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Reading network in dyslexia: Similar, yet different

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ABSTRACT

Dyslexia is a developmental disorder characterized by reading and phonological difficulties, yet important questions remain regarding its underlying neural correlates. In this study, we used partial least squares (PLS), a multivariate analytic technique, to investigate the neural networks used by dyslexics while performing a word-rhyming task. Although the overall reading network was largely similar in dyslexics and typical readers, it did not correlate with behavior in the same way in the two groups. In particular, there was a positive association between reading performance and both right superior temporal gyrus and bilateral insula activation in dyslexic readers but a negative correlation in typical readers. Together with differences in lateralization unique to dyslexics, this suggests that the combination of poor reading performance with high insula activity and atypical laterality is a consistent marker of dyslexia. These findings emphasize the importance of understanding right-hemisphere activation in dyslexia and provide promising directions for the remediation of reading disorders.

1. Introduction

Reading is a complex process: unlike less effortful aspects of language, such as verbal acquisition (Kuhl, 2000), the ability to read needs to be acquired through repetitive and consistent practice. This process draws on phonological awareness, the awareness of the sound structure of words (Høien, Lundberg, Stanovich, & Bjaalid, 1995; Joubert et al., 2004) and on orthographic knowledge, the ability to recognize letter combinations or whole words (Loveall, Channell, Phillips, & Conners, 2013). Both abilities are thought to play an important role in reading acquisition, with the former being a strong predictor of reading fluency (Ziegler & Goswami, 2005).

Functional Magnetic Resonance Imaging (fMRI) studies have repeatedly demonstrated that skilled word reading depends heavily on a left-lateralized cortical network including frontal, temporoparietal and occipitotemporal areas (Cohen & Dehaene, 2004; Pugh, 2006; Richlan, 2012; Rumsey et al., 1997; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003). The temporoparietal cortex is involved in grapheme-phoneme conversion (Pugh, 2006), while the occipitotemporal (OT) region is important for visual and orthographic encoding (whole word recognition) and includes the visual word-form area (VWFA, Cohen & Dehaene, 2004). The OT region has a strong reciprocal relationship with the left inferior frontal gyrus (IFG; Broca's area), a region associated with articulation and involved in phonological processing (Richlan, 2012). Furthermore, IFG functional activation during a reading task is positively correlated with reading ability (Turkeltaub et al., 2003), further emphasizing its critical role in the development of reading ability. Consistent with these findings, developmental models of reading expertise show that early stages of reading induce bilateral activation (Waldie & Mosley, 2000), subsequently declining to left hemispheric predominance in skilled readers (Shaywitz et al., 2007). Learning to read fluently is also associated with decreasing reliance on right extrastriate and inferotemporal cortices (Turkeltaub et al., 2003).

Some children have great difficulty attaining fluent decoding and, if this persists, may have a specific reading disability (herein called dyslexia). Dyslexia is a persistent and unexplained difficulty in achieving accurate and/or fluent word recognition skills, despite adequate intelligence and opportunity (Lyon, Shaywitz, & Shaywitz, 2003). While many adults who had reading difficulties in childhood are eventually able to read accurately, their reading often remains slow and effortful with persistent spelling and written expression deficits (Habib, 2000).

The primary cognitive deficit in dyslexia can be traced back to deficient phonological coding, which impairs the way that speech sounds are represented, stored and retrieved (Shaywitz & Shaywitz, 2005). Dyslexic children are typically unable to decode written words phonetically, have great difficulty reading nonwords

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but are able to recognize and correctly pronounce familiar words (Castles & Coltheart, 1993). Coltheart (1980) first speculated that this so-called phonological dyslexia might be the developmental form of deep dyslexia. Patients with acquired deep dyslexia are thought to rely on their right hemisphere for reading as a result of left hemisphere damage (typically resulting from left temporal or parietal-occipital lesions). Zaidel and Peters (1981) later proposed that individuals with phonological dyslexia rely on the right hemisphere for reading because of the similarity between their reading errors and the ideographic reading ability of the disconnected right hemisphere.

A disruption in the ability to link graphemes and phonemes in dyslexia has been shown to be related to anatomical (Galaburda & Kemper, 1979; Galaburda, Rosen, & Sherman, 1990; Pernet, Andersson, Paulesu, & Demonet, 2009; Rimrodt, Peterson, Denckla, Kaufmann, & Cutting, 2010; Steinbrink et al., 2008; Temple, 2002) and functional (Helenius, Tarkiainen, Cornelissen, Hansen, & Salmelin, 1991; Shaywitz, Mody, & Shaywitz, 2006; Shaywitz & Shaywitz, 2008) abnormalities. For example, the parietal operculum is less asymmetrical in dyslexics than in controls and the degree of asymmetry is inversely related to phonological task performance (Habib & Demonet, 2000). Adults with dyslexia also show reduced left temporoparietal activity during phonological processing, a pattern opposite of that observed in typical readers (Shaywitz et al., 1998).

Besides weaker activation in the left posterior areas during pseudoword rhyming (Shaywitz et al., 1998) and pseudoword decisions (Waldie, Haigh, Badzakova-Trajkov, Buckley, & Kirk, 2013), individuals with dyslexia also show overactivation in the corresponding areas in the right hemisphere (Waldie et al., 2013), in line with prior research on the neural systems predicting long-term outcomes of dyslexia (Hoeft et al., 2011). That is, Hoeft et al. (2011) found, in their prospective, longitudinal study, that reading improvements in their participants with dyslexia were associated with greater right prefrontal activation during a phonological reading task. Therefore, right-hemisphere activation also appears to be diagnostic of impaired reading performance, in contrast with the traditional focus on left hemisphere activation in the study of reading ability.

Current research trends reflect this new direction in the study of dyslexia. For example, a recent meta-analysis pointed out that right hemisphere activation is largely inconsistent across studies (Richlan, Kronbichler, & Wimmer, 2009), thus highlighting the need to better understand how activity in this area and subregions is associated with reading impairment. As noted, dominant theories have consistently demonstrated that dyslexia develops from deficient phonological coding (Pennington, Van Orden, Smith, Green, & Haith, 1990), which entails how sounds are encoded and retrieved. Although phonological coding is typically thought to be a left lateralized process, with skilled readers showing strong left laterality when processing speech sounds, empirical evidence suggests that individuals with dyslexia recruit a more bilateral neural network to perform the same type of tasks (Shaywitz et al., 1998). This is consistent with structural (Rimrodt et al., 2010; Saygin et al., 2013) and functional (Richlan et al., 2010; Shaywitz & Shaywitz, 2008; Shaywitz et al., 2002) differences between individuals with dyslexia and typical readers, the former group showing less asymmetrical patterns than the latter. The precise underpinnings of the increased right hemisphere activation in dyslexia have yet to be identified, however, given that the interest bilateral studies have sparked is only recent.

The current study was designed to refine our understanding of the asymmetrical neural activation typical in dyslexia, by assessing the relationship between neural activation, both within and outside of the traditional reading areas, and reading performance, either in the presence (dyslexia, comorbid) or absence (dyscalculia, control) of a reading disability. Specifically, we used partial least squares (PLS; Krishnan, Williams, McIntosh, & Abdi, 2011; McIntosh & Lobaugh, 2004), to investigate two independent questions. First, we assessed the similarities and differences between normal readers and individuals with reading difficulties in regards to the regions activated in response to a rhyming task. We predicted that, as shown by others (Hoeft et al., 2006), both groups would activate a set of regions largely restricted to the left hemisphere. In addition, we predicted that group differences would emerge showing the reading difficulty group to have reduced activity in certain regions of the left hemisphere (e.g. McCrory, Mechelli, Frith, & Price, 2004; Paulesu et al., 2001; Shaywitz et al., 2002), as well as increased activity in right hemisphere regions (Waldie et al., 2013).

In addition to investigating group similarities and differences in regions activated by a rhyming task, we assessed whether the relationship between reading ability and BOLD activity differed between the two groups. Here, we predicted that regions within left-hemisphere regions associated with the rhyming task would correlate with reading performance in the control group, but not the reading difficulty group. This is motivated by previous research showing that activity in—and task-related functional connectivity between—left hemisphere regions is linearly related to reading ability in normal readers, but not reading difficulty groups (Hampson et al., 2006; Hoeft et al., 2007; van der Mark et al., 2011). We also predicted that BOLD signal in regions outside the left-lateralized "reading network" would correlate with reading performance in the reading difficulty group (but not the normal reading group). Besides refining theoretical models of reading disorders, identifying patterns of neural activation that correlate with reading performance may also provide an avenue for the development of evidence-based interventions.

