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Adaptive compensation of arcuate fasciculus lateralization in developmental dyslexia

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ABSTRACT

Previous studies have reported anomalies in the arcuate fasciculus (AF) lateralization in developmental dyslexia (DD). Still, the relationship between AF lateralization and literacy skills in DD remains largely unknown. The purpose of our study is to investigate the relationship between lateralization of three segments of AF (AF anterior segment (AFAS), AF long segment (AFLS), and AF posterior segment (AFPS)) and literacy skills in DD. A total of 26 children with dyslexia and 31 age-matched control children were included in this study. High angular diffusion imaging, combined with spherical deconvolution tractography, was used to reconstruct the AF. Connectivity measures of hindrance-modulated orientational anisotropy (HMOA) were computed for each of the three segments of the AF. The lateralization index (LI) of each AF segment was calculated by (right HMOA - left HMOA)/(right HMOA + left HMOA). Results showed that the LIs of AFAS and AFLS were positively correlated with reading accuracy in children with dyslexia. Specifically, the LI of AFAS was positively correlated with nonword and meaningless text reading accuracy, while the LI of AFLS accounted for word reading accuracy. The results suggest adaptive compensation of arcuate fasciculus lateralization in developmental dyslexia and functional dissociation of the anterior segment and long segment in the compensation.

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1. Introduction

Developmental dyslexia (DD) is known as a developmental learning disorder with impairment in reading, not caused by a disorder of intellectual development, sensory impairment (vision or hearing), neurological or motor disorder, lack of education availability, lack of proficiency in the language of academic instruction, or psychosocial adversity (World Health Organization, 2018). The prevalence of developmental dyslexia ranges from 1.3% to 17.5% (Di Folco, Guez, Peyre, & Ramus, 2021; Shaywitz & Shaywitz, 2005). In the last decade, DD was identified as a disconnection syndrome with defects in the connectivity of white matter pathways (Gullick & Booth, 2015; Langer, et al., 2017; Saygin, et al., 2013; Su, et al., 2018; Vanderauwera, Wouters, Vandermosten, & Ghesquière, 2017; Vandermosten et al., 2012).

Arcuate fasciculus (AF) is the most important and well-studied white matter pathway in DD, as it connects two language brain regions, Broca's area and Wernicke's area. A number of studies have reported reduced connectivity indexed by fractional anisotropy (FA) in the left AF in individuals with DD compared to their controls (Christodoulou, et al., 2017; Gullick & Booth, 2015; Langer, et al., 2017; Saygin, et al., 2013; Su, et al., 2018; Vanderauwera et al., 2017; Vandermosten et al., 2012; Zhao, Thiebaut de Schotten, Altarelli, Dubois, & Ramus, 2016). In contrast to deficiency in the left AF, some studies suggest that the right AF is related to reading compensation in DD, manifesting as an increase in connectivity of the right AF and a positive correlation between the FA of the right AF and reading behavioral metrics. In a longitudinal study, Hoeft et al. (2011) reported that FA of the right AF predicted improved reading ability in children with DD over the next 2.5 years. Similarly, studies focusing on children with a family risk of dyslexia have shown that FA of the right AF at pre-school age is correlated with children's further ability to read (Vanderauwera et al., 2017; Van Der Auwera, Vandermosten, Wouters, Ghesquière, & Vanderauwera, 2021; Wang et al., 2017; Zuk et al., 2020). Other research also demonstrates a positive correlation between FA of the right AF and rapid automatic naming (RAN) in children with dyslexia (El-Sady et al., 2020). These results indicate that the right AF provides considerable adaptive compensation in individuals with dyslexia or risk of dyslexia.

Considering previous findings of a deficiency of the left AF and an adaptive compensation of the right AF in DD, these results might indicate a possibility of atypical rightward lateralization of the AF and an adaptive compensatory role of the right lateralization of the AF. Indeed, atypical rightward lateralization of the AF has been reported in adults with dyslexia: DD showed less left lateralization in the AF than the control groups (Vandermosten, Poelmans, Sunaert, Ghesquière, & Wouters, 2013), although this atypical rightward lateralization in the AF was failed to be replicated in children with dyslexia (Zhao et al., 2016). In terms of compensatory role of the AF, most previous studies focused on the compensatory role of the right AF in DD. It is unclear whether the rightward lateralization of the AF can compensate literacy skills in DD. We previously observed that rightward lateralization of inferior frontal-occipital fasciculus (IFOF) and local network centered at the right fusiform gyrus (FG) could provide maladaptive compensation for reading skills in children with dyslexia (Liu, Thiebaut de Schotten, Altarelli, Ramus, & Zhao, 2021; Zhao et al., 2016). Both rightward lateralization of IFOF and the right FG connectivity were negatively correlated with reading ability of children with dyslexia. In particular, rightward lateralization of IFOF is more associated with word reading ability, while right FG is more associated with pseudoword reading ability. It should be noted that the maladaptive compensations in the rightward lateralization of IFOF and the right FG subnetwork were specific to reading ability, but not to spelling ability. Based on these observations, the present study is intended to test whether compensation exists in the rightward lateralization of the AF and whether it is adaptive compensation or maladaptive compensation. Specifically, we aim to test: 1) whether right lateralization of the AF is correlated with reading skills, 2) whether the correlation is specific to reading ability but not to spelling ability, and 3) whether the correlation is positive (adaptive compensation) or negative (maladaptive compensation).

