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Phonological decoding ability is associated with fiber density of the left arcuate fasciculus longitudinally across reading development

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ABSTRACT

Numerous studies have linked reading ability to white matter microstructure using diffusion tensor imaging, but findings have been inconsistent and lack specificity. Fiber-specific diffusion-weighted magnetic resonance imaging (dMRI) models offer enhanced precision in measuring specific microstructural features, but they have not yet been applied to examine associations between reading ability and white matter microstructure development as children learn to read. We applied constrained spherical deconvolution (CSD) and fiber-specific modelling to characterize developmental changes in fiber density of key white matter tracts of the reading network, and investigated associations between tract-wise fiber density and children's phonological decoding abilities. Fiber density was measured from ages 2–13 years, and decoding ability (pseudoword reading) was assessed at ages 6 years and older. Higher decoding ability was associated with greater fiber density in the left arcuate fasciculus, and effects remained consistent over time. Follow-up analysis revealed that asymmetry from early childhood onward, while poorer decoders shifted toward leftward asymmetry over time. These results suggest that densely organized fibers in the left arcuate fasciculus serve as a foundation for the development of reading skills from the pre-reading stage through fluent reading.

1. Introduction

Reading is critical to academic success and daily functioning beginning in childhood, and persistent reading difficulties can have detrimental consequences for academic performance, as well as social and mental well-being (Haft et al., 2016). Reading ability varies widely among individuals; those who fall at the lowest tail of the continuum may be diagnosed with a reading disability (i.e., dyslexia). A distributed network of brain regions support reading, including structures involved in sensory processing (auditory & visual), language, motor planning/control (articulation), and executive functions. The neural connections among these brain regions play an important role in reading; they coordinate functions required to convert text in its visual/orthographic form to phonological representations, meaning, and possibly verbal output. "Phonological decoding" refers to "sounding out" words by converting text (orthographic) input to its associated speech sounds (phonology). This ability is fundamental for the development of fluent reading (Hudson et al., 2009), and is thought to depend primarily on the neural connections linking left hemisphere occipito-temporal regions that process orthographic input to temporo-parietal and inferior frontal regions involved in phonological processing and speech output (D'Mello and Gabrieli, 2018; Richlan, 2019).

These regions constitute the putative "reading network", a set of cortical regions and their white matter connections that support fluent reading (D'Mello and Gabrieli, 2018; Martin et al., 2015). Prior research using diffusion tensor imaging (DTI) has shown associations between reading ability and diffusion properties in white matter of the reading network, including the arcuate fasciculus (AF), superior longitudinal

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fasciculus (SLF), inferior longitudinal fasciculus (ILF), and inferior fronto-occipital fasciculus (IFOF) (for reviews, see: (D'Mello and Gabrieli, 2018; Vandermosten et al., 2012a). Case-control studies comparing groups with and without reading disabilities tend to show reduced diffusion indices of white matter microstructural integrity in left hemisphere reading network tracts (Christodoulou et al., 2017; Vandermosten, Boets, Poelmans, et al., 2012a), though some reports vary in the direction and location of effects, e.g. (Arrington et al., 2017; Banfi et al., 2019) or report null effects (Meisler and Gabrieli, 2022a). Other studies have identified continuous associations between individual differences in reading abilities and white matter microstructure, including tract-specific associations with different reading sub-skills (Broce et al., 2019; Cross et al., 2023; Lebel et al., 2013; Meisler and Gabrieli, 2022a; Niogi and McCandliss, 2006; Yeatman et al., 2011). Phonological processing and phonological decoding (i.e., pseudoword reading) appear to exhibit robust associations with white matter microstructure, with several studies linking these sub-skills to diffusion properties in left AF microstructure, even after controlling for other reading sub-skills and cognitive ability (Broce et al., 2019; Cross et al., 2023)

