001$). Experiment 2 showed a slightly different picture (Fig. 7B). We found a significant group × condition interaction ($F(1,30) = 7.15$, $p < .05$), driven by a significant difference between groups in the pseudoword condition ($t(30) = 2.133$, $p < .05$), with no difference in the falsefont condition.

The ROI analysis of the left MOG showed similar results as the VWFA for Experiment 1 (Fig. 7C). Activations in this ROI were characterized by a significant group difference ($F(1,27) = 6.58$, $p < .05$), with the main effect of condition indicating that symbols elicited the strongest activations ($F(2,54) = 5.87$, $p < .001$). No significant interaction between group and stimulus type was present. However, the MOG pattern of results for Experiment 2 differed from the VWFA (Fig. 7D). A significant difference between groups ($F(1,30) = 8.45$, $p < .001$) and a significant group × condition interaction was obtained ($F(1,30) = 5.28$, $p < .05$). However, the two groups showed a reversed pattern: control children exhibited stronger activations for pseudowords than falsefonts, while the

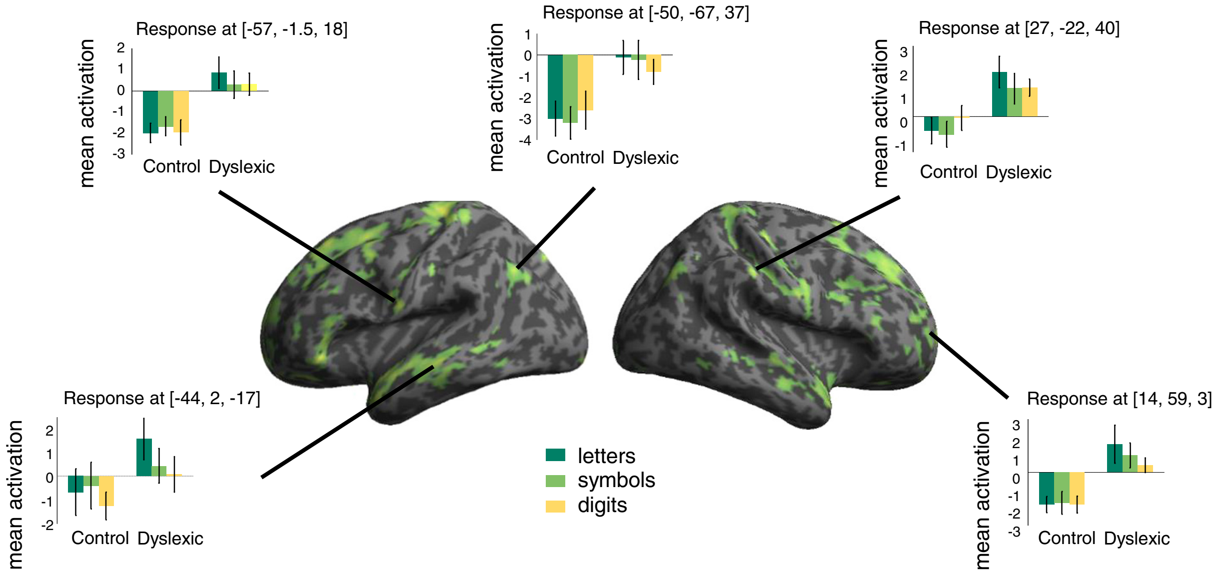

Fig. 5. Areas showing more activation for dyslexic than control children in the letter condition of Experiment 1 (the non-reading task). Plots show activation profiles at the five strongest peaks for the above contrast. All of the locations demonstrate strong disengagement during task execution for control children but not for dyslexic subjects. BOLD activations are rendered on an inflated canonical SPM brain. Thresholds: $p < 0.001$, uncorrected for multiple comparisons at the voxel level, and a FWE-corrected threshold of $p < 0.05$ at the cluster level.

dyslexics responded more strongly to falsefonts than to pseudowords in the MOG.

4. Discussion

The main focus of our study was on the interplay between the dorsal and ventral streams in basic orthographic processing. We used a visual search task with letters, digits and symbols to tap the dorsal stream