On the other hand, although compensation of the right AF in DD has been reported, not enough research has been done on the compensatory roles for different segments of the AF in DD. It is well-accepted that the AF can be divided into three distinct segments (AFLS: long frontotemporal, AFAS: anterior frontoparietal, and AFPS: posterior temporoparietal segments) (Catani, Jones, & Ffytche, 2005). The long segment, AFLS, connects the language areas in the frontal (Broca's area) and temporal (Wernicke's area) lobes, which is the mostly studied segment of AF in reading and dyslexia and is also the segment representing AF if a study does not specifically divide AF into different segments. The anterior segment, AFAS, connects the language areas in the frontal and parietal lobes. The posterior segment, AFPS, connects the language areas in the temporal and parietal lobes. In fact, the compensation of the right AF observed in most previous studies actually referred to AFLS (Vanderauwera et al., 2017; Van Der Auwera et al., 2021; Wang et al., 2017; Zuk et al., 2020; except for Hoeft et al., 2011, which included both AFAS and AFLS). Although no significant differences of lateralization in AFLS were observed between control and children with DD in our earlier study, we indeed discovered more rightward lateralization of AFAS and AFPS in children with DD compared with controls using FA as an index for white matter connectivity (see validation analysis in Zhao et al., 2016). However, no studies have systematically examined whether rightward lateralization of AFAS, AFLS, and AFPS could compensate for dyslexia and whether different segments of AF play different roles (e.g., word reading versus pseudoword reading) in compensation for dyslexia. Thus, another goal of the present study is to establish whether rightward lateralization of AFAS, AFLS, and AFPS can compensate for literacy skills in DD and whether they play different compensatory roles for literacy skills (e.g., word reading, pseudoword reading, and text reading) in DD.

In sum, the aim of the present study is twofold. First, whether there is compensation in the lateralization of the AF and its potential adaptive or maladaptive nature. In the case of a positive correlation between the LI of the AF and reading ability, the hypothesis is that the compensation of the AF LI would be adaptive. In the case of a negative correlation between the AF LI and reading ability, the compensation of AF LI

would be maladaptive. Second, whether the lateralization of the three segments of the AF (AFLS, AFAS, and AFPS) has the same compensation mechanism. Specifically, this study explores whether different segments of the AF compensate for the same literacy skills or play different roles in the compensation for different literacy skills (e.g., word reading, pseudoword reading, and text reading).

As AF passes regions including crossing fibers which might result in failure to reconstruct AF (especially for right AFLS) using standard DTI model (e.g., Vandermosten et al., 2012), we therefore used spherical deconvolution tractography model to reconstruct AF with hindrance-modulated orientational anisotropy (HMOA) as an index of white matter connectivity for the three segments of AF (AFLS, AFAS, and AFPS). Our earlier studies showed that spherical deconvolution tractography can reconstruct all segments of AF, while standard DTI model cannot (Zhao et al., 2016). HMOA, defined as the absolute amplitude of each lobe of the fiber orientation distribution, can be used as a compact metric to characterize the diffusion qualities along each fiber orientation in white matter areas with complex structures. HMOA has been indicated to be more accurate than FA for a white matter pathway with crossing fibers and could detect white matter alterations that standard DTI indices such as FA cannot (Dell'Acqua, Simmons, Williams, & Catani, 2013; Dubois et al., 2014).

2. Materials and methods

2.1. Research transparency and data availability

This study's experimental procedures and analyses were not registered prior to the research being conducted. The sample size, all the inclusion/exclusion criteria, data exclusions, manipulations, and measures in the study were reported. Inclusion/exclusion criteria were established before the data analysis. Further details can be found in our previous published paper, where we used the same dataset (Zhao et al., 2016).

The conditions of our ethics approval do not permit public archiving of anonymized study data. Readers seeking access to the data should contact the lead authors, Franck Ramus and Jingjing Zhao. Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data. Legal copyright restrictions prevent publicly archiving various assessment tests used in the current study. They can be obtained from the copyright holders in the cited references. The analysis code used in this study can be obtained from the supplementary materials.

2.2. Participants

The study included 26 children with dyslexia, and 31 controls matched for age, gender, handedness, and nonverbal IQ. The age range of the children was 109–169 months. All the children's native language was French. Children with dyslexia were referred from a clinic for reading and language disabilities. They were required to show more than an 18-month delay on reading age based on the accuracy and speed of the Alouette test (Lefavrais, 1967), while the control children had to be no more than 12 months behind. All the subjects had normal hearing and vision abilities, no history of brain injury, mental illness, or cognitive impairment. The study was approved by the ethics committee of Bicetre Hospital, and informed consent was obtained from all children and their parents. Analyses of group differences in white matter pathways and white matter network connectivity in the same sample were previously published; no difference in head motion parameters was found between dyslexia and controls (Liu et al., 2021, 2022; Lou et al., 2019; Zhao et al., 2016).