In addition to direct associations with diffusivity metrics, some studies have examined white matter microstructural asymmetries in relation to reading ability. Functional left-lateralization for language is established early in life (Olulade et al., 2020), and leftward asymmetry of the AF is apparent by age 2 years (Dubois et al., 2009; Langer et al., 2015; Reynolds et al., 2019). Functional and microstructural left-lateralization increases throughout childhood, as connectivity within the left hemisphere increases and language-related activation of the right hemisphere decreases (Olulade et al., 2020; Reynolds et al., 2019). Better reading ability has been associated with leftward asymmetry of both dorsal (SLF, AF) and ventral (ILF, IFOF) tracts (Banfi et al., 2019; Broce et al., 2019; Niogi and McCandliss, 2006; Zhao et al., 2016), suggesting that greater coherence in left-hemisphere compared to right hemisphere tracts within individuals is advantageous for reading. However, it remains unknown whether these asymmetries are a cause or a consequence of reading ability.

Research on pre-reading children with and without family or behavioral risk of reading disability aims to determine whether observed white matter differences in children with reading disability are present prior to the onset of reading instruction. Several studies have shown white matter differences in at-risk children in early childhood and infancy (Kraft et al., 2016; Langer et al., 2015; Vandermosten et al., 2015). White matter macro- and microstructural features have also been associated with individual differences in reading-related skills in pre-readers, such as phonological processing and rapid naming (Manning et al., 2022; Reynolds et al., 2019; Saygin et al., 2013; Walton et al., 2018). These studies provide support for the notion that the brain's structural connections can facilitate or constrain reading development, but the findings are not sufficient to determine causality.

Longitudinal research provides important insight into the role of brain structure and function in learning to read (Chyl et al., 2021). Numerous longitudinal studies have linked white matter structure to later reading abilities (Borchers et al., 2019; Gullick and Booth, 2015; Myers et al., 2014; Van Der Auwera et al., 2021; Vanderauwera et al., 2017; Zuk et al., 2020), suggesting that strong white matter connections may facilitate the development of reading skills. In retrospective analyses, white matter differences prior to formal reading instruction have been identified between children who do and do not go on to develop reading difficulties, pointing to putative neurobiological risk factors (Vanderauwera et al., 2017) and protective/compensatory mechanisms (Zuk et al., 2020). There is also evidence that the trajectories of white matter development differ between good and poor readers, indicating that white matter plasticity may be associated with the development of reading skills (Lebel et al., 2019; Wang et al., 2017; Yeatman et al., 2012). Thus, it is important to consider how white matter-reading associations unfold over the course of reading development in order to understand the reciprocal relationship between white matter microstructural development and reading development.

Despite a large body of research linking white matter structure to reading ability, recent evaluations of the literature question the reproducibility of previous findings and point out methodological limitations of DTI as a potential source of this heterogeneity (Huber et al., 2019; Koirala et al., 2021; Meisler and Gabrieli, 2022b; Moreau et al., 2018; Ramus et al., 2018). First, the tensor usually does not accurately reflect the complex organization of brain white matter, in which crossing, curving, and kissing fibers are highly prevalent (Jeurissen et al., 2013). Further, the metrics derived from DTI are not specific to microstructural features of white matter, which leads to vague or ambiguous interpretation (Raffelt et al., 2012; Raffelt, Tournier, et al., 2017). More advanced microstructural models with longitudinal data are needed to better characterize links between reading ability and white matter in the developing brain.

One such method is constrained spherical deconvolution (CSD; (Calamuneri et al., 2018; Jeurissen et al., 2014). CSD is applied to dMRI data acquired with higher diffusion weightings and more directions than standard DTI to model multiple fiber populations within each voxel (modelled as a fiber orientation distribution function [FOD]) and more accurately represents complex fiber organization. It also separates intraand extra-axonal water compartments to model specific white matter microstructural features, such as fiber density (Calamante et al., 2015; Raffelt et al., 2012; Raffelt, Tournier, et al., 2017). Apparent fiber density (henceforth, 'fiber density'), fiber cross-section, and composite 'fiber density and cross section' metrics can be computed for independent fiber populations within each voxel (termed 'fixels').

