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Maladaptive compensation of right fusiform gyrus in developmental dyslexia: A hub-based white matter network analysis

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ABSTRACT

Cognitive theories have been proposed to clarify the causes and symptoms of dyslexia. However, correlations between local network parameters of white matter connectivity and literacy skills remain poorly known. An unbiased hypothesis-free approach was adopted to examine the correlations between literacy symptoms (reading and spelling) and hub-based white matter networks' connectivity parameters [nodal degree fractional anisotropy (FA) values] of 90 brain regions based on Anatomical Atlas Labels (AAL) in a group of French children with dyslexia aged 9–14 years. Results revealed that the higher the right fusiform gyrus's (FFG) nodal degree FA values, the lower the reading accuracy for words and pseudowords in dyslexic children. The results indicate that the severity of word/pseudoword reading symptoms in dyslexia relates to a white matter network centered around the right FFG. The negative correlation between right FFG network connectivity and reading accuracy, in particular pseudoword reading accuracy, suggests that right FFG represents a maladaptive compensation towards a general orthography-to-phonology decoding ability in developmental dyslexia.

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1. Introduction

Dyslexia is one of the most significant learning disabilities, with a prevalence rate ranging from 1.3% to 17.5% (Di Folco et al., 2020; Shaywitz & Shaywitz, 2005). It is characterized by difficulties in the acquisition of fluent reading skills despite normal intelligence and schooling (Lyon et al., 2003). Although cognitive theories, e.g., phonological deficit hypothesis (Brady & Shankweiler, 1991; Ramus, 2003; Shankweiler & Liberman, 1972), have been proposed to elucidate the causes and symptoms of dyslexia, there is considerable value in identifying quantitative measures of the brain anatomy that can directly correlate with the severity of dyslexia symptoms.

In terms of symptoms of dyslexia, it has been widely reported in various orthographies that children with dyslexia exhibited less accurate word and pseudoword reading (poor decoding ability) compared with controls in various languages, e.g., English (Rack et al., 1992), French (Saksida et al., 2016), and German (Wimmer, 1996; Ziegler et al., 2003). Besides, dyslexia is associated with a slower reading speed for words/pseudowords and texts (Norton & Wolf, 2012) across both opaque and transparent languages (Serrano & Defior, 2008). Other than reading abilities, evidence indicates that most children with dyslexia also have spelling difficulties that usually persist through their life span (Berninger et al., 2008; Bruck, 1993; Lefly & Pennington, 1991).

Regarding correlations between literacy symptoms of dyslexia and white matter anatomy, most studies have revealed positive correlations between literacy skills and white matter connectivity, indexed by the fractional anisotropy (FA) in regions or pathways of the left hemisphere. Significant positive correlations between FA of the left temporoparietal region and word/pseudoword reading accuracy have been consistently reported in studies on adults and children with dyslexia (Deutsch et al., 2005; Klingberg et al., 2000; Niogi & McCandliss, 2006; Odegard et al., 2009). Similarly, FA values of the left temporoparietal region have also been found to be positively correlated with spelling abilities in children with dyslexia (Deutsch et al., 2005). Positive correlations were reported between FA in regions of the left perisylvian language and reading fluency (Rimrodt et al., 2010). Besides, tractography studies in recent years further demonstrated that FA values of the left inferior fronto-occipital fasciculus (Vandermosten et al., 2012) and the left arcuate fasciculus (Banfi et al., 2019) were positively correlated with spelling abilities in children with dyslexia.

On the other hand, white matter connectivity in the white matter pathways of the right hemisphere or right lateralization of some white matter pathways has also been reported to be correlated with literacy skills. However, both positive and negative correlations have been observed. In particular, FA in the right superior longitudinal fasciculus (SLF), a dorsal pathway, positively predicted the dyslexia group's word reading accuracy (Hoeft et al., 2011) and children at risk of dyslexia's pseudoword reading accuracy (Zuk et al., 2020) two to three years later. In contrast, Zhao and colleagues reported that right lateralization of the inferior fronto-occipital fasciculus (IFOF), an important ventral pathway, negatively correlated with reading and spelling accuracy in the dyslexia group (Zhao et al., 2016). Furthermore, significant negative correlations were observed between FA and reading accuracy and fluency in the right inferior longitudinal fasciculus (ILF), another key ventral pathway (Banfi et al., 2019).