2.3. Behavioral measures

We determined the subjects' intelligence and literacy skills through a series of behavioral tests. Intelligence abilities were tested through the WISC blocks, matrices, similarities, and comprehension subtests (Wechsler, 2005). The text reading ability was measured by the "Alouette" test (Lefavrais, 1967), a test of reading ability for meaningless text. The "Alouette" text required participants to read a 265-word text, which does not convey any meaning, as quickly and as accurately as possible in 3 min. Reading abilities for words and pseudowords were measured by Odedys, in which participants have to read 60 isolated items, consisting of 20 regular words, 20 irregular words, and 20 pseudowords (Jacquier-Roux, Valdois, & Zorman, 2005). Spelling skills were measured by a word spelling-to-dictation test (Martinet & Valdois, 1999).

To analyze the relationship between AF lateralization and literacy skills, two composite measures were defined as follows: reading accuracy (READACC) was defined by averaging z scores from the word, pseudoword, and text reading accuracy; spelling (SPELL) was simply the z-score of the word spelling accuracy.

2.4. Image acquisition and analysis

3 T MRI scanner (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 were used for all children's MRI exams at the Neurospin center, Gif-sur-Yvette, France. T1-weighted structural MRI scans were performed using the MPRAGE sequence (acquisition matrix = 230 × 230 × 224, repetition time (TR) = 2,300 ms, echo time (TE) = 3.05 ms, flip angle = 9°, the field of view (FOV) = 230 mm, voxel size = .9 × .9 × .9 mm^3).

The spin-echo single-shot EPI sequence was utilized 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 brain was imaged in full, with an isotropic spatial resolution of 1.7 mm^3 (matrix size = 128 × 128, the field of view = 218 mm) and 70 interleaved axial slices. Diffusion gradients were applied along 60 uniformly distributed orientations, with a diffusion weighting of b = 1400 s/mm^2 (repetition time = 14,000 msec, echo time = 91 msec). In addition, three photographs were taken without any diffusion gradient (b = 0). Each sequence took about 6 min, for a total of 18 min of acquisition time.

2.5. DTI analysis

The three sequences' raw DW data were first concatenated into a single data format, using ExploreDTI (http://www.

exploredti.com, see Leemans & Jones, 2009); the images were simultaneously recorded and corrected for subject motion and geometrical distortions. A damped Richardson-Lucy algorithm for spherical deconvolution (SD) was used to estimate multiple orientations in voxels containing different populations of crossing fibers (Dell'Acqua et al., 2010). The algorithm parameters were chosen following Thiebaut de Schotten et al. (2011).

For whole-brain tractography, per brain voxel with at least one fiber orientation was chosen as a seed voxel. Euler integration with a phase size of 1 mm was used to propagate streamlines from these voxels and for each fiber's orientation (as described in Dell'Acqua et al., 2013). When entering a region with crossing white matter tracts, the algorithm adopted the least curvature orientation vector (as described in Schmahmann et al., 2007). When a voxel without fiber orientation was reached, or the curvature between two phases exceeded a threshold of 60, the streamlines were halted. In-house software developed with MATLAB v7.8 was used to perform spherical deconvolution, fiber orientation vector estimations, and tractography (The Mathworks, Natick, MA).

TrackVis (http://www.trackvis.org, see Wedeen et al., 2008) was used to dissect each participant's tracts in their native space. TrackVis allows tract recognition, visualization in three dimensions, and quantitative analysis on each tract. To extract the tracts of interest, a region-of-interest (ROI) approach was used, with the protocol for defining the ROIs for the three segments of AF (AFLS: long frontotemporal, AFPS: posterior temporoparietal, and AFAS: anterior frontoparietal segments) based on previous tractography studies (Catani et al., 2005).

The ROIs were specified on the MNI152 template, provided with the FMRIB Software Library package (FSL, http://www.fmrib.ox.ac.uk/fsl/) to automate some steps of tract dissection and restrict inter-subject variability related to the operator expertise. The Richardson-Lucy spherical deconvolution lgorithm was used to calculate the convergence map (CS maps; Dell'Acqua et al., 2006). Advanced Normalization Tools (ANTs, http://www.picsl.upenn.edu/ANTS/) were used to register each subject's convergence map to the MNI152 prototype that combined affine and diffeomorphic deformations (Avants, Epstein, Grossman, & Gee, 2008; Klein et al., 2009). After that, the ROIs identified on the MNI152 template were inverse deformed to bring them to the native space of each participant.

Individual dissections of the tracts were then visually examined and corrected by two anatomists in each participant's native brain space (JZ and MTS). For each dissected pathway, hindrance-modulated orientational anisotropy (HMOA; Dell'Acqua et al., 2013) was extracted and used as a compact measure of fiber density and connectivity characterizing the diffusion properties along with each tract orientation. The critical variable of interest was HMOA summed across each entire tract.

2.6. *Statistical analysis*

Statistical analysis was performed using SPSS software (SPSS26, Chicago, IL). The lateralization index [HMOA LI = (right HMOA - left HMOA)/(right HMOA + left HMOA)] for each of the three segments of the AF (AFLS, AFPS, and AFAS) was calculated.