2. Methods

2.1. Subjects

Subjects were recruited as part of a larger study, the Auckland Comorbidity Study (Wilson et al., 2015), which included 85 adults, selected from an initial 127 volunteers. From this pool of 85 participants, n = 47 were selected for the current study. All participants with dyslexia reported a history of reading difficulties dating back to primary school, as well as current difficulties. Initial screening included a detailed clinical history, the administration of the Wechsler Abbreviated Scale of Intelligence (WASI), standardized tests of reading, spelling and mathematics (Woodcock Johnson Word ID and Word Attack, and the Wide Range Achievement Test spelling and mathematics), and screening for ADHD using the ASRS (Adult Self Report Scale; ASRS). A second clinical interview was performed to diagnose any participants presenting with high ASRS scores, who were screened out of the current fMRI study.

In the current study, almost all participants (n = 45) were included based on a cutoff criterion; for dyslexia, this was at least one score ≤25th percentile on the three reading and spelling tests (WJ Word ID and Word Attack, and WRAT spelling), as well as another score ≤50th percentile on the same tests. A further two participants were included based on a cutoff + discrepancy criterion (≤35th percentile on one reading/spelling test, and ≥1.5 SD between FSIQ and the average of all the reading/spelling tests). Exclusion criteria for the current study were neurological disorder (except mild depression or anxiety), history of major head injury or non-standard schooling, English as a second language, vision or hearing impairment, Full Scale Intelligence Quotient (FSIQ) < 85, clinical diagnosis of ADHD, fMRI contraindications, or left handedness. The final sample of n = 47 included 11 dyslexics, 11 dyscalculics, 13 comorbids (dyslexia and dyscalculia) and 12 controls. For the purpose of the present report, the Dyscalculia and Control groups were combined into a single Normal Reading group, while the Dyslexia and Comorbid groups constituted a Reading Difficulty group (see Table 1).

2.2. Behavioral tasks

Prior to scanning, participants were tested on a cognitive profiling battery targeting core cognitive networks involved in reading and mathematics. Tasks included: response speed, short term memory (letters, digits), phonological processing, rapid naming (letters, digits), word decoding (regular, irregular, non-word), and spelling (regular, irregular words), as well as mathematical tasks. Here we briefly describe domain general and reading-related tasks relevant the current study. The performance of the current sample on these tasks is shown in Table 2. A description of other tasks included in the larger study can be found in Wilson et al. (2015).

Table 1
Sample characteristics for the Normal Reading (controls and dyscalculics) and Reading Difficulty (dyslexics and comorbids) groups.

	Normal Reading group	Reading Difficulty group
n	23	24
Average age, yrs	29 (1)	31 (1)
Female	48%	42%
Education, yrs from age 6	15.1 (0.4)	15.2 (0.4)
Parents education, yrs from age 6	13.7 (0.4)	13.7 (0.4)
WJ word ID standard score	109 (2)	85 (1)***
WJ word attack standard score	114 (2)	89 (2)***
WRAT spelling standard score	109 (2)	83 (2)***
WRAT math standard score	94 (3)	92 (3)
WASI IQ – full	118 (2)	116 (2)
WASI IQ – verbal	121 (2)	114 (3)*
WASI IQ – performance	110 (2)	115 (2)
ASRS score, average	5 (1)	8 (1)*
Born premature	17%	4%
Pregnancy/birth complications	26%	27%
Taking medication for depression/anxiety at the time of the study	30%	8%

Notes: Parentheses contain standard errors. *Group difference significant $p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, using independent *t*-test, or chi-square.

Table 2
Descriptive statistics (M and SEM) for Normal Reading and Reading Difficulty groups.

	Normal Reading group	Reading Difficulty group
Processing speed, RT (msec)	270 (6)	281 (8)
Processing speed standard deviation (msec)	54 (7)	59 (5)†
Short term memory span (digits)	6.2 (0.2)	5.5 (0.2)**
Short term memory span (letters)	4.9 (0.2)	4.3 (0.1)**
Rapid naming (digits/min)	167 (6)	142 (5)**
Rapid naming (letters/min)	156 (5)	133 (3)**
Phonemic Reversal (percent correct)	53 (4)	23 (4)***
Word decoding accuracy, regular (%)	100 (0)	94 (1)***,†
Word decoding accuracy, irregular (%)	95 (1)	86 (1)***,†
Word decoding accuracy, nonword (%)	90 (1)	61 (3)***,†
Word decoding RT, regular (msec)	533 (13)	713 (26)***,†
Word decoding RT, irregular (msec)	560 (13)	752 (32)***,†
Word decoding RT, nonword (msec)	621 (37)	1213 (127)***,†
Spelling accuracy, regular (%)	85 (3)	36 (5)***
Spelling accuracy, irregular (%)	73 (6)	8 (2)***

Notes: Parentheses contain standard errors. *Group difference significant $p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, using independent *t*-test, or †Mann-Whitney U.

2.2.1. Processing speed

Reaction time was recorded for a simple key press response to a pink dot (16 pixels in diameter), which appeared centrally on screen with irregular timing (ISI randomly jittered to either 2500 or 4500 ms). Participants completed 40 trials.

2.2.2. Verbal short term memory

The digit version of this task was taken from the Comprehensive Test of Phonological Processing (CTOPP; Wagner, Torgesen, & Rashotte, 1999), and the letter version was made by exchanging letters for digits (C, F, H, K, N, R, S, T, & Z; chosen to reduce visual/phonological similarity). Sequences of digits and letters were recorded and presented by computer (for standardization), and accuracy was recorded. Task order was counterbalanced across subjects.

2.2.3. Rapid naming

The RAN task was also from the CTOPP (Wagner et al., 1999) using four 9 × 4 matrices of digits and letters (two of each), and presenting matrices of digits or letters on the computer. Task order was counterbalanced across subjects.

2.2.4. Phonemic Reversal

This task from the CTOPP (Wagner et al., 1999) required participants to say words backwards. Words were presented by computer, for standardization.

2.2.5. Word decoding

We used the 90 words from Coltheart and Leahy (1996); 30 regular, 30 irregular, and 30 nonwords. Words were presented in a pre-randomized order by computer in Times New Roman 18pt font.

2.2.6. Spelling

Twenty difficult words from the Boder lists (Boder & Jarrico, 1982), 10 regular, 10 irregular, were presented in a pre-randomized order by computer. Participants spelt each word on paper. Regular and irregular word lists were matched as closely as possible length (written and recorded), frequency (written and spoken; CELEX), bigram frequency, and imageability, using NWatch (Davis, 2005).

Performance of the RD group on the tasks was typical of adults with developmental dyslexia; showing impairments in short term memory, rapid naming, phonemic tasks, word decoding, and spelling (Hatcher, Snowling, & Griffiths, 2002; Parrila, Georgiou, & Corkett, 2007; Ramus et al., 2003; Shaywitz et al., 2002). The slightly lower verbal IQ, but normal performance IQ, is also typical of adult dyslexia (Ransby & Lee Swanson, 2003), probably because vocabulary is affected by reduced exposure to print (Lyon et al., 2003). An examination of data within the RD group (at the request of a reviewer) suggested that the group can be accurately characterized as phonological, rather than orthographic developmental dyslexia (Castles & Coltheart, 1993). The greatest impairment was in tasks with a high phonological or non-lexical load (e.g. phonemic reversal, decoding of nonwords), and there was no evidence of bimodality in score distributions. RD participants were less accurate and slower decoding and spelling irregular words compared to regular words, however so was the control group, suggesting this was merely a difficulty effect. Furthermore, a median split of the RD group by performance on phonemic reversal did not change the direction of this word regularity effect.