For some neural underpinnings that were not typically involved in reading processing, such as the right SLF, some researchers interpreted the positive correlation between these neural underpinnings and reading performance as a compensatory mechanism for children with dyslexia (Hoeft et al., 2011). However, the use of the term “compensatory mechanism” has thus far been equivocal, partially due to vague definitions used in the literature (Fleming et al., 2018; Hancock et al., 2017). As described by Cabeza et al. (2018) in a review article, two criteria have to be met to define a neural compensation. First, it should be clear what the neural underpinning is being compensated for (e.g., deficits in reading skills that children with dyslexia exhibited). Second, the enhanced activation related to a beneficial effect on cognitive performance (e.g., the right SLF was positively related to the dyslexia group's reading performance) (Cabeza et al., 2018). Thus, previous functional MRI studies, which consistently showed hyperactivation in the right hemisphere analog of the left occipitotemporal visual word form area, might not be appropriate enough to be considered a neural compensation in children with dyslexia since these hyperactivation results lacked linking to better reading performance (Pugh et al., 2000; Shaywitz et al., 2002, 2003). Alternatively, some studies observed negative correlations between white matter measures in these areas (such as IFOF and ILF) and reading performance in children with dyslexia, and these negative correlation results of right IFOF and ILF might be a maladaptive compensatory strategy in children with dyslexia (Banfi et al., 2019; Zhao et al., 2016). Nevertheless, the nature of this compensation remains unclear.

Reading is a process regulated by multiple brain areas working as a complex network (Dehaene, 2010). Apart from previous studies examining correlations between the symptoms of dyslexia and white matter connectivity and focusing on a region or a pathway, a few studies adopted the graph theory to investigate network characteristics associated with reading disabilities. These studies showed decreased global parameters such as the small worldness of grey matter network in children with dyslexia (Qi et al., 2016) and familial risk for reading difficulties (Hosseini et al., 2013). Recent studies on normally developing children and normal adults further revealed developmental differences in topological measures of large-scale functional brain networks during reading tasks (Liu et al., 2018; Zhou et al., 2021). Nonetheless, only one recent study investigated the topological properties of white matter networks in children with dyslexia (Lou et al., 2019). Lou et al. (2019) reported that literacy skills were positively correlated with some global network parameters (e.g., clustering coefficient, local efficiency, transitivity, global efficiency) of whole-brain white matter network. However, this study provided limited information on correlations between literacy skills and local white matter network parameters (e.g., nodal degree), which might provide novel information of hub-based impaired subnetworks in dyslexia.

Therefore, the main objective of this study was to explore variations of connectivity of hub-based white matter subnetworks associated with literacy difficulties in children with dyslexia. We adopted an unbiased data-driven approach to facilitate a hypothesis-free analysis and examine correlations between hub-based white matter network connectivity and broad literacy skills, including word/pseudoword/text reading accuracy and fluency, and spelling accuracy. We anticipate these clinical–anatomical correlations could facilitate the understanding of the relationship between literacy symptoms of dyslexia and the brain, and potentially improve objective clinical diagnosis and intervention in reading disability.

2. Materials and methods

2.1. *Research transparency and data availability*

The experimental procedures and analyses in this study were not preregistered prior to the research being conducted. We reported how we determined our sample size, all inclusion/exclusion criteria, all data exclusions, all manipulations, and all measures in the study. Inclusion/exclusion criteria were established prior to data analysis. Further details can also be found in our previous published paper in which we used the same dataset (Zhao et al., 2016).

The conditions of our ethics approval do not permit public archiving of anonymised study data. Readers seeking access to the data should contact the lead author Franck Ramus and Jingjing Zhao. Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data. Specifically, requestors must provide a research proposal following the guidelines at the Open Science Framework (OSF) approved by Franck Ramus and preregistered the study at OSF (https://osf.io) to obtain the data.

2.2. *Participants*

Twenty-six children with dyslexia and 31 matched (sex, age, handedness, and nonverbal IQ) control children (aged 109–169 months) were included in this study. All the children were native French-speaking with normal vision and hearing abilities, and none of them was diagnosed with a history of brain damage or psychiatric or any other cognitive disorders. The dyslexia group subjects were referred by a clinic for reading and language disabilities and presented with a delay of >18 months on text reading age based on accuracy and speed of the Alouette test, a meaningless text that assesses both reading accuracy and speed (Lefavrais, 1967). The control children were no more than 12 months behind on text reading age of the Alouette test. Demographics for the two groups are shown in Table 1. The study was approved by the Ethics Committee of Bicetre Hospital, and informed consent was obtained from all the children and their parents. Analyses of group differences of some white matter pathways and whole-brain white matter network connectivity in the same sample have previously been published (Lou et al., 2019; Zhao et al., 2016).