Sample size determination was conducted using G-Power software (version 3.1). The correlation analysis required for this study was based on a bivariate normal model of two-tailed test with an anticipated correlation of .55, a significance level of .05, and a statistical power of .8. These parameters were chosen to ensure sufficient statistical power to detect the expected correlation. By inputting the aforementioned parameters into G-Power, we obtained a minimum required sample size of 23 participants. The Pearson's partial correlations between literacy skills (READACC and SPELL) and HMOA LI of each segment of the AF were calculated respectively in children with dyslexia and the control group, after regressing out age, gender, parental education, handedness, and non-verbal and verbal IQ. Fisher's z scores for all correlation values of the two groups were transformed and compared using Fisher's z test.

Regression analysis was used to confirm the dissociation between LIs of the three segments of the AF and the three dimensions of reading accuracy (word, pseudoword, and text) in children with dyslexia. We conducted hierarchical linear regression analyses with age, sex, parental education, handedness, non-verbal and verbal IQ, and spelling accuracy as controlled variables in the first step. The LIs of AFLS, AFAS, and AFPS were included in the second step. Word reading accuracy, pseudoword reading accuracy, and text reading accuracy was incorporated as a dependent variable, respectively.

Finally, we conducted correlation analyses between the three dimensions of reading accuracy and the LIs of the three segments of the AF, and created scatterplots to further validate the linear regression results.

3. Results

3.1. *Demographics and behavioral results*

Table 1 shows descriptive statistical information on all participants' demographics and behavioral performance. There was no difference in age, sex, handedness, maternal education, and non-verbal IQ between dyslexia and control groups. However, children with dyslexia performed worse than the control group in verbal IQ and all aspects of literacy skills.

3.2. *Correlation between LI of AF and reading ability*

Partial correlation analyses showed significant correlations between LI of AFAS and READACC as well as between LI of AFLS and READACC in children with dyslexia: the more right-lateralized the AFAS ($r = .571$, $R^2 = .326$, $p = .011$) and AFLS ($r = .471$, $R^2 = .222$, $p = .042$), the better READACC in children with dyslexia. In the control group, we found positive correlations between LI of AFPS and SPELL ($r = .533$, $R^2 = .284$, $p = .006$) as well as READACC ($r = .422$, $R^2 = .178$, $p = .035$). The results from Fisher's z tests showed that the correlation difference between the two groups was only significant for the correlation between LI of AFAS and READACC ($p = .006$). The correlation differences between the two groups were

Table 1 – Demographical data and scores 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	$\chi2$ (1) = .371, -p = .543
Handedness (left/right)	31	2/29	26	3/23	$\chi2$ (1) = .457, p = .449
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
Reading accuracy (READACC)					
Word reading accuracy (/20)	31	18.65 (1.64)	25	10.52 (4.33)	t (54) = 9.650, p < .0001
Pseudoword reading accuracy (/20)	31	17.45 (1.73)	25	11.36 (3.37)	t (54) = 8.759, p < .0001
Text reading accuracy (%)	31	96.41 (2.02)	24	77.81 (17.78)	t (53) = 5.791, p < .0001
Spelling accuracy (SPELL)					
Spelling (%)	31	82.75 (13.77)	26	37.94 (20.18)	t (55) = 9.922, p < .0001

marginally significant for the correlations between LI of AFLS and READACC (p = .071), between LI of AFAS and SPELL (p = .071), and between LI of AFPS and SPELL (p = .071). Details of the correlation results are shown in Table 2 and Fig. 1.

3.3. *Regression analysis*

Three dimensions of reading abilities (word reading, pseudoword reading, and text reading) were further analyzed separately in a series of regression analyses (Tables 3–5). The results showed that AFLS is significantly related to word reading accuracy (β = .434, p = .023), but not to pseudoword reading accuracy and text reading accuracy. In contrast, AFAS is significantly related to pseudoword reading accuracy (β = .690, p = .041) and text reading accuracy (β = 0.623, p = .003), but not to word reading accuracy.

Fig. 2 shows individual scatterplots for the relationship between the three dimensions of reading accuracy (word reading, pseudoword reading, and text reading) and LIs of AFLS and AFAS. In the dyslexia group, AFLS was positively related to word reading accuracy (r = .525, R^2 = .276, p = .030), while AFAS was positively related to pseudoword reading accuracy (r = .526, R^2 = .277, p = .030) and text reading accuracy (r = .569, R^2 = .324, p = .017).

4. Discussion

The present study revealed two main facts. First, the results showed a significant positive correlation between rightward lateralization of the AFAS and AFLS and reading accuracy, suggesting an adaptive compensatory role of the rightward lateralization of the two segments of AF. Secondly, we found that the compensatory roles of the rightward lateralization of the AFAS and AFLS are functionally independent. The rightward lateralization of the AFLS plays a compensatory role in word reading accuracy, while the rightward lateralization of the AFAS plays a compensatory role in pseudoword and meaningless text reading accuracy.