2.3. fMRI protocol

We used a block fMRI design, with three 7-min functional runs, each comprised of 14 × 30 s blocks (6 trials each). Block order was counterbalanced using a partial Latin square across runs and across

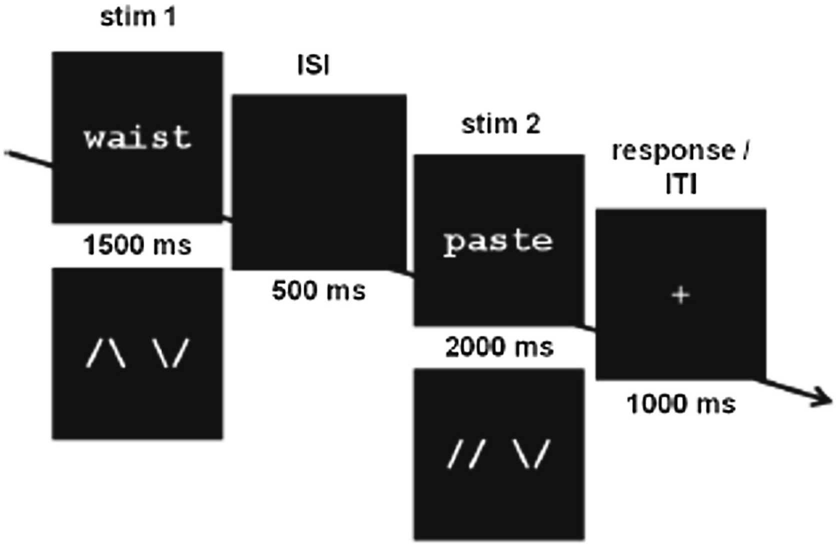

Fig. 1. Rhyming and line-judgment tasks. The top row shows orthographically dissimilar words (waist/paste) in the rhyming task. Participants had to make a response after the second word was presented (rhyming/not rhyming). The bottom row shows two presentations of four oriented lines. Participants were required to detect if any of the lines changed orientation between the first and second presentation (change/no change).

subjects. The two conditions investigated here were a rhyming task and a line-judgment control task (see Fig. 1). In the rhyming task participants determined if two sequentially presented orthographically dissimilar words (e.g. waist/paste) rhymed (stimuli based on Hoeft et al., 2007). In the control line-judgment task participants detected any orientation changes in two sequentially presented patterns of oriented lines (stimuli based on Shaywitz et al., 1998). Stimuli were presented and key press responses collected using E-Prime (Schneider, Eschman, & Zuccolotto, 2002). Four tasks related to mathematical cognition were also presented but were not analyzed for the current study.

We chose an in-scan rhyming task to elicit reading-related activity that would load primarily on phonological processing. Bryant, MacLean, Bradley, and Crossland (1990) convincingly showed that, over time, children's rhyming ability is related to reading success. They claimed that awareness of rhyme makes a distinctive contribution to reading that cannot be accounted for in terms of general language ability and goes beyond the learning of grapheme-phoneme correspondences (e.g., learning to make inferences about spelling patterns).

Scanning was performed on a 1.5 T Siemens Avanto with a 12-channel head matrix coil. Gradient echo echo-planar imaging (EPI) was performed with TR = 2000 ms, TE = 1.91 ms, FA = 90°, with 23 axial interleaved slices per volume, parallel AC–PC, thickness = 5 mm (no gap). In-plane spatial resolution was 3 mm, with FOV = 192 mm, matrix = 64 × 64, voxels: $3 \times 3 \times 5\ \text{mm}^3$. T1 Anatomical was MPRAGE with TE = 4.94 ms, TR = 11 ms, FA = 15°, matrix = 256 × 256, FOV = 256 mm, 176 slices, thickness = 1 mm, voxels: $1 \times 1 \times 1\ \text{mm}^3$.

fMRI images were preprocessed in SPM8 (http://www.fil.ion.ucl.ac.uk/spm/doc/). Standard preprocessing of functional images was performed, including rigid-body motion correction and unwarping, spatial normalization to the Montreal Neurological Institute (MNI) template (resampled at $2 \times 2 \times 2\ \text{mm}^3$ voxels) and spatial smoothing (using an 8 mm full-width half maximum isotropic Gaussian kernel).

2.4. Analyses

Analyses were performed using partial least squares (PLS); a multivariate procedure that identifies latent variables (LVs) specifying the relationship between brain activity and experimental conditions (Krishnan et al., 2011). In PLS, the latent variables are defined by three components: a singular value specifying the amount of covariance explained by the LV; a linear contrast of conditions; and a set of voxel weights or "saliences" specifying brain regions showing reliable covariance with the condition contrast. To assess the statistical significance of LVs, 1000 permutations that randomly assigned brain activity to conditions (within subjects) were computed, and the significance of the LV was determined based on the proportion of permuted singular values exceeding the observed singular value. The reliability of each voxel's salience was determined by a bootstrapping procedure (McIntosh, Chau, & Protzner, 2004). Participants were randomly resampled with replacement, and the standard error of the saliences was computed based on 1000 bootstrap samples. In addition to group-averaged spatial maps, a "brain score" was calculated for each condition in each subject, which is a weighted average of brain activity across the brain associated with a given condition. More precisely, for each participant, a brain score is calculated as the dot product of a vector containing saliences for all voxels in the brain (derived from the group PLS analysis) and a vector containing BOLD percent signal change values[1] of all voxels for that participant. This is done separately for each condition and produces a single measure, similar to a component score in PCA, which indexes how strongly each participant expresses the spatial pattern associated with each condition (Krishnan et al., 2011).

Two versions of PLS were performed on these data: task PLS, which detects differences in patterns of activity between experimental conditions and/or groups; and behavioral PLS, which produces correlation maps for each condition by correlating BOLD signal in each voxel with behavioral variables, and then identifies similarities and differences in correlation maps between conditions and/or groups (McIntosh, Bookstein, Haxby, & Grady, 1996; McIntosh & Lobaugh, 2004). Because PLS is a multivariate approach performed in one analytic step, it is a more powerful analysis than standard GLM, with no correction required for multiple comparisons. In addition, it is model-free, i.e. it makes no assumptions about the shape of the BOLD response.

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[1] Note that in PLS, the BOLD signal is normalized to the first TR of each trial; thus percent signal change values reflect mean change relative to the start of blocks rather than an implicit baseline (as is generally the case in univariate, general linear model methods)

Table 3
Accuracy and response times for Normal Reading and Reading Difficulty groups in fMRI tasks.

	Normal Reading group		Reading Difficulty group	
	Proportion Correct	Response Time	Proportion Correct	Response Time
Rhyming Task	0.94 (0.01)	974 (37)	0.86 (0.02)	1133 (35)
Line Judgment Task	0.92 (0.01)	822 (31)	0.93 (0.01)	860 (30)

Notes: Parentheses contain standard errors of the mean.

A number of non-rotated PLS analyses[2] were subsequently performed, each targeting a separate research question. First, to determine the reading network common to both Normal Reading and Reading Disability groups, a task-PLS analysis was performed that contrasted *Rhyming* and *Line-judgment* tasks (i.e. a main effect of condition, or regions showing a reliable Words > Lines effect for both groups). Next, we assessed whether there was a reliable *Task* × *Group* interaction.

Following these task analyses, we determined the neural correlates of reading ability across the groups. First, we correlated the brain scores attained from the common reading network with reading and phonological ability (as indexed by participants' performance on the Woodcock-Johnson Word Attack and the Comprehensive Test of Phonological Processing Phonemic Reversal task). These measures were chosen because the primary cognitive deficit in dyslexia can be traced back to deficient phonological coding, which impairs the way that speech sounds are represented, stored and retrieved (Shaywitz & Shaywitz, 2005). Second, we performed a non-rotated behavioral-PLS analysis to determine if any regions *outside* the common reading network were differentially correlated with reading performance across our two groups.

3. Results

3.1. Behavioral results

Behavioral data from two participants in the typical readers group are not included in these analyses due to a setup error and an equipment failure error. Accuracy and response time (RT) data, summarized in Table 3, were submitted to a 2 × 2 mixed ANOVA with condition (Rhyming/Lines) and group (Typical/Dyslexic) as factors. For accuracy, there was a main effect of condition, $F(1,43) = 9.00$, $p = 0.004$, with the line-judgment task producing a higher proportion of correct response ($M = 0.93$) than the rhyming condition ($M = 0.90$). A main effect of group was also significant, $F(1, 43) = 7297.50$, $p < 0.001$; typical readers ($M = 0.93$) were more accurate than dyslexic readers ($M = 0.90$). The interaction effect was also significant, $F(1, 43) = 26.36$, $p < 0.001$. Bonferroni-corrected *t*-tests showed that the interaction was driven by the group difference being significant for the rhyming task, $t(43) = 3.00$, $p = 0.005$, but not the line-judgment task, $t(43) = -0.51$, $p = 0.64$. The pattern of results for the RT analyses was similar. The line-judgment task produced faster responses ($M = 840$) than the rhyming task ($M = 1053$), $F(1, 43) = 82.56$, $p < 0.001$. Typical readers ($M = 898$) were generally faster than dyslexic readers ($M = 996$), $F(1, 43) = 2131.05$, $p < 0.001$. The significant interaction, $F(1, 34) = 6.71$, $p = 0.013$, indicated the difference between the two groups was more pronounced in the rhyming task relative to the line-judgment task. Bonferroni corrected *t*-tests showed that only the rhyming condition produced a difference between the two groups, $t(43) = 3.11$, $p = 0.003$ – see Table 3 for means and standard errors of the mean.