2.3. *Behavioral measures*

Behavioral assessments were employed to determine each child's intellectual abilities and literacy skills. Intellectual abilities were measured using the WISC blocks, matrices, similarities, and comprehension subtests (Wechsler, 2005). Text reading skills (accuracy and fluency) were estimated by the Alouette test (Lefavrais, 1967). Word and pseudoword reading skills (accuracy and fluency) were measured by the Odedys word and nonword reading fluency test (Jacquier-Roux et al., 2005). Spelling ability was assessed by a word spelling-to-dictation test (Martinet & Valdois, 1999). Parental education was recorded as the highest degree obtained, coded on a 1–6 scale, from 1: a postgraduate degree to 6: neither a high school diploma nor a professional certificate. Handedness was based on each child's writing hand.

We defined three composite measures for the brain-behavior correlation analysis: reading accuracy, reading fluency, and spelling accuracy, consistent with our previous study (Zhao et al., 2016). Reading accuracy (READACC) was

Table 1 – Demographical data and behavioral results of literacy skills.

	Control children		Dyslexia children		Test statistics
	N	Mean (SD)	N	Mean (SD)	
Subject characteristics					
Sex (male/female)	31	18/13	26	13/13	χ^2 (1) = .371, p = .543
Handedness (left/right)	31	2/29	26	3/23	χ^2 (1) = .457, p = .499
Age (months)	31	137.90 (16.33)	26	139.27 (15.77)	t (55) = .320, p = .751
Maternal education	31	2.65 (1.38)	26	3.08 (1.80)	t (55) = 1.029, p = .308
Paternal education	31	2.52 (1.61)	26	3.62 (1.92)	t (55) = 2.352, p = .022
Non-verbal IQ	31	110.29 (17.09)	26	106.00 (15.69)	t (55) = .980, p = .332
Verbal IQ	31	123.84 (18.70)	26	107.88 (18.22)	t (55) = 3.246, p = .002
Reading age (months)	31	145.94 (18.65)	26	87.27 (11.43)	t (55) = 13.979, p < .0001
Literacy skills					
Word reading accuracy (/20)	31	18.65 (1.64)	25	10.52 (4.33)	t (54) = 9.650, p < .0001
Word reading time (sec)	31	15.30 (4.00)	25	65.68 (39.45)	t (54) = −7.082, p < .0001
Pseudoword reading accuracy (/20)	31	17.45 (1.73)	25	11.36 (3.37)	t (54) = 8.759, p < .0001
Pseudoword reading time (sec)	31	22.00 (5.37)	25	57.80 (34.81)	t (54) = −5.656, p < .0001
Text reading accuracy (%)	31	96.41 (2.02)	24	77.81 (17.78)	t (53) = 5.791, p < .0001
Text reading speed (nb of correct words/3 min)	31	397.88 (67.52)	24	112.73 (80.55)	t (53) = 14.277, p < .0001
Spelling (%)	31	82.75 (13.77)	26	37.94 (20.18)	t (55) = 9.922, p < .0001

computed by averaging z-scores of the word, pseudoword, and text reading accuracy. Reading fluency (READFUL) was computed by averaging z-scores of the word and pseudoword reading time and text reading speed. Spelling accuracy (SPELL) simply was the z-scores of the word spelling test. Signs were adjusted such that positive z-scores represented above-average performance. Legal copyright restrictions prevent publicly archiving of the various assessment tests used in the current study, which can be obtained from the copyright holders in the cited references.

2.4. *Image acquisition*

All the children were scanned on a 3T MRI system (Tim Trio, Siemens Medical Systems, Erlangen, Germany), equipped with a whole-body gradient (40 m T/m, 200 T/m/sec), and a 32-channel head coil. For T1-weighted structural MRI scans, a MPRAGE sequence with following parameters was used: acquisition matrix = 230 × 230 × 224, repetition time (TR) = 2,300 msec, echo time (TE) = 3.05 msec, flip angle = 9°, field of view (FOV) = 230 mm, voxel size = .9 × .9 × .9 mm^3. A spin-echo single-shot EPI sequence was used for diffusion MRI scans, with parallel imaging (GRAPPA reduction factor 2), partial Fourier sampling (factor 6/8), and bipolar diffusion gradients to reduce geometric distortions. The whole brain was imaged with an isotropic spatial resolution of 1.7 mm^3 (matrix size = 128 × 128, field of view = 218 mm) and 70 interleaved axial slices. Diffusion gradients were applied along 60 orientations, uniformly distributed, with a diffusion weighting of $b = 1400$ sec/mm^2 (repetition time = 14,000 msec, echo time = 91 msec). Additionally, three images were acquired with no diffusion gradient applied ($b = 0$). Each sequence took about 6 min, resulting in a total acquisition time of 18 min.