Firstly, the present study reports the association between rightward lateralization of the AF and reading ability in DD for the first time. The results show a positive correlation between rightward lateralization of the AF and reading accuracy in children with dyslexia, suggesting an adaptive compensatory

Table 2 – Partial correlation coefficients and Fisher'z test (controlled for age, sex, parental education, handedness, non-verbal and verbal IQ) between lateralization index (LI) of three segments of arcuate fasciculus (anterior segment: AFAS, long segment: AFLS, and posterior segment: AFPS) and behavioral measures of reading accuracy (READACC), and spelling accuracy (SPELL). #p < .10, *p < .05, **p < .01.

			r	*p*	fisher's z	*p*
AFAS_LI	READACC	Dyslexia	**.571***	**.011***	0.649	**.006****
		Control	−.078	.713	−0.078	
	SPELL	Dyslexia	.247	.308	0.252	.071#
		Control	−.159	.447	−0.161	
AFLS_LI	READACC	Dyslexia	**.471***	**.042***	.511	.071#
		Control	.089	.674	.089	
	SPELL	Dyslexia	.343	.150	.358	.298
		Control	.205	.327	.208	
AFPS_LI	READACC	Dyslexia	.025	.921	.025	.071#
		Control	**.422***	**0.035***	.450	
	SPELL	Dyslexia	.143	.558	.144	.071#
		Control	**.533****	**.006****	.594	

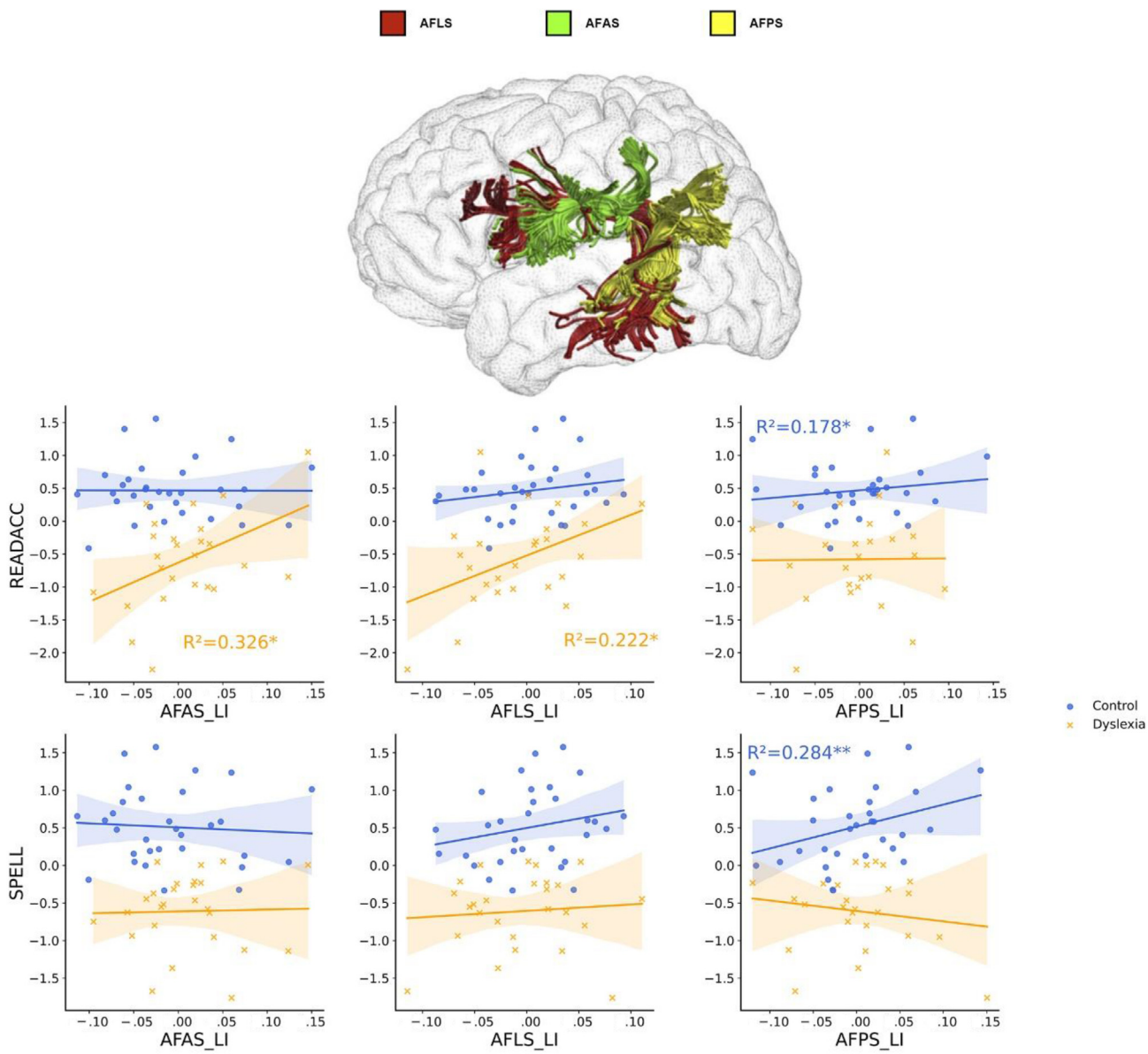

Fig. 1 – Individual scatterplots for the correlation of lateralization index (LI) of AFLS and AFAS and reading accuracy (READACC) and spelling accuracy (SPELL) with age, sex, parental education, handedness, and non-verbal and verbal IQ controlled. *p < .05, **p < .01.