3.2. Commonalities and differences in brain activity between normal readers and dyslexics

The task-PLS analysis yielded a significant LV corresponding to a main effect of condition ($p < 0.001$). Inspection of the mean brain scores and associated confidence intervals, presented in Fig. 2, showed that this effect was reliable for both groups. Listed in Table 4, clusters with a minimum of 10 voxels showing bootstrap ratios greater than 4 (approximate $p < 0.0001$) were regarded as reliably contributing to this effect.

As shown in Fig. 2, a reading network predominantly lateralized to the left-hemisphere was recruited by the rhyming/words task. Many of these regions are commonly reported nodes of the adult reading network, including the left inferior frontal gyrus (Broca's Area) and our left fusiform gyrus peak, which is consistent with the location of the "Visual Word Form Area" (for recent relevant reviews and meta-analyses Dehaene, Cohen, Morais, & Kolinsky, 2015; Martin, Schurz, Kronbichler, & Richlan, 2015; Price & Mechelli, 2005). The left middle temporal gyrus is adjacent to temporo-parietal regions normally implicated in adult reading, and is often active in studies involving rhyming or phonological tasks in adults (e.g. Booth et al., 2004; Lurito, Kareken, Lowe, Chen, & Mathews, 2000), as well as in broader reading tasks in children (Martin et al., 2015). Fig. 3 shows key regions of the left-lateralized reading network where greater activation was found in the rhyming task relative to the line-judgment task for both typical and dyslexic readers. These include the inferior frontal gyrus, the fusiform gyrus, and the middle temporal gyrus. Conversely, regions responsive to the line judgment task included bilateral parietal and occipitotemporal cortices (not shown in Fig. 3).

The LV corresponding to the interaction effect failed to reach significance ($p = 0.767$), suggesting no reliable whole-brain group differences between the two groups. To further address this issue, a region of interest (ROI) approach was adopted. First, we tested whether any regions showing a Rhyming > Line judgment effect for both groups showed this effect to a greater degree for the control group. 2-way mixed ANOVAs (with *Condition* and *Group* as factors) were performed on signal extracted from all voxels listed in Table 4 showing the Rhyming > Line judgment effect. Each of these analyses failed to produce any significant interactions, even when uncorrected for multiple comparisons (all p's > 0.07). Next, we determined if regions previously shown to respond differentially to reading in typical and dyslexic groups also showed similar effects in these data. ROIs were selected based on the meta-analysis of Maisog and colleagues (Maisog, Einbinder, Flowers, Turkeltaub, & Eden, 2008) and are listed in Table 5... As shown in Table 5, none of these ROIs exhibited a significant *Group* × *Condition* interaction. In conjunction, the PLS and ROI analyses suggest the reading network recruited by the Rhyming task is activated to similar degrees for both typical and dyslexic reading groups.

3.3. Brain-behavior correlations

Next, we investigated the relationship between BOLD responses in the Rhyming task and reading proficiency, with the latter

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[2] Non-rotated PLS analyses are hypothesis driven and require the specification of a specific contrast (in contrast to mean-centred PLS analyses which are exploratory and generate contrasts that account for the most cross-block covariance).

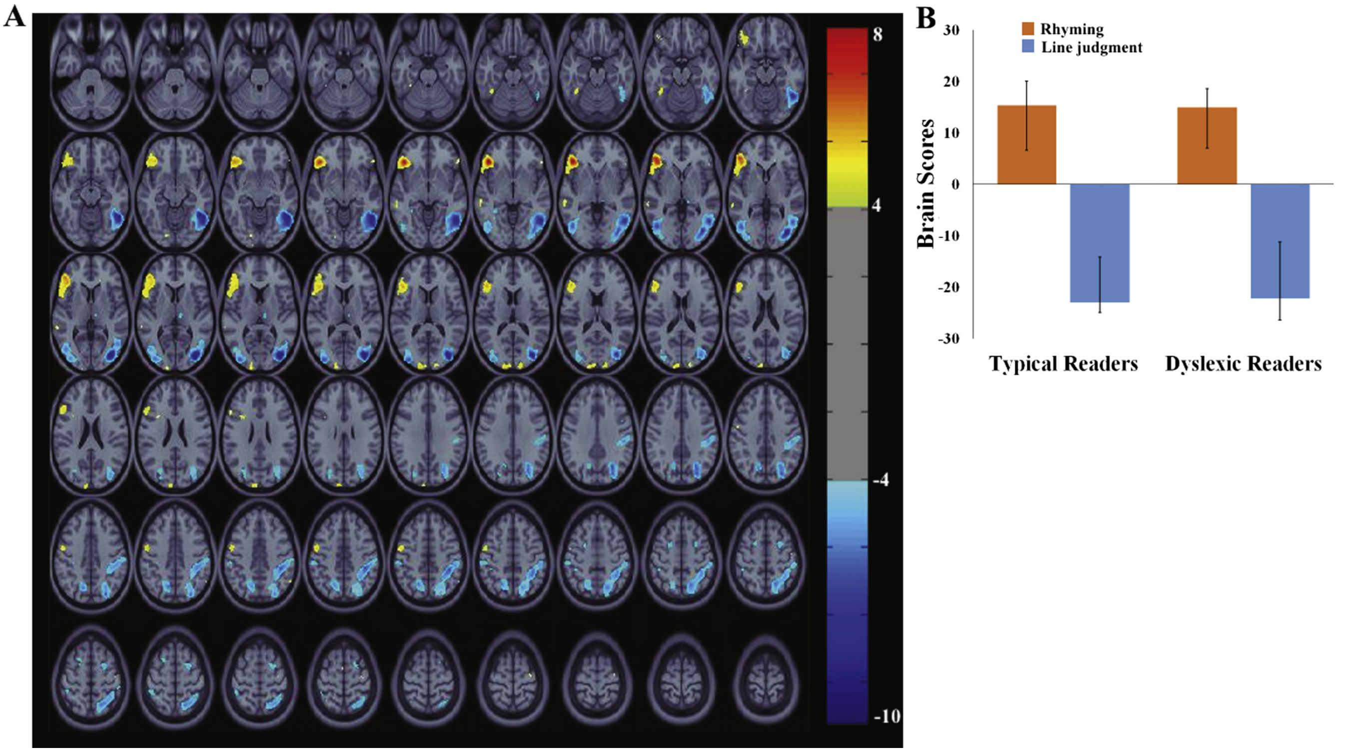

Fig. 2. (A) Singular image of the main effect of condition LV. Warm regions are more active during the Rhyming task; cool regions are more active during the line-judgment task. Images are thresholded at BSR > 4 ($p < 0.0001$). (B) Mean brain scores with 95% confidence intervals for rhyming and line-judgment conditions in typical and dyslexic readers associated with the main effect of condition. Brain scores are weighted averages of activity across all voxels associated with particular conditions. This contrast was significant ($p < 0.0001$).

Table 4
Regions associated with latent variable corresponding to a main effect of condition.