Despite these advantages, few studies to date have applied CSD or other advanced dMRI models to investigate white matter microstructure in relation to reading ability (Geeraert et al., 2020; Huber et al., 2019; Koirala et al., 2021; Meisler and Gabrieli, 2022b; Vanderauwera et al., 2015; Zhao et al., 2016). Vanderauwera et al. (2015) compared DTI and spherical deconvolution models in a study examining associations between phonological awareness and microstructure of left hemisphere temporo-parietal tracts in pre-reading children (ages 5-6 years). They found significant associations between FA and phonological awareness in both the arcuate fasciculus and left projection tracts, but the spherical deconvolution model showed enhanced specificity with significant associations between fiber-specific anisotropy and phonological awareness limited to the arcuate fasciculus. Zhao et al. (2016) applied spherical deconvolution to examine tract anisotropy and asymmetry in children with and without dyslexia. They reported higher fiber-specific anisotropy in the right SLF in children with dyslexia relative to controls; in addition, the children with dyslexia had reduced leftward microstructural asymmetry of the IFOF and elevated rightward microstructural asymmetry of the middle SLF branch that links the inferior parietal lobule to the precentral gyrus (SLF-II). These findings are consistent with alterations in the left hemisphere reading network and putative compensatory mechanisms in the right hemisphere. In another study, Huber et al. (Huber et al., 2019) applied two advanced dMRI models to examine microstructure in the posterior corpus callosum in relation to reading ability, and reported reading-related associations with metrics related to tissue density. Geeraert et al. (2020) identified multivariate white matter microstructural components based on principal components analysis of dMRI (DTI and Neurite Orientation Density and Dispersion Imaging [NODDI; (Zhang et al., 2012)] models) and myelin-specific imaging (magnetization transfer imaging and multicomponent relaxometry). However, the white matter components were not significantly associated with reading ability in a sample of typically developing children and adolescents. Together, these studies illustrate the potential utility of advanced dMRI models in studies of reading ability, but further research using larger samples and longitudinal designs is needed to fully characterize associations between reading and white matter microstructure.

Advanced dMRI models have been applied in two recent studies of

reading in large samples drawn from the Healthy Brain Network Biobank (Alexander et al., 2017). Koirala et al. (2021) found that the neurite density index (NDI) and orientation dispersion index (ODI) were negatively correlated with both phonological processing and composite reading ability (timed word and pseudoword reading) in tracts throughout the brain; in contrast, DTI metrics showed limited relations to phonological processing and no associations with reading ability. Meisler and Gabrieli (2022b) applied the CSD model and fixel-based analysis to show widespread associations between composite reading ability (timed word and pseudoword reading) and fiber density and cross-section (a metric thought to reflect capacity of white matter tracts to efficiently transmit information), with largest effect sizes identified in left temporo-parietal and cerebellar white matter. Follow-up analyses testing associations between reading abilities and alternative dMRI metrics (from DTI, diffusion kurtosis imaging [DKI], and NODDI models) did not reveal any significant associations between reading and DTI or DKI metrics; NODDI metrics were associated with reading ability, including negative associations with NDI in the cerebellum and with ODI in the left temporoparietal region and cerebellum, though these effects did not pass correction for multiple comparisons (Meisler and Gabrieli, 2022b). Together, these studies illustrate the enhanced sensitivity of non-tensor dMRI models to individual differences in reading ability. However, these findings were derived from a single dataset that was oversampled for children with/at risk for neurodevelopmental conditions, so it remains unclear whether these effects generalize to typically developing children. Furthermore, no study to date has examined associations between reading ability and fiber-specific microstructure longitudinally from pre-reading to fluent reading.