2.5. *DTI analysis*

The diffusion MRI dataset was implemented using a pipeline toolbox, PANDA (Cui et al., 2013), mainly programmed based on FSL (Jenkinson et al., 2012). Raw DICOM files were first converted to 4D NIFTI files using the dcm2nii tool embedded in MRIcron. A brain mask for each individual was then generated by removing the skull to extract the brain tissues. Head motion was corrected using the eddy-current method by registering the diffusion-weighted images to the b0 image, with the affine transformation of diffusion gradient direction adjusted accordingly. Fractional anisotropy (FA) metrics of each individual were calculated by fitting diffusion tensors to each participant's native head motion-corrected diffusion-weighted image. Then, each individual's fractional anisotropy (FA) image in the native space was normalized to the MNI space using a standard FA template (FMRIB58_FA). We manually checked all the DWI data and registrations during the data processing. All of them showed good quality. Finally, whole-brain tractography was performed using the deterministic fiber tracking method employed by continuous tracking (FACT) algorithms (http://trackvis.org/dtk). Fiber tracking was terminated if two consecutive moving directions had a crossing angle of >45°. Fiber tracking was also terminated if the FA was out of the threshold range of .2–1 because the tissue with FA out of this range is thought to be grey matter or CSF.

2.6. *Network node definition*

Nodes of the white matter network were defined by automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). According to the AAL atlas, the whole-brain gray matter (excluding cerebellum) of each child was divided into 90 regions of interest (ROIs). To obtain a better grey-matter image, a utility in PANDA named Brain Extraction (T1) with parameters of the eye and optic nerve clean-up and bias field and neck clean-up was used to extract the T1 image. The T1 image of each individual was then co-registered to the fractional anisotropy (FA) image in the diffusion tensor imaging (DTI) space using a linear transformation. Subsequently, the transformed T1 image was normalized to the ICBM152 template in the MNI space using non-linear transformation. Finally, the AAL mask from the MNI space was warped to the DTI native space using the resultant inverse transformation.

2.7. *Define backbone network in the control group children*

We first computed the backbone network in the control group to identify the highly consistent cortical connections (Gong et al., 2009). A nonparametric one-tailed sign test was applied with a null hypothesis of no existing connection for each pair of cortical nodes (fiber bundle number = 0). The results were Bonferroni corrected for multiple comparisons ($C_{90}^{2} = 4005$ pairs of regions) at $p < .05$. Finally, a symmetric binarized matrix with 396 tracts survived the threshold (Figure S1). The sparsity of the resultant network (9.89%) was similar to that reported in previous studies on adults (Chen et al., 2020; Gong et al., 2009).

2.8. *Identifying anatomical hubs in dyslexia*

Using the backbone network mask acquired in the control group, we then extracted the fractional anisotropy (FA) metrics of the backbone network in the dyslexia group and computed the nodal degree FA value of each AAL region, which referred to the sum of FA values of all the edges that were linked to the node. To identify neural hubs for literacy skills in dyslexia, partial correlation test was performed between the nodal degree FA value of each AAL node and the pre-defined literacy z-scores (READACC, READFUL, SPELL) by regressing the effects of age, sex, handedness, and parental education level. Correlation results were corrected for multiple testing with Bonferroni correction ($p < .05/90 \approx .00056$).

2.9. *Post hoc analyses*

As a negative correlation was observed between the right fusiform gyrus (FFG) network and READACC in the present study, similar to what we reported in a previous study between right lateralization of a ventral white matter pathway (IFOF) and READACC (Zhao et al., 2016) and similar to the results reported in Banfi et al. (2019)'s study between FA of another ventral pathway (right ILF) and reading measures (word reading and pseudoword reading), we carried out a hierarchical linear regression analysis to determine the added value of the right FFG network above the right lateralization of IFOF and right ILF in explaining the variance in READACC. In this model, age, sex, handedness, and parental education level were included in the first step. The lateralization index (LI) of IFOF and right ILF were included in the second step. The nodal degree FA value of the right FFG were included in the third step.