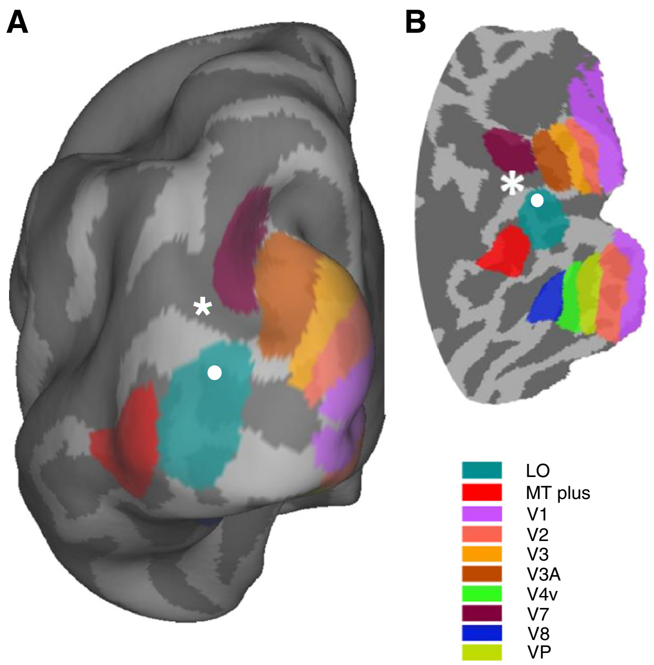

Fig. 6. Peak activation for the letter and pseudoword conditions overlaid on the human PALS B12 brain atlas (Van Essen, 2005) showed on inflated (A) and flat surface (B). Peak activation for the letters (Control > Dyslexic) contrast is marked by a dot, peak activation for the pseudowords (Control > Dyslexic) contrast is marked by an asterisk. Visuotopic areas represented according to the SumsDB database (Van Essen et al., 2003; Dickson et al., 2001).

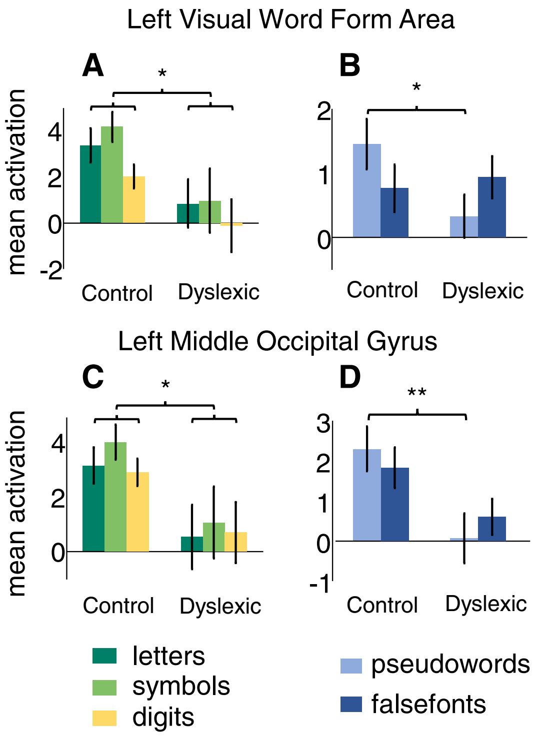

Fig. 7. ROI analysis. Mean activations in the left VWFA (A–B) and the left middle occipital gyrus (C–D) of Control and Dyslexic subjects for the non-reading (Experiment 1) and reading (Experiment 2) tasks. In the VWFA significantly lower responses in Dyslexic group relative to the Control group were found for Experiment 1 but not Experiment 2. (A, B). In addition significant subject group × condition interaction was apparent in Experiment 2 (B) driven by a significant difference between groups for the pseudoword condition ($t(30) = 2.133$, $p < .05$), with no difference for the falsefont condition. In the case of the left middle occipital gyrus both Experiment 1 and 2 showed significant group differences (C, D). However in the case of the MOG a significant group × condition interaction in Experiment 2 revealed a reverse pattern of activations between the two groups than in the case of the VWFA. Control children exhibited stronger activations for pseudowords than falsefonts, while dyslexic participants responded more strongly to falsefonts than to pseudowords in the case of the MOG (D). Error bars represent the SEM across subjects after subtraction of the individual subjects' mean. (*) — $p < .05$, (**) — $p < .005$.

involved in sequencing, attentional guidance and visuo-spatial processing (Jones et al., 2008; Vidyasagar and Pammer, 2010), and an implicit reading task with pseudowords and falsefonts known to tap automatized letter processing in the ventral stream (Cohen et al., 2002; Dehaene and Cohen, 2011).

4.1. Ventral stream deficits

We found the VWFA to be underactivated in dyslexic children, a finding that has been previously reported in several studies (Blau et al., 2010; Schulz et al., 2009; Shaywitz et al., 2002; van der Mark et al., 2009). Importantly, our results replicate this finding in dyslexic children in both the classic implicit reading task with pseudowords and falsefonts (Experiment 2) but also in a visual search task with letters, digits and symbols (Experiment 1). Given that we found underactivation of the VWFA even with digit and symbol strings in a non-reading task, it is tempting to conclude that the underactivation of the VWFA is a primary deficit that is not simply the consequence of the lack of reading experience. However, it is impossible to fully rule out this possibility because it has been shown that learning-to-read profoundly changes basic visual processes (for review, see Dehaene et al., 2015). For example, literates show increased occipital activation compared to illiterates not only for letters but also for faces and pictures (Dehaene et al., 2010). Literacy even enhances the retinotopic fMRI responses to checker-boards in primary visual areas suggesting that the visual cortex has become specifically responsive to the location at which alphabetic words appear on the retina (Dehaene et al., 2015).