Structure	MNI Coordinate			Percent Signal Change				BSR	Cluster Size
	X	Y	Z	Rhyming		Line Judgment			
				Typical	Dyslexic	Typical	Dyslexic		
Rhyming > Line Judgment									
L IFG	−46	32	−4	0.29 (0.24)	0.31 (0.22)	−0.08 (0.19)	−0.02 (0.2)	9.39	1625
L PoCG	−52	−6	44	0.17 (0.21)	0.24 (0.17)	−0.02 (0.21)	0.00 (0.2)	6.07	108
L SOG	−14	−102	14	0.19 (0.24)	0.11 (0.25)	−0.19 (0.22)	−0.11 (0.23)	5.80	177
R SOG	14	−98	14	0.18 (0.27)	0.02 (0.29)	−0.13 (0.15)	−0.12 (0.16)	4.89	46
L FusG	−36	−46	−20	0.28 (0.22)	0.13 (0.2)	0.05 (0.15)	0.04 (0.13)	4.87	46
L LinG	−16	−86	−10	0.08 (0.17)	0.14 (0.18)	−0.05 (0.11)	0.03 (0.14)	4.76	13
L MTG	−60	−38	−6	0.18 (0.23)	0.18 (0.23)	−0.02 (0.22)	0.08 (0.17)	4.64	55
L IFG	−32	12	24	0.09 (0.14)	0.12 (0.18)	−0.02 (0.16)	−0.04 (0.15)	4.52	14
R IFG	54	34	−8	0.22 (0.35)	0.28 (0.35)	−0.05 (0.43)	0.00 (0.29)	4.49	21
Line Judgment > Rhyming									
R MOG	38	−84	8	−0.05 (0.16)	−0.06 (0.21)	0.36 (0.16)	0.26 (0.16)	−11.24	3937
R IPL	40	−36	46	−0.06 (0.16)	−0.04 (0.16)	0.13 (0.12)	0.19 (0.14)	−7.57	1611
L MOG	−36	−88	10	−0.05 (0.17)	0.02 (0.18)	0.23 (0.15)	0.18 (0.18)	−7.44	887
L SPL	−14	−66	42	−0.05 (0.11)	−0.01 (0.11)	0.09 (0.12)	0.11 (0.15)	−7.06	423
R SFG	24	0	58	−0.04 (0.17)	−0.04 (0.15)	0.08 (0.15)	0.13 (0.13)	−5.21	109
L PHG	−32	−46	−4	0.01 (0.1)	−0.02 (0.12)	0.05 (0.12)	0.11 (0.12)	−5.17	17
L IPL	−58	−28	50	0.05 (0.26)	−0.06 (0.36)	0.18 (0.3)	0.35 (0.26)	−5.09	71
R Thal	10	−18	8	0.02 (0.13)	−0.03 (0.19)	0.08 (0.23)	0.17 (0.15)	−5.08	23
L MOG	−28	−74	26	0 (0.12)	−0.01 (0.08)	0.12 (0.15)	0.11 (0.13)	−4.96	89
L SFG	−22	0	54	−0.06 (0.12)	0.01 (0.1)	0.08 (0.12)	0.09 (0.12)	−4.87	50
L PoCG	−46	−40	62	−0.03 (0.37)	0.04 (0.39)	0.41 (0.34)	0.27 (0.4)	−4.67	59

Note: reported clusters survived a bootstrap ratio (BSR) of ±4.0 (approximate $p < 0.0001$) and had a spatial extent of at least 10 voxels. FusG = fusiform gyrus; IFG = inferior frontal gyrus; IPL = inferior parietal lobule; L = left; LinG = lingual gyrus; MOG = middle occipital gyrus; MTG = middle temporal gyrus; PHG = parahippocampal gyrus; PoCG = post-central gyrus; R = right; SFG = superior frontal gyrus; SOG = superior occipital gyrus; SPL = superior parietal lobule; Thal = thalamus.

indexed based on performance in the Word Attack and Phonemic Reversal tasks (assessed at study intake). These tasks, measures of phonological decoding and phonological awareness respectively, were chosen because they have shown to be reliable correlates of reading skill in previous studies (e.g. Shaywitz & Shaywitz, 2005; Vellutino, Fletcher, Snowling, & Scanlon, 2004) and because phonological deficit is typically regarded as the primary marker of dyslexia (Shaywitz & Shaywitz, 2005). We assessed whether activity

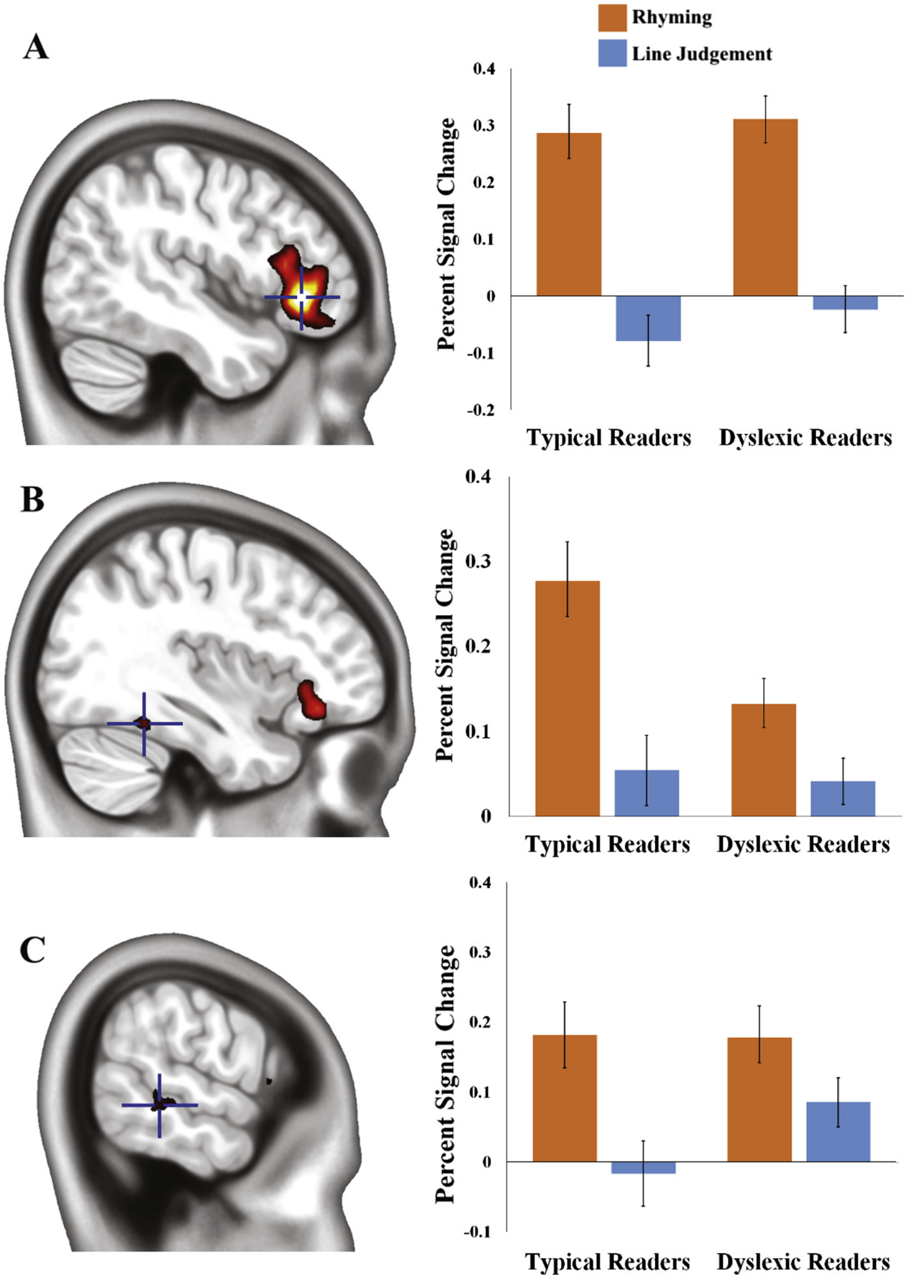

Fig. 3. Key regions of the left-lateralized reading network showing greater BOLD signal change in response to the rhyming task relative to the line-judgment task for both typical and dyslexic readers. (A) Inferior frontal gyrus (−46, 32, −4). (B) Fusiform gyrus (−36, −46, −20). (C) Middle temporal gyrus (−60, −38, −6). Error bars show SE of the mean.

in the reading network produced in the main effect of condition was associated with reading proficiency, and whether this relationship differed between the two groups. This was achieved by correlating Rhyming task brain scores — a measure of how strongly each individual expresses the spatial pattern associated with the Rhyming task — with Word Attack and Phonemic Reversal scores for each group.