To determine which subset test of READACC correlated with the nodal degree FA value of the right FFG, we further recalculated the partial correlation coefficients between the three subtests of the z-score component of READACC (word, pseudoword, and text reading accuracy) and the nodal degree FA value of the right FFG.

To further compare the roles of the right FFG and IFOF in explaining pseudoword reading accuracy, word reading accuracy, and spelling accuracy, we conducted a second set of hierarchical linear regression analyses with age, sex, handedness, and parental education as statistically controlled variables in the first step; nodal degree FA value of right FFG and lateralization of IFOF were included in the second step. Pseudoword reading accuracy, word reading accuracy, and spelling accuracy were included as dependent variables, respectively. Notably, when testing one literacy measurement (e.g., pseudoword reading accuracy), we also added other literacy measurements (e.g., word reading accuracy, spelling accuracy) as controlled variables in the first step.

3. Results

3.1. *Demographic statistics*

Table 1 presents the descriptive statistics for behavioral measures for dyslexia and control groups. Dyslexia and control groups showed no significant differences in sex, age, handedness, and non-verbal IQ. The dyslexia group exhibited a significantly worse performance than the controls on all the measures of literacy skills.

3.2. *Brain-behavior correlation*

The whole-brain partial correlation between the nodal degree FA value of each region in the AAL atlas and the READACC, READFUL, and SPELL after controlling for age, sex, handedness, and parental education level yielded only one significant result: a negative correlation between READACC and nodal degree FA value of the right fusiform gyrus (FFG) in the dyslexia group ($r = -.66$, $p < .0005$, surviving Bonferroni corrected $p < .05$). None of the other correlations was significant in the dyslexia group, and no significant results were found in the control group. Table S1 presents the partial correlation results for the control and dyslexia groups, separately. Fig. 1 (top) presents the ten nodes in the right hemisphere linked to the right FFG, including the superior occipital gyrus, middle occipital gyrus, inferior occipital gyrus, calcarine fissure and the surrounding cortex, lingual gyrus, middle temporal gyrus, temporal pole, middle temporal gyrus, inferior temporal gyrus, hippocampus, and parahippocampal gyrus. Individual scatterplots for the correlation between nodal degree FA value of the right FFG and the READACC are shown in the bottom part of Fig. 1.

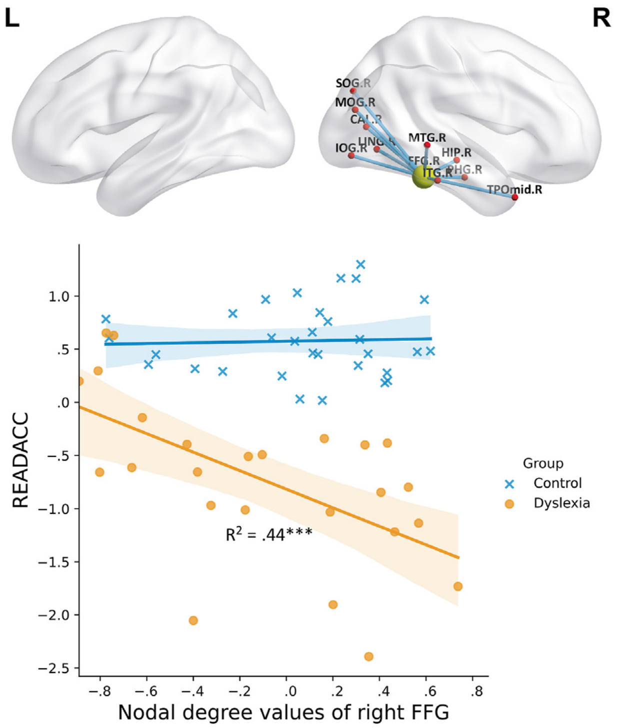

Fig. 1 – Ten nodes in the right hemisphere linked to the right fusiform gyrus (FFG), including the superior occipital gyrus (SOG), middle occipital gyrus (MOG), inferior occipital gyrus (IOG), calcarine fissure and surrounding cortex (CAL), lingual gyrus (LING), middle temporal gyrus (MTG), temporal pole: middle temporal gyrus (TPOmid), inferior temporal gyrus (ITG), hippocampus and parahippocampal gyrus (HIP). Individual scatter plots for the correlation between nodal degree FA value of the right FFG and reading accuracy (READACC) after controlling for sex, handedness, age, and education level for the control group and dyslexia group respectively.