4.2. Deficits beyond the ventral stream

A deficit was also found outside of the ventral stream, namely a strong underactivation of the left middle occipital gyrus (MOG) in children with dyslexia. The underactivation of the MOG was found for all three kinds of stimuli in the visual search task (Experiment 1) but also in the implicit reading task (Experiment 2). To our knowledge, only one previous study reported underactivation of the MOG in dyslexics in a letter matching task (Temple et al., 2001). In order to better specify the location of the group differences we found in MOG, Fig. 6 shows that the peak of the activation difference for pseudowords lies dorsally to LO and in the vicinity of V7. The peak difference for letters was found at the dorsal edge of the area identified as the LO complex/dorsolateral occipital area/V4d (Grill-Spector et al., 2001, 1998; Tootell and Hadjikhani, 2001; Tyler et al., 2005).

Can we unequivocally classify these peaks as belonging either to the ventral (shape, identity, …) or dorsal (position, …) stream? Recent work has shown that shape- and motion-sensitive regions overlap (Denys et al., 2004; Grill-Spector and Weiner, 2014; Grill-Spector et al., 2001, 1998; Weiner and Grill-Spector, 2013). This overlap is particularly prominent in the area that has been referred to as the dorsolateral part of the LO complex (Grill-Spector et al., 2001, 1998), V4d (Tootell and Hadjikhani, 2001) or the dorsolateral occipital area (DLO) (Tyler et al., 2005). Arguably, peaks of the control vs. dyslexic difference (Figs. 4 and 6) could also lie in area V3B, a visuotopic region identified superior to LO-1 and lateral to V3A (Brewer and Barton, 2012; Press et al., 2001; Wandell et al., 2007, not shown on the map in Fig. 6), which, according to Press et al. (2001), might be incorporated in the putative V4d. Interestingly, Ban et al. (2012) found that V3B performs fusion of motion and depth cues, and suggested that this computation might be generalized to other types of information.

We therefore believe that the proximity/overlap of space and shape sensitive areas enables the MOG to integrate spatial processing with object recognition necessary for ordering symbols in a string. This fusion of information is particularly important in the case of stimuli which due to lack of automatization do not go exclusively through the ventral, but engage also the dorsal stream. It might be arguable, whether our MOG activation difference lies in the dorsal stream, as some researchers suggested that the human visual system might best be described as being made of not two, but three processing streams, the third one being a lateral stream, which would contain lateral visuotopic maps like the LO and hMT+ (Wandell et al., 2007, 2005). It is indeed difficult to determine the exact location of our MOG activation difference relative to visual maps without proper, subject-level retinotopic mapping in 2D cortical space and direct experimental evidence of overlapping visuotopic areas. Nevertheless we are confident that that all areas that correspond to our Control > Dyslexic difference in MOG are involved in visuospatial processing.

4.3. Role of spatial attention in reading

Current models of orthographic processing and reading aloud acknowledge that serial letter-by-letter reading is an important stage of early reading development. According to the dual route approach to orthographic processing (Grainger and Ziegler, 2011), mastering reading requires a transition from a serial letter-by-letter phonological recoding to a parallel independent letter processing leading to the formation of two types of location-invariant, sublexical orthographic codes that form the basis of skilled reading. On the one hand, the so-called coarse-grained coding involves mapping of letters onto whole-word orthographic representations and enables readers to access the visual form and the meaning of the word at once. At the neuronal level, this is suggested to happen in the VWFA (Cohen et al., 2002; Grainger and Ziegler, 2011). On the other hand, the fine-grained processing route is used to precisely specify letter position within a string, which is necessary for the coding of multi-letter graphemes and grapheme–phoneme conversion (Grainger and Ziegler, 2011; Perry et al., 2007; Share, 1995). Indeed, recent computational models of skilled reading (Perry et al., 2007, 2010) and reading development (Ziegler et al., 2014) postulate an orthographic parsing mechanism, which provides the input to the nonlexical fine-grained processing route. This mechanism is implemented as an "attentional window" that moves serially over a string in order to parse individual letters into a position-specific grapho-syllabic template (Perry et al., 2013, 2010, 2007; Ziegler et al., 2014). Focused spatial attention is needed for this process.