As shown in Fig. 4, there was no association between Rhyming brain scores and Word Attack scores ($r = 0.04$, $p = 0.86$) and only a weak, non-significant positive association between brain scores and Phonemic Reversal scores ($r = 0.31$, $p = 0.14$) for the normal readers group. Surprisingly, robust negative associations were found between Rhyming brain scores and both Word Attack ($r = -0.52$, $p = 0.008$) and Phonemic Reversal scores ($r = -0.51$, $p = 0.01$) in the dyslexia group. Fisher Z-tests confirmed that the correlation coefficients between brain scores and each reading task were significantly different between the two groups for both Word Attack ($z = 1.99$, $p < 0.05$) and Phonemic Reversal ($z = 2.8$, $p < 0.005$). This pattern suggests that while the reading network was activated to similar degrees in both groups, increasing levels of activation in this network are associated with lower reading proficiency in the group with dyslexia.

To further investigate brain-behavior correlations, we performed a non-rotated behavioral-PLS analysis to determine if there were reliable spatial patterns of brain activity outside of the reading network that showed differential correlations with reading proficiency between the two groups. Permutation tests showed this LV to be significant ($p = 0.009$). As shown in Fig. 5, correlations

Table 5
Results of the group × condition interaction effect for regions reported in the Maisog et al. (2008) meta-analysis as showing a difference in activation between typical and dyslexic readers. None of the regions showed a significant effect.

Structure	MNI coordinate			Percent Signal Change				*Group × Condition* Interaction	
	X	Y	Z	Rhyming		Line Judgment		F	p
				Typical	Dyslexic	Readers	Dyslexic		
L PrCu	−4	−76	28	0.13 (0.16)	0.08 (0.2)	0.08 (0.2)	0.10 (0.16)	1.24	0.27
L ITG	−48	−58	−10	0.11 (0.2)	0.07 (0.16)	0.11 (0.19)	0.10 (0.14)	0.13	0.72
L FusG	−48	−42	−22	0.18 (0.28)	0.04 (0.32)	0.10 (0.33)	−0.01 (0.26)	0.45	0.51
L IPL	−46	−44	26	0.11 (0.12)	0.04 (0.14)	0.08 (0.16)	0.05 (0.08)	0.48	0.49
L ITG	−52	−36	8	0.11 (0.15)	0.17 (0.21)	0.04 (0.19)	0.06 (0.19)	0.26	0.61
L Thal	−18	−24	10	0.02 (0.14)	0.06 (0.15)	0.06 (0.1)	0.1 (0.15)	0.01	0.93
L IFG	−22	32	−4	0.04 (0.13)	0.03 (0.15)	0.04 (0.14)	0.02 (0.14)	0.00	0.98
R PoCG	50	−26	32	0.02 (0.15)	−0.08 (0.15)	0.11 (0.15)	0.11 (0.1)	3.78	0.06
R ITG	44	−22	−4	0.08 (0.16)	0.04 (0.15)	0.03 (0.16)	0.02 (0.16)	0.25	0.62
R Thal	14	−20	12	0.05 (0.18)	0.02 (0.18)	0.03 (0.19)	0.11 (0.15)	2.91	0.10
R Ins	34	18	2	0.00 (0.24)	0.03 (0.18)	0.05 (0.17)	0.02 (0.16)	0.70	0.41

FusG = fusiform gyrus; IFG = inferior frontal gyrus; Ins = insula; IPL = inferior parietal lobule; ITG = inferior temporal gyrus; PoCG = post-central gyrus; PrCU = precuneus; Thal = thalamus.

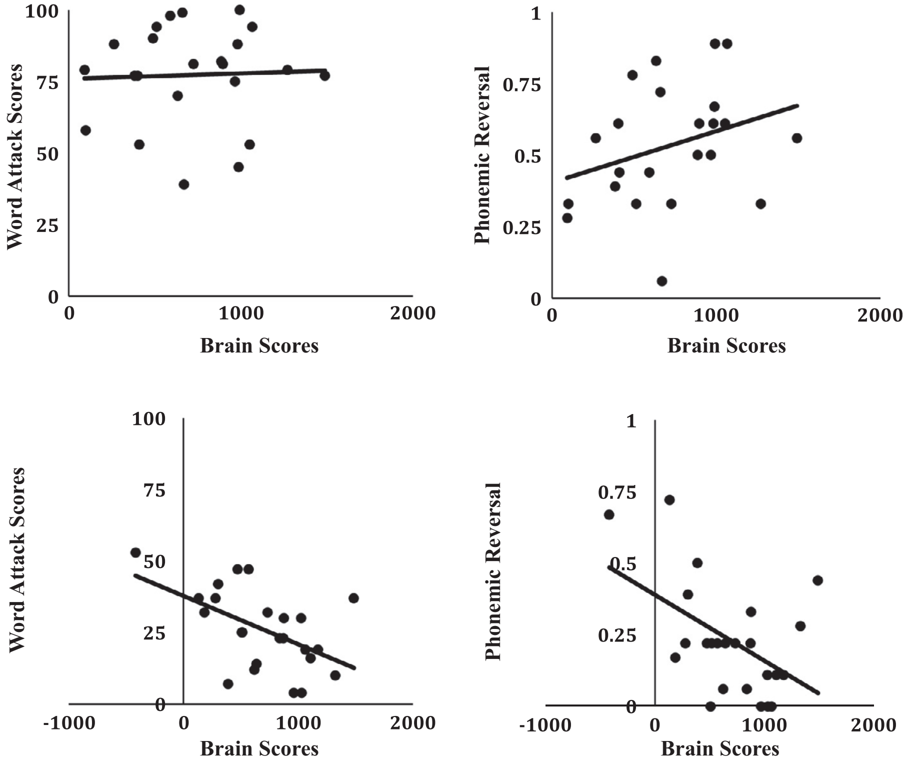

Fig. 4. Correlation profiles showing relationships between brain scores from the Rhyming condition and performance in Word Attack and Phonemic Reversal tasks. The top row shows typical readers; the bottom row dyslexic readers.

between brain activity in the regions expressing the LV and both Word Attack and Phonemic Reversal scores were different for the two groups. The spatial patterns (shown in Fig. 5) contributing to this effect (BSR threshold −/+ 3; approx. $p < 0.001$) are dominated by clusters exhibiting negative saliences (i.e. clusters in cool colors), showing that the effect was generally driven by regions showing more positive brain-behavior correlations in the Dyslexia group. The spatial extent of this network was widespread and included clusters in bilateral insula, temporal and parietal lobes: for a full list of regions contributing to the LV, see Table 6. As shown by the correlation plots in Fig. 6, increased activity in these regions during the Rhyming tasks was associated with increased performance in Word Attack and Phonemic Reversal scores, but only for the Dyslexia group.

4. Discussion

A number of interesting findings emerged from the current study. First, using task PLS, we showed that both normal and dyslexic reading activated a left-lateralized reading network well characterized in previous studies (see for reviews and meta-analyses Dehaene et al., 2015; Martin et al., 2015; Price & Mechelli, 2005). Next, we found that even though dyslexic and non-dyslexic readers differed in behavioral performance for the Rhyming task (but not the control line-judgment task), this behavioral interaction was not mirrored in our fMRI results: this was the case both for a whole-brain PLS analysis and when testing for group effects in specific ROIs, based on the main effect ROIs or on regions previously shown to be affected in individuals with