3.3. *White matter network connectivity, and reading accuracy*

Post hoc hierarchical linear regression analysis revealed that when the control variables and LI of IFOF and right ILF were statistically controlled, the nodal degree FA value of the right FFG remained significantly associated with the READACC ($\beta = -.474$, $p < .01$; Table 2).

Post hoc partial correlation analysis showed that the nodal degree FA value of the right FFG showed a significant correlation with pseudoword reading accuracy ($r = -.738$, $p < .001$) and word reading accuracy ($r = -.614$, $p < .01$), but not text reading accuracy ($r = -.296$, $p = .21$). Fig. 2 presents the scatterplots.

As shown in Table 3, when age, sex, handedness, parental education, and word reading and spelling accuracy were statistically controlled, nodal degree FA value of the right FFG

Table 2 – Hierarchical linear regression analysis of reading accuracy (READACC).

Step		READACC		
		ΔR^2	*Beta*	SE
1	*Control variables*	.262		
	Age		.206	.011
	Sex		.368	.349
	Handedness		.160	.551
	Parental Education		-.379	.049
2	*Tractography measures*	**.300****		
	Right ILF		-.007	.005
	LI of IFOF		**-.619****	4.214
3	Right FFG	**.188****	**-.474****	.204

*$p < .05$, **$p < .01$. ΔR^2 is the R^2 change at each hierarchical step; *Beta* is the standardized regression coefficient. SE is the standard error. ILF: inferior longitudinal fasciculus. IFOF: inferior fronto-occipital fasciculus. LI: lateralization index. Fusiform gyrus: FFG.

showed a strong association with pseudoword reading accuracy ($\beta = -.562$, $p < .01$), but the LI of IFOF did not associate with pseudoword reading accuracy ($\beta = -.157$, $p = .546$). In contrast, as shown in Table 4, when age, sex, handedness, parental education, and pseudoword reading and word spelling accuracy were statistically controlled, the LI of IFOF was significantly associated with word reading accuracy ($\beta = -.391$, $p < .05$), but the right FFG did not associate with word reading accuracy ($\beta = -.119$, $p = .498$). As shown in Table 5, when age, sex, handedness, parental education, and pseudoword and word reading accuracy were statistically controlled, neither the LI of IFOF ($\beta = -.249$, $p = .241$) nor the nodal degree FA value of the right FFG ($\beta = -.254$, $p = .190$) could predict the word spelling accuracy.

4. Discussion

This study investigated the local network parameters of white matter connectivity (nodal degree FA values) related to literacy symptoms of dyslexia by using a data-driven hub-based white matter network analysis. The nodal degree FA value of the right fusiform gyrus (FFG) was negatively correlated with reading accuracy in the dyslexia group. In particular, the nodal degree FA value of the right FFG best accounted for individual differences in pseudoword reading accuracy.

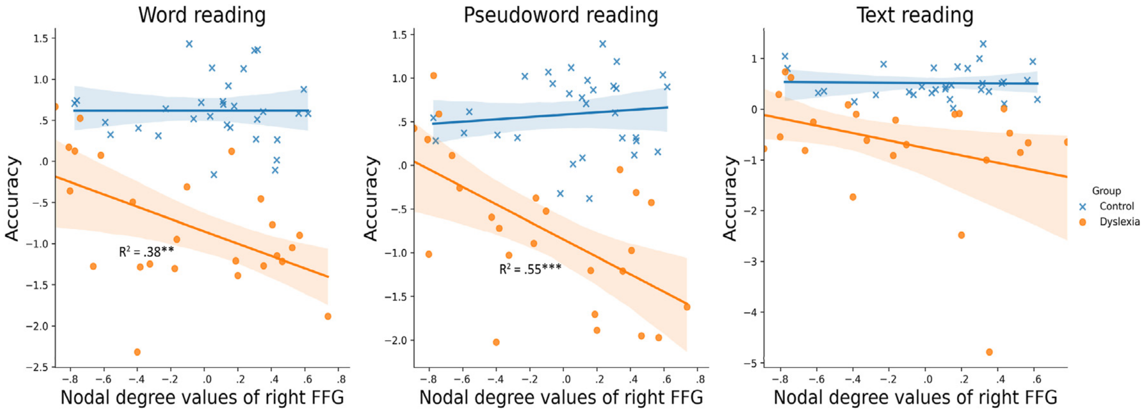

Fig. 2 – Individual scatter plots for the correlation between nodal degree FA value of the right fusiform gyrus (FFG) and word reading, pseudoword reading, and text reading accuracy after controlling for age, sex, handedness, and education level for the control group and dyslexia group respectively.