role of the rightward lateralization of the AF for reading ability. These correlations were only shown between reading accuracy and the rightward lateralization of the AFAS and AFLS in DD, but not between reading accuracy and the rightward lateralization of the AFPS, also not between spelling accuracy and the rightward lateralization of the AF. In addition, the associations between reading accuracy and the rightward lateralization of the AFAS and AFLS in DD were remained after regressing out spelling ability. These results suggesting that the adaptive compensatory role of the rightward lateralization of the AFAS and AFLS are specific to reading ability, but not to spelling ability. These results are consistent with the previous findings that suggest the adaptive compensation of the right AF in DD or children with risk of DD (Hoeft, et al., 2011; Vander Stappen, Dricot, & Van Reybroeck, 2020; Vanderauwera et al., 2017; Wang, et al., 2017). For instance, Hoeft et al. (2011) reported that integrity of the right superior longitudinal fasciculus (SLF), including AF anterior and long segments, could predict long-term improvement of the reading performance in children with dyslexia. The stronger the integrity of the right SLF/AF, the better the reading level over the next two and a half years. However, Hoeft and colleagues did not further anatomize the right SLF/AF into more refined anterior and long segments of the AF. Our results provide the first examination of the compensatory role of the rightward lateralization of the AFAS and AFLS, respectively. Our findings, together with the previous results, suggest that the impairment of the left AF in DD might be able to be repaired or compensated by the right AFAS and AFLS through later development or training.

Table 3 – Hierarchical linear regression analysis of word reading accuracy (WDREADACC) predicted by the lateralization index (LI) of arcuate fasciculus long segment (AFLS), anterior segment (AFAS), and posterior segment (AFPS) with age, sex, parental education, handedness, non-verbal and verbal IQ, and spelling accuracy (SPELL) controlled in children with dyslexia. *$p < .05$, **$p < .01$.

				WDREADACC		
				Unstandardized		Standardized
				Coefficients		Coefficients
Step		ΔR^2	Adjusted R^2	*B*	*SE*	*Beta*
1	Control variables	.661**	.522**			
	Sex			.182	1.602	.021
	Age			−.032	.049	−.118
	EDUC			.119	.257	.090
	Handedness			.992	2.190	.076
	Non-verbal IQ			.013	.052	.047
	Verbal IQ			.014	.051	.061
	SPELL			5.349**	1.595	.881**
2	lateralization index	.115	.616			
	AFAS_LI			4.916	13.339	.076
	AFLS_LI			**35.372***	13.863	**.434***
	AFPS_LI			15.979	12.338	.189

Secondly, it is essential to emphasize the following finding: the rightward lateralization of the AFLS and AFAS compensate for different aspects of reading abilities. Generally, the lateralization of AFLS compensates for word reading accuracy, while the lateralization of AFAS compensates for pseudoword reading and meaningless text reading ability. Due to the connection with the Broca's area, AFAS and AFLS are both thought to be involved in articulation-related processes of speech, while with the connection to Wernicke' area, AFLS is possibly also taking on a more complex task with semantic processing (Catani et al., 2005). In the present study, word reading task includes both regular and irregular words, thus requires both lexical-semantic and phonological processing. In contrast, both pseudoword reading task and meaningless text reading task do not emphasize semantic processing, so they might induce more phonological decoding and speech retrieval. We therefore postulate that the rightward lateralization of AFLS might be related to the adaptive compensation of the lexical-semantic and phonological processing in DD. In contrast, the rightward lateralization of AFAS might be more associated with the adaptive compensation of speech articulation and phonological decoding in DD. These data provide evidence for further understanding the adaptive compensatory functions of the different segments of the AF. Alternatively, previous studies have also suggested that AFLS is related to phonological processing, such as phonemic awareness, language fluency, and verbal working memory, while AFAS is related to the phonological storage and articulatory rehearsal module (Duffau, 2008; Li, et al., 2017; Meyer, Cunitz, Obleser, & Friederici, 2014; Nakajima, Kinoshita, Shinohara, & Nakada, 2020; Papagno, et al., 2017; Vandermosten et al., 2012; Yeatman et al., 2011). These data

Table 4 – Hierarchical linear regression analysis of pseudoword reading accuracy (NWDREADACC) predicted by the lateralization index (LI) of arcuate fasciculus long segment (AFLS), anterior segment (AFAS), and posterior segment (AFPS) with age, sex, parental education, handedness, non-verbal and verbal IQ, and spelling accuracy (SPELL) controlled in children with dyslexia. *$p < .05$.