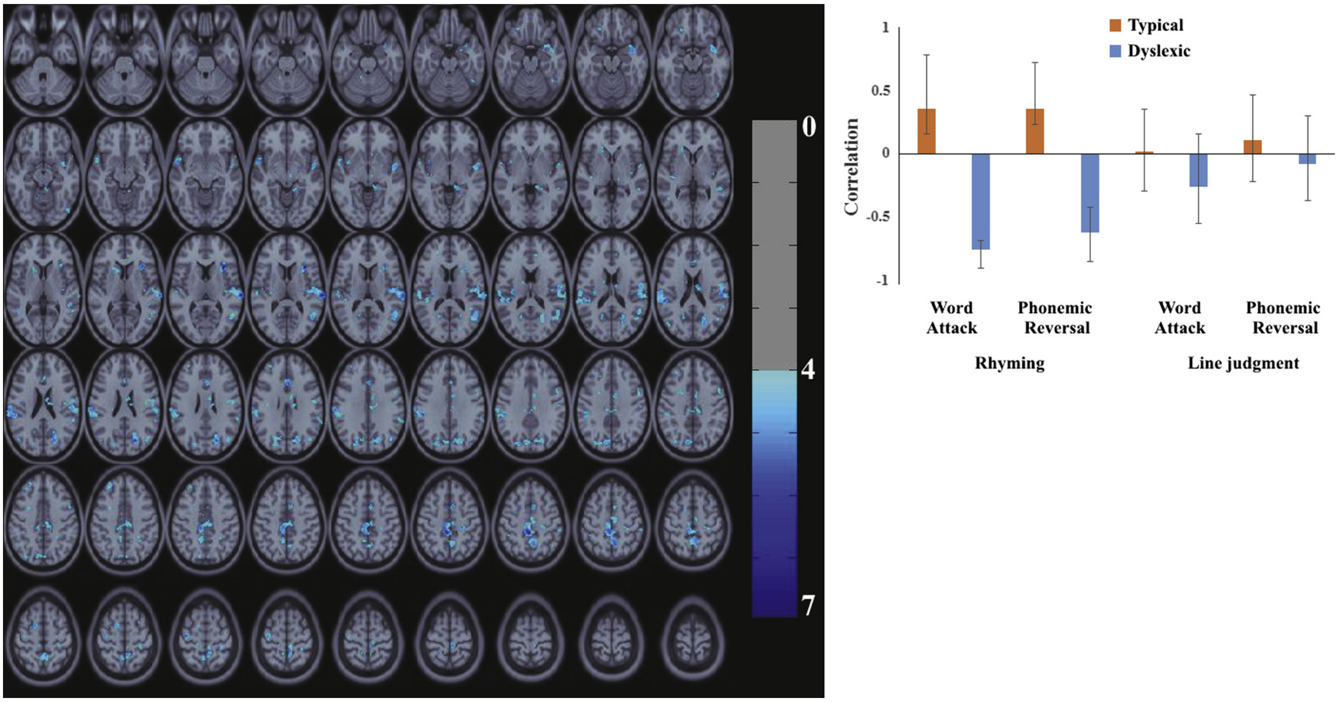

Fig. 5. (A) Singular image of the behavioral PLS LV. The image is dominated by voxels exhibiting negative saliences (cool colors), which exhibit greater brain-behavior correlations between reading performance and BOLD signal during the Rhyming condition in the Dyslexic group. Images are thresholded at BSR > 4 ($p < 0.0002$). (B) Correlation profile of the behavioral PLS LV. Note that only the Rhyming condition contributed to the effect. This LV was significant ($p = 0.009$).

dyslexia (Maisog et al., 2008). This finding was not consistent with our initial hypothesis. One possibility is that this finding was due to the behavioral differences observed in the rhyming task, with control participants obtaining higher accuracy (close to ceiling) and faster response times than the reading difficulty group. A consequence of this is that the reading network in the control group may not have been recruited to the same degree as would be the case in a more difficult task, highlighting the importance of matching for behavioral performance when analyzing group differences in neuroimaging. Although speculative, a related explanation is that the reading network, while activated to a similar degree in the group with dyslexia, does not operate as efficiently as in the control group, thus leading to reduced performance. Indeed, the finding that the level of activation in the reading network during the Rhyming task was negatively correlated with reading ability is tentative support for this hypothesis. Future work designed to test this particular question could provide additional validation to this assumption.

Next, we showed that while both groups activate a left-lateralized reading network to the same degree, activation in this network showed distinct relationships with reading ability for each group. Specifically, while normal readers showed no relationship between reading ability and activation in this network, this relationship was negative for the reading difficulty group. While this finding aligns with previous research showing differences in brain-behavior relationships between controls and dyslexics (Hampson et al., 2006; Hoeft et al., 2007; van der Mark et al., 2011), the nature of this difference in the current study (i.e. the dyslexia group showing a negative relationship) was unexpected. One possibility for the difference in the current study is the nature of the variable being correlated with behavior: while previous studies have generally correlated signal from specific ROIs with reading ability (e.g. Hampson et al., 2006), the brain-behavior correlations reported here involved brain scores, which are weighted averages of activity indicating how strongly each participant expresses the spatial pattern associated with the Rhyming task. This measure provides a more global index of brain function during a cognitive task as opposed to single ROIs, and this finding requires further investigation using multivariate techniques.

Most importantly, our findings indicate that reading performance is mediated by a distinct set of regions in individuals with dyslexia relative to typical readers. Many of the regions in this network were lateralized to the right, in line with other earlier research (e.g. Shaywitz et al., 1998; Waldie et al., 2013). Specifically, dyslexic readers showed a positive correlation between right superior temporal gyrus (STG) activity and phonological task performance, as well as between bilateral insula activation and reading performance. Given that the left STG is thought to be involved in grapheme-phoneme conversion (Pugh, 2006), it was not surprising that typical readers showed an inverse association between *right* STG activity and task performance; this finding is consistent with greater reading skill being associated with left lateralisation of reading-related areas. Conversely, our findings for dyslexic readers suggest that these right hemisphere areas are not only playing a compensatory role in dyslexia, consistent with the idea of reversed lateralization (Illingworth & Bishop, 2009).

Increased bilateral anterior insula activation was associated with higher accuracy on both nonword decoding and phonological processing in participants with dyslexia. This is consistent with findings from Maisog et al.'s (2008) meta-analysis, which found right anterior insula overactivation in dyslexia, and also with Richlan et al's (2009) meta-analysis, which found overactivation in the same region but in the left hemisphere (Maisog et al., 2008; Richlan et al., 2009). The association of greater insula activity with better performance in dyslexics in the current study is particularly interesting because the positive correlation between insula activity and reading performance was not found in the group without reading disability (which included those with dyscalculia), suggesting that this pattern does not emerge as a consequence of shared properties of dyslexia and dyscalculia (Vellutino et al., 2004), but rather is specific to dyslexia.

Table 6
Regions associated with the behavioral PLS analysis. For the dyslexic group, brain activity in all regions listed showed reliably greater correlation coefficients with Word Attack and Phonemic Reversal performance relative to typical readers.

	MNI coordinate				
Structure	X	Y	Z	BSR	Cluster Size
R Ins	34	20	10	−7.75	81
R STG	70	−24	8	−7.1	684
L CinG	−4	−38	52	−6.9	529
L Ins	−38	4	−4	−6.48	20
L STG	−54	−34	18	−6.44	563
R PoCG	24	−28	50	−6.24	36
R STG	52	−4	−6	−6.23	111
R Cun	20	−74	24	−6.22	300
L PrCG	−36	−16	62	−6.14	43
R SMA	6	6	50	−5.93	145
R PrCu	4	−54	54	−5.92	281
L Ins	−34	−20	14	−5.91	53
R ACinG	4	18	28	−5.87	90
L STG	−54	6	−8	−5.84	76
R PCL	8	−34	66	−5.79	40
L SFG	−16	2	58	−5.74	48
R LinG	16	−42	−6	−5.59	52
L CalC	−18	−62	18	−5.47	34
L Cun	−10	−78	38	−5.45	123
L SOG	−24	−80	32	−5.39	117
R MTG	50	−62	10	−5.35	182
R STP	40	−6	−18	−5.34	109
L Cau	−20	24	2	−5.28	52
L MTG	−50	−56	4	−5.19	11
R Thal	8	−10	20	−5.19	68
R ACinG	10	44	20	−5.04	16
R MOG	46	−72	26	−5.02	34
R IOG	48	−78	−16	−4.92	18
L MFG	−34	46	30	−4.91	16
L STG	−40	−20	0	−4.91	25
R MTG	54	−40	4	−4.89	32
R IPL	28	−44	42	−4.88	12
L PrCu	−10	−50	44	−4.82	40
R PrCG	50	6	40	−4.74	55
L OFC	−24	34	−18	−4.74	18
L SFG	−28	42	42	−4.74	41
R PoCG	30	−38	62	−4.71	17
L MTG	−48	−72	22	−4.63	19
R SMG	62	−42	28	−4.56	25
R Cun	4	−78	40	−4.2	11

ACinG = anterior cingulate gyrus; CalC = calcarine cortex; Cau = caudate; CinG = cingulate gyrus; Cun = cuneus; Ins = insula; IOG = inferior occipital gyrus; IPL = inferior parietal lobule; L = left; LinG = lingual gyrus; MFG = middle frontal gyrus; MOG = middle occipital gyrus; MTG = middle temporal gyrus; OFC = orbitofrontal cortex; PCL = paracentral lobule; PrCG = precentral gyrus; PrCu = precuneus; R = right; SFG = superior frontal gyrus; SMA = supplementary motor area; SMG = supramarginal gyrus; SOG = superior occipital gyrus; STP = superior temporal pole; Thal = thalamus.