Several researchers associate spatial selection and sequencing with parietal attentional regions (Lobier et al., 2012a; Pammer et al., 2006; Peyrin et al., 2011; Reilhac et al., 2013). In a recent fMRI study, Ossmy et al. (2014) used a support vector machine (SVM) classifier to demonstrate that left intraparietal sulcus (IPS) activity carries sufficient information to discriminate between two letter positions. In line with these results a number of recent studies demonstrated functional and anatomical connectivities between the IPS and the VWFA (Bouhali et al., 2014; Finn et al., 2014; Ossmy et al., 2014). This connectivity might enable the transfer of letter position information from attentional areas to the ventral visual stream. Parietal activations, however, might merely reflect modulatory mechanisms of attention on spatial processing in reading. This is supported by the fact that dyslexics with visual-attentional span disorder who show an underactivation of SPL or IPL (Peyrin et al., 2012, 2011) exhibit normal pseudoword reading, which at least partly requires sequencing of the letters that build them. In contrast, dyslexic children with deficits in focusing visual (or auditory) spatial attention exhibit deficits in pseudoword reading (Facoetti et al., 2010, 2006). Thus, it is possible that the role of the parietal attention areas would be limited to subserving a serial mechanism of visual attention required for shifting attention from one letter to another (Bosse et al., 2007; Pammer et al., 2006; Rosazza et al., 2009; Vidyasagar and Pammer, 2010). Indeed a reading intervention study found an increase of intrinsic functional connectivity between the left VWFA and right MOG after a successful reading intervention in dyslexic children (Koyama et al., 2013). Thus, visuospatial areas rather than parietal attention areas might play an important role in orthographic processing, grapheme-parsing (sequencing) and letter position coding.

4.4. Interplay between ventral and dorsal streams

There is a growing consensus that dorsal/attention and ventral/recognition based processes in reading should not be regarded as separated, but rather as complementary functions (Pammer et al., 2006; Reilhac et al., 2013; Rosazza et al., 2009; Stein, 2014; Vidyasagar and Pammer, 2010). As suggested in the Introduction, the ventral route, which hosts the VWFA, can recognize letter strings but it cannot code their precise location. Hypothetically, the rapid dorsal route provides feedback to V1 and the VWFA about where to attend in order to identify letters and specify their order in a word (Vidyasagar and Pammer, 2010).

Here, we argue that MOG is involved in coding for letter order and grapheme parsing. The underactivation found in our dyslexic population suggests that this process is impaired in dyslexia. The MOG might be particularly strongly associated with the processing of stimuli that lack automatization in the ventral stream. Our results suggest that in 8–12 year old children such automatization is not yet fully achieved. Consequently, a failure to properly activate the dorsal stream might result in reading impairments in the course of reading development.

In line with this view, familiar letter strings can be processed in the VWFA without any involvement of the PPC in skilled readers (Cohen and Dehaene, 2004; Dehaene and Cohen, 2011; Dehaene et al., 2010; McCandliss et al., 2003; Rosazza et al., 2009). However, the effortful reading of degraded or unfamiliar word formats requires the engagement of the dorsal stream (Cohen and Dehaene, 2009; Cohen et al., 2008; Rosazza et al., 2009). Thus whenever fast, holistic processing is not possible, the role of the PPC is to assist the reading process providing appropriate spatial selection and sequencing mechanisms, which are particularly required for orthographic processing in visual word recognition (Pammer et al., 2006). This idea is supported in a recent fMRI study by Takashima et al. (2014), who obtained dorsal visual stream activation for novel letter combinations and showed reduced engagement of this area with training. In an earlier study, Tagamets et al. (2000) argued that this activation reflects spatial processing demands necessary for ordering the symbols in unfamiliar strings.

In sum, given that VWFA activation is developmentally a result of shifting from serial letter-by-letter recoding to automatic and parallel whole word reading, we speculate that the underactivation reported in VWFA in this and several other studies (Paulesu et al., 2001; Richlan et al., 2011, 2009) might be secondary to a MOG/dorsal stream deficit that happens earlier in time and/or development. Further studies are needed to establish developmental and temporal dependencies between the two brain regions.

4.5. DMN suppression

The dyslexic underactivation in the VWFA and the MOG was accompanied by a failure to disengage the default mode network (DMN) during task performance (Fig. 5). This large scale distributed network is usually suppressed in externally driven cognitive tasks (Anticevic et al., 2012; Greicius et al., 2009). In our study, group differences in the DMN were driven by more negative activations in control children, suggesting that only the control children successfully disengaged their DMN. To our knowledge, this is the first study to report systematic DMN dysfunction in dyslexics using task-fMRI. Our results are supported by functional connectivity studies which showed atypical synchronization of the posterior cingulate cortex with other DMN nodes in dyslexic readers (Finn et al., 2014). Although the abnormal balance between brain regions in dyslexia has often been interpreted in terms of compensatory mechanisms (Zhang et al., 2013), we argue that DMN dysfunction is associated with reading disability rather than compensatory mechanisms (see also Schurz et al., 2014). These results provide further evidence for the importance of DMN suppression in perception (Singh and Fawcett, 2008).

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.01.014.

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