Table 3 – Hierarchical linear regression analysis of pseudoword reading accuracy (NWREADACC) with age, sex, handedness, parental education, word reading accuracy (WDREADACC), and word spelling accuracy (SPELL) controlled.

Step		ΔR^2	*Adjusted* R^2	NWREADACC		
				Unstandardized Coefficients		Standardized Coefficients
				B	SE	Beta
1	*Control variables*	.515*	.354*			
	Age			-.005	.011	-.085
	Sex			-.121	.348	-.072
	Handedness			.001	.493	.001
	Parental Education			-.007	.047	-.027
	WDREADACC			.849**	.282	.837**
	SPELL			-.147	.388	-.123
2	*Brain measures*	.171*	.530*			
	LI of IFOF			−3.842	6.227	-.157
	Right FFG			**-.890****	.301	**-.562****

*$p < .05$, **$p < .01$. IFOF: inferior fronto-occipital fasciculus. Fusiform gyrus: FFG.

Table 4 – Hierarchical linear regression analysis of word reading accuracy (WDREADACC) with age, sex, handedness, parental education, pseudoword reading accuracy (NWREADACC), and word spelling accuracy (SPELL) controlled.

Step		ΔR^2	*Adjusted* R^2	WDREADACC		
				Unstandardized Coefficients		Standardized Coefficients
				B	SE	Beta
1	*Control variables*	.768***	.690***			
	Age			-.001	.007	-.015
	Sex			.040	.238	.024
	Handedness			.094	.336	.036
	Parental Education			-.009	.032	-.035
	NWREADACC			.395**	.131	.401**
	SPELL			.705**	.208	.600**
2	*Brain measures*	.061$^{\#}$	.743$^{\#}$			
	LI of IFOF			**−9.405***	3.945	**-.391***
	Right FFG			-.187	.269	-.119

\# $p < .10$, *$p < .05$, **$p < .01$, ***$p < .001$. IFOF: inferior fronto-occipital fasciculus. Fusiform gyrus: FFG.

Table 5 – Hierarchical linear regression analysis of word spelling accuracy (SPELL) with age, sex, handedness, parental education, pseudoword reading accuracy (NWREADACC), and word reading accuracy (WDREADACC) controlled.

Step		ΔR^2	*Adjusted* R^2	SPELL		
				Unstandardized Coefficients		Standardized Coefficients
				B	SE	Beta
1	*Control variables*	.748***	.664***			
	Age			.011	.006	.251
	Sex			.295	.199	.209
	Handedness			-.217	.294	-.098
	Parental Education			-.022	.028	-.103
	NWREADACC			-.054	.142	-.064
	WDREADACC			.554**	.163	.651**
2	*Brain measures*	.037	.677			
	LI of IFOF			−5.106	4.189	-.249
	Right FFG			-.337	.246	-.254

**$p < .01$, ***$p < .001$. IFOF: inferior fronto-occipital fasciculus. Fusiform gyrus: FFG.

First, the negative correlations between the right FFG and reading skills in the dyslexia group suggest a maladaptive compensation mechanism of the right FFG in dyslexia (poorer literacy was accompanied by higher FA). More importantly, the nodal degree FA value of the right FFG accounted for the variance in reading accuracy independent of the lateralization index (LI) of IFOF in our earlier study, in which we observed negative correlations between the right-lateralization of IFOF and the severity of reading disability in children with dyslexia (Zhao et al., 2016). These results thus provide a complement to our previous white matter pathway analysis (Zhao et al., 2016). The results are also consistent with a more recent study, in which researchers reported that the FA of the right ILF negatively correlated with reading measures (Banfi et al., 2019). All these white matter connectivity results might also be in line with previous functional MRI studies, which consistently showed hyperactivation in the right hemisphere analog of the left occipitotemporal visual word form area, an area close to the right FFG, in individuals with dyslexia compared with the controls (Démonet et al., 2004; Pugh et al., 2000; Shaywitz & Shaywitz, 2005). Nevertheless, these functional MRI studies lacked linkage of the hyperactivation to an individual's performance, which might be relevant to distinguish compensation from activation differences due to inefficiency or neuropathology (Cabeza et al., 2018). Indeed, some recent studies showed that these hyperactivated regions were positively correlated with reading performance (Hancock et al., 2017; Hoeft et al., 2011), whereas others showed that structural connectivity of these regions negatively correlated with reading performance (Banfi et al., 2019; Zhao et al., 2016). Such differences shed light on two distinct neural compensation mechanisms; one was adaptive, the other was maladaptive. Our negative correlation results indicate that increased anatomical connectivity in the right FFG were associated with poorer reading accuracy in dyslexia provide further support for a maladaptive compensatory hypothesis in the right FFG.