				NWREADACC		
				Unstandardized		Standardized
				Coefficients		Coefficients
Step		ΔR^2	Adjusted R^2	*B*	*SE*	*Beta*
1	Control variables	.283	−.012			
	Sex			−.508	1.813	−.077
	Age			−.043	.056	−.205
	EDUC			.074	.291	.073
	Handedness			.335	2.478	.033
	Non-verbal IQ			.032	.059	.153
	Verbal IQ			−.004	.057	−.022
	SPELL			3.104	1.804	.657
2	lateralization index	.215	.141			
	AFAS_LI			**34.848***	15.521	**.690***
	AFLS_LI			12.843	16.130	.202
	AFPS_LI			5.023	14.357	.077

Table 5 – Hierarchical linear regression analysis of text reading accuracy (TEXTREADACC) predicted by the lateralization index (LI) of arcuate fasciculus long segment (AFLS), anterior segment (AFAS), and posterior segment (AFPS) with age, sex, parental education, handedness, non-verbal and verbal IQ, and spelling accuracy (SPELL) controlled in children with dyslexia. *$p < .05$, **$p < .01$.

				TEXTREADACC		
				Unstandardized		Standardized
				Coefficients		Coefficients
Step		ΔR^2	Adjusted R^2	*B*	*SE*	*Beta*
1	Control variables	.614*	.445*			
	Sex			.828	7.693	.024
	Age			−.090	.211	−.081
	EDUC			−2.511*	1.072	−.465*
	Handedness			31.602**	9.865	.600**
	Non-verbal IQ			−.461	.222	−.419
	Verbal IQ			−.144	.230	−.141
	SPELL			18.398*	6.780	.732*
2	lateralization index	.222**	.710**			
	AFAS_LI			**174.205****	47.538	**.623****
	AFLS_LI			50.964	43.478	.160
	AFPS_LI			−58.383	39.275	−.200

might therefore support a possible hypothesis that different segments of the AF also represent compensatory neural bases related to different aspects of the phonological deficit in dyslexia (Ramus, 2001, 2003; Ramus & Szenkovits, 2008).

Lastly, the adaptive compensation pathway, observed in the AF in the present study, was in the dorsal language network, consistent with other previous studies (Hoeft et al., 2011; Vanderauwera et al., 2017; Van Der Auwera et al., 2021; Wang et al., 2017; Zuk et al., 2020). Comparatively, our previous findings reported negative correlations between the rightward lateralization of inferior frontal-occipital fasciculus (IFOF) and reading accuracy (Zhao et al., 2016), as well as between the right fusiform subnetwork and reading accuracy (Liu et al., 2021). Similarly, Banfi et al. (2019) reported a negative correlation between the right inferior longitude fasciculus (ILF) and pseudoword reading. These findings point to a