Insula activity has been related to increased cognitive challenge, including linguistic effort (Gasquoine, 2014), and is also prominent during periods of increased emotional arousal (Damasio et al., 2000). It is also associated with several regions involved in decision-making and interference resolution, especially the anterior cingulate and dorsolateral prefrontal cortex (Eckert et al., 2009; Fleck, Daselaar, Dobbins, & Cabeza, 2006; Nee, Wager, & Jonides, 2007). In the present study, it is not entirely clear why the correlations between phonological performance and insula activity were in opposite directions in the two groups. One explanation could be that the anterior insula supports the increased load of linguistic decision-making in the dyslexic group, but not in typical readers. However, this seems unlikely given that significant brain-behavior correlations were observed during the rhyming task but not the line judgment task. In our view, a more plausible interpretation is that increased insula activation in dyslexia reflects a negative emotional association with reading, and that this activity is therefore increased with effortful task engagement in the dyslexia group, but not in the typical reading group, since they do not have the same negative emotional association (Maisog et al., 2008).

A possible limitation of the tasks used in the present study is that activations might not solely reflect the phonological demands of the rhyme task, compared to the control line orientation judgment task, but could also be related to additional verbal short-term memory demands. In the rhyming task, participants had to remember the first word (e.g. waist) for the rest of the trial in order to decide if the second word (e.g., paste) rhymed. Although this time period was short (3500 ms maximum), this could have been achieved using a sub-vocal rehearsal strategy (whereas the line judgment stimuli obviously could not be represented in this way). This is consistent with the influential neural model of the articulatory loop (comprised of sub-vocal rehearsal and phonological encoding) postulated by Paulesu, Frith, and Frackowiak (1993), which includes the right and the superior temporal gyrus, the supermarginal gyrus, and the insula. Because verbal short-term memory is known to be affected in dyslexia, including in the current sample (Wilson et al., 2015), the hypothesis of increased short-term memory demands cannot be ruled out and should be investigated in future research. However, given that verbal short-term memory is in any case a crucial cognitive component of reading, this does not reduce the interest of the current findings.

Our findings suggest several avenues for future research. It has been suggested that the right hemisphere should be given more consideration in the study of dyslexia, as atypical laterality seems

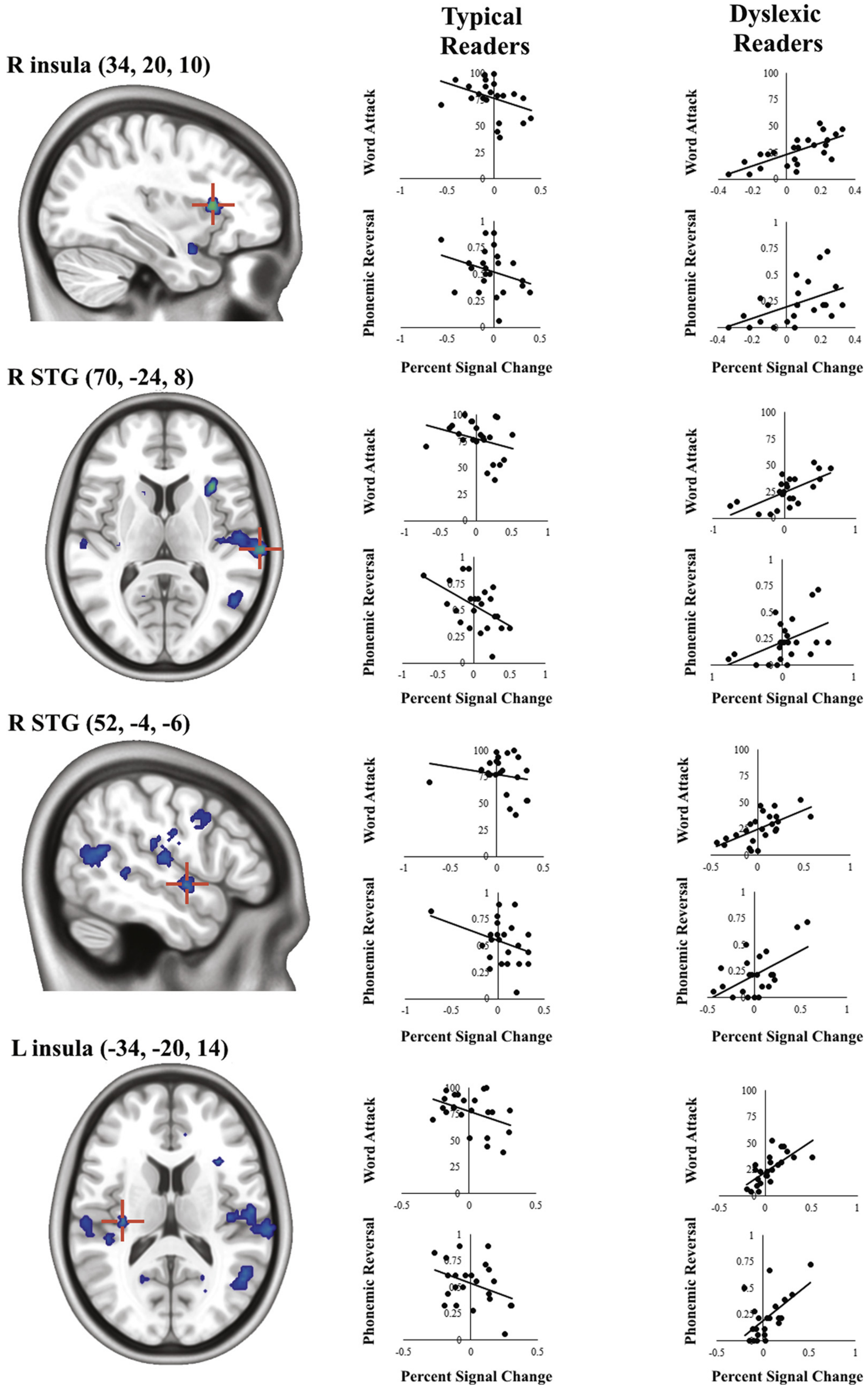

Fig. 6. Selected regions showing a positive association between reading performance (word attack and phonemic reversal) and BOLD signal during the rhyming task for dyslexic readers only.

to correlate with reading difficulties (e.g. Waldie et al., 2013). As noted earlier, inconsistencies in right hemisphere activation highlight the necessity of investigating its specificity in reading disorders, yet in our view this has not translated to a systematic study of right cortical networks in reading. In addition, establishing a neural signature of dyslexia has broad implications for refining screening and diagnosis, in both adults and children. Current diagnosis is usually based on behavioral testing with only a fairly acceptable rate of individuals positively identified (Pennington et al., 2012). In some cases, however, a sole reliance on behavioral results is insufficient, and could be coupled with neural data to better identify the source of the problem and confirm initial interpretations. The present findings suggest that the right STG and the insula might both play an important compensatory reading role in dyslexia, and that the combination of poor reading performance with high insula activity could be used as a marker of dyslexia. Moreover, identifying the precise neural underpinnings of dyslexia can also inform the design and content of cognitive remediation programs, with the potential for more focused and theoretically informed training programs (Moreau & Waldie, 2016). Previous work has shown that patterns of activation in dyslexia can be altered following intensive phonological processing training (e.g. Temple et al., 2003). However, the extent to which normalizing neural activity transfers to sustained behavioral improvement remains to be confirmed.

The present findings warn against focusing solely on simple comparisons of neural activation in diagnosis or remediation; similar activation in typical readers and dyslexics may not reflect equivalent underlying cognitive processes. In this respect, the present paper contributes to challenging a common assumption in the remediation of dyslexia. Perhaps normalization in neural activity is not essential, or even desirable, and remediation efforts should instead focus on developing and increasing the efficiency of compensatory strategies? Intervention research using pre/post brain imaging has the potential to shed light on whether the unique right hemisphere activity patterns seen in dyslexia help or hinder reading, and whether they are a consequence or a cause of reading difficulties.

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