Second, the right FFG and lateralization of IFOF showed functional dissociation concerning pseudoword reading accuracy and word reading accuracy. Specifically, the nodal degree FA value of the right FFG accounted for individual differences in pseudoword reading accuracy but not in word reading accuracy. In contrast, the right-lateralization of IFOF accounted for the individual differences in word reading accuracy but not in pseudoword reading accuracy. This dissociated correlation pattern might reveal a dissociated maladaptive compensatory effect towards a general orthography-to-phonology decoding ability for the right FFG and an orthographic processing ability for the right IFOF. It is well established that the left FFG is involved in the reading process (Dehaene & Cohen, 2011; Démonet et al., 2004; McCandliss et al., 2003), and there is a dysfunctional activation in the left FFG in dyslexia (Maisog et al., 2008; Martin et al., 2016; Richlan et al., 2009). Furthermore, previous functional MRI studies showed that the left FFG responded with higher activation to pseudowords than to real words (Brunswick et al., 1999; Cohen et al., 2002; Xu et al., 2001). Training studies also showed that these areas are sensitive to language-specific orthographic and phonological processing (Sandak et al., 2004; Zhao et al., 2014). Our findings in the right FFG showed a particularly strong correlation with pseudoword reading, a process involving orthography-to-phonology decoding. Therefore, it might indicate that right FFG represents a maladaptive compensation for the corresponding left FFG areas towards a general orthography-to-phonology decoding ability. By contrast, a previous study suggests a relationship between the structural integrity and connectivity of the left IFOF and orthographic processing in reading (Vandermosten et al., 2012). Together with other studies indicating a semantic involvement of the left IFOF (Duffau et al., 2005; Han et al., 2013; Turken & Dronkers, 2011), our negative correlation results in IFOF with reading accuracy might indicate a maladaptive compensatory effect towards general orthographic ability or a compensatory orthography-to-semantics reading route (Seidenberg & McClelland, 1989).

Finally, it has to be admitted that a potential limitation of the present study is that we could not disentangle the causal relations between these behavioral symptoms and white matter structural changes in dyslexia. It remains an open question when this maladaptive compensation occurs and whether these anatomical changes could be found in an earlier time (even in children with family risk). Besides, although the maladaptive compensatory mechanism might provide valuable information for individualized clinical interventions, further investigations are required to determine whether interventions targeting the maladaptive compensatory areas are effective or not (Hope et al., 2017). Moreover, future studies might be helpful to determine whether these structural changes are specifically related to developmental dyslexia, or more generally, to other clinical populations or even normally developing populations with varied literacy skills.

In summary, based on a hypothesis-free analysis, we found a significant negative correlation between reading accuracy and nodal degree FA value of the right FFG. Nodal degree FA value of the right FFG specifically correlated with pseudoword reading accuracy. These results suggest that the right FFG might reveal a maladaptive compensation for the corresponding left FFG towards a general orthography-to-phonology decoding ability. The results shed light on understanding the etiology and brain-behavior correlation of developmental dyslexia. For clinical practice, our results might provide potential objective individual-based neural diagnoses and interventions of reading disabilities.

Credit author statement

Jingjing Zhao conceived of the presented idea. Irene Altarelli and Franck Ramus collected the behavioral, MRI, and diffusion tensor imaging data. Tianqiang Liu and Jingjing Zhao analyzed the behavioral data, performed the MRI and diffusion tensor imaging analyses, and wrote the main manuscript. Michel Thiebaut de Schotten and Franck Ramus verified the analytical methods and supervised the findings of this work.

Declaration of competing interest

No conflicts of interest.

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Supplementary data

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