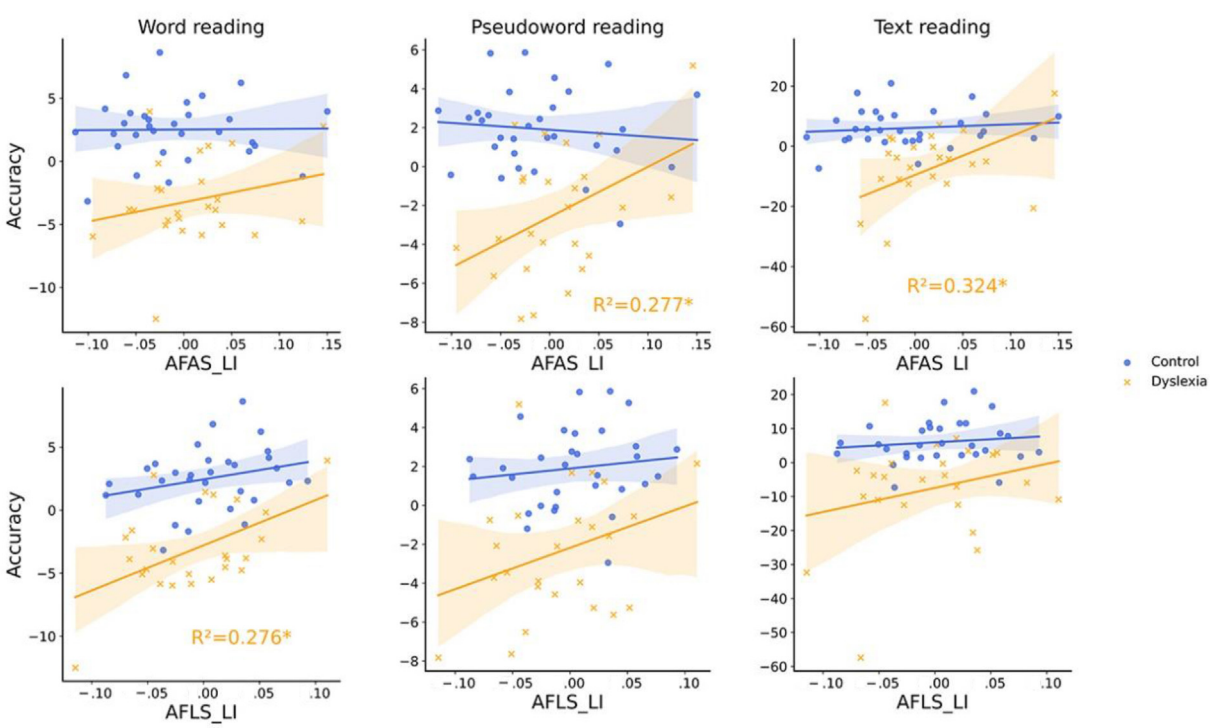

Fig. 2 – Individual scatterplots for the correlation of lateralization index (LI) of arcuate fasciculus long segment (AFLS) and arcuate fasciculus anterior segment (AFAS) and word reading accuracy, pseudoword reading accuracy and text reading accuracy with age, sex, parental education, handedness, non-verbal and verbal IQ, and spelling accuracy controlled. *$p < .05$, **$p < .01$.

maladaptive compensation network in the ventral language pathway. Altogether, these results might suggest that different neural pathways correspond to different compensation modes: adaptive compensation in the dorsal language pathway and maladaptive compensation in the ventral language pathway. This hypothesis might be consistent with the meta-analysis results by Paulesu, Danelli, and Berlingeri (2014), in which the authors highlighted that dyslexia might involve dysfunctions (hypo-activations) in both ventral and dorsal language networks in the left hemisphere and hyper-activations in the dorsal network in the right hemisphere. Our findings of the maladaptive compensation in the rightward lateralization of IFOF and the right fusiform subnetwork in the dyslexic group might be a structural reflection of the dysfunction within the left ventral network found by Paulesu et al. which included two key cortical regions: the left inferior frontal cortex and the left inferotemporal and fusiform region. Our findings of the adaptive compensation in the rightward lateralization of AFLS in the dyslexic group might be a counterpart of the dysfunction in the left dorsal language network. The adaptive compensation in the rightward lateralization of AFAS in the dyslexic group might correspond to the functional hyper-activations in the right dorsal network that Paulesu et al. found, which included the inferior parietal lobule where AFAS connects.

Finally, it should be acknowledged that our successful observation of associations between the rightward lateralization of the AF and reading ability in the present study also benefited from spherical deconvolution tractography with HMOA measurement from the three segments of the AF in all participants. Previous studies using standard DTI models to reconstruct AF revealed limitations in fiber-crossing regions where AF cross and have consistently shown that it is less effective in tracking the right AF, especially the right long segment of AF (Su et al., 2018; Vanderauwera, Vandermosten, Dell'Acqua, Wouters, & Ghesquiere, 2015; Vandermosten et al., 2012; Zhao et al., 2016). In the present dataset, when we used the standard DTI model for fiber tracking of AF, 15 of the participants could not be reliably reconstructed for the AF (eight in the right long segment, four in the left anterior segment, two in the left posterior segment, and one in the left long segment). This was also why the standard DTI model was not suitable for the current study to examine the association between rightward lateralization of the AF and reading ability.

Despite of interesting implications for adaptive compensation in the rightward lateralization of the AF, our study still included some limitations. First, we did not observe any compensation effect in the rightward lateralization of the AFPS in dyslexic children. However, we revealed a positive correlation between the rightward lateralization of the AFPS and literacy skills (spelling and reading accuracy) in control children. This was the first time that we observed a positive correlation between rightward lateralization of a white matter pathway and literacy skills in the control children of this dataset. We previously have discovered a negative correlation between the rightward lateralization of SLF II and literacy skills in control children (Zhao et al., 2016). Because previous studies have reported important roles of the left AFPS in literacy acquisition (Thiebaut de Schotten, Cohen, Amemiya, Braga, & Dehaene, 2012), phonological processing in reading (Zemmoura, Herbet, Moritz-Gasser, & Duffau, 2015) and vocabulary development speed (Su et al., 2018), we tend to speculate that the rightward lateralization of the AFPS might be associated with better literacy and related language skills in general population. Second, our study is a cross–sectional correlation study. Thus, no longitudinal follow-up was conducted, unlike in the previous studies (Hoeft, et al., 2011; Zuk, et al., 2020). Therefore, it was impossible to explore the long-term prediction of the AF compensation lateralization for reading ability in DD. Last, given the limited dyslexia sample in each age group across 9–14 years in our study, the age effect of the AF lateralization compensation was not examined. These are the suggested areas of future research.

In summary, our study revealed an adaptive compensatory role of the rightward lateralization of the long and anterior segments of the AF in developmental dyslexia. Additionally, a different adaptive compensatory role was found for the long and anterior segments of the AF. The long segment of the AF is compensatory for word reading accuracy, whereas the anterior segment of the AF is compensatory for pseudoword and meaningless text reading accuracy.

Credit author statement

Jingjing Zhao conceived of the presented idea. Irene Altarelli and Franck Ramus collected the behavioral, MRI, and diffusion tensor imaging data. Jingjing Zhao, Yueye Zhao and Zujun Song analyzed the data and wrote the manuscript. Michel Thiebaut de Schotten supervised the analytical methods. Franck Ramus verified the analytical methods and supervised the findings.

Declaration of competing interest

No conflicts of interest.

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Supplementary data

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