In this study, we applied an advanced dMRI model to characterize the development of fiber density in reading-related white matter tracts over the course of reading development, and examine associations between fiber density and decoding ability in children learning to read English. Phonological decoding ability is fundamental for the development of fluent reading, as decoding precedes automatic word recognition and supports the formation of orthographic representations (Perfetti and Helder, 2022). Thus, we focused on decoding ability assessed via pseudoword reading. We predicted that fiber density would increase with age, and that better decoding ability would be associated with greater fiber density and faster increases of fiber density in left hemisphere reading-related tracts, with strongest effects in dorsal tracts (AF and SLF) thought to support phonological decoding (Broce et al., 2019; Cross et al., 2023; Vandermosten et al., 2012b). We performed post-hoc analyses to test associations between microstructural asymmetry and reading ability in tracts that showed significant associations with decoding ability in the main analysis.

2. Methods

2.1. Participants

Participants were drawn from a large accelerated longitudinal study of brain development spanning early childhood-early adolescence (Reynolds et al., 2020). All participants were born full term (\geq 37 weeks gestation), and no participants had diagnosed neurological, genetic, or neurodevelopmental conditions upon enrollment. This study was approved by the conjoint health research ethics board (CHREB) at the University of Calgary (REB13–0020). Parents provided written informed consent and children provided verbal assent prior to participation.

Children who completed an assessment of reading ability at one or more study visits at ages 6 years and older and had good quality dMRI data (with $b=2000 \text{ s/mm}^2$) from at least one study visit were included in analysis (quality assurance procedures described below). Analyses included 280 dMRI scans from 66 participants (34 females, 32 males, 59 right-handed, scan age range = 2.41–12.92 years [mean = 7.23, SD=2.43], reading assessment age range = 6–12.71 years [mean = 8.5, SD=1.82]); see Fig. 1. The socioeconomic status of the sample was



Fig. 1. Age at scan acquisition by participant. Each scan is represented by a circle; each participant is shown in a different row with their scans connected by a straight line. Participants are colored by decoding ability (mean Word Attack standardized score across visits), with darker colors indicating poorer decoding ability.

generally high. Based on parent report at study enrollment, all mothers completed at least some postsecondary education, with the majority of mothers attaining at least an undergraduate degree (N = 54). Total family income (at study enrollment) ranged from under \$25,000 to over \$175,000 with a median range of \$150,000-\$174,999.

2.2. dMRI acquisition and processing

dMRI data were acquired using a 3 T GE MR750w MR system with a 32-channel head coil at the Alberta Children's Hospital (Calgary, AB, Canada) without the use of sedation. dMRI data were acquired using a single shot spin echo EPI sequence (TR = 6750 ms, TE = 97 ms, $1.6 \times 1.6 \times 2.2 \text{ mm}^3$ resolution [resampled on scanner to $0.78 \times 0.78 \times 2.2 \text{ mm}^2$, and five interleaved volumes at b = 0 s/mm². The imaging protocol also included acquisition of a separate dMRI sequence at b = 750 s/mm², but these data were excluded from the present analyses due to the increased influence of extra-axonal water on apparent fiber density measures at low b-values (Calamante et al., 2015; Genc et al., 2020; Raffelt et al., 2012).

dMRI data were resampled to $2.2 \times 2.2 \times 2.2 \text{ mm}^3$ isotropic voxels to match the slice thickness of the original acquisition, Gibb's ringing correction was performed via MRTrix3 (v. 3.0.4, https://mrtrix.readth edocs.io/en/latest; [Kellner et al., 2016; Tournier et al., 2019]), and eddy current correction and motion correction with outlier replacement was performed using FSL's *EDDY* (Andersson et al., 2016; Andersson and Sotiropoulos, 2016) via the *dwifslpreproc* function in MRTrix3. Preprocessed images were upsampled to 1 mm isotropic voxels, then binary brain masks were generated using *bet2* in FSL with fractional intensity threshold adjusted to .4, as this level performed best on our data (Smith, 2002). Brain masks were visually inspected to ensure full brain coverage; errors in the masks (holes) were identified in two subjects and manually filled using edit mode in FSLeyes (https://open.win.ox.ac. uk/pages/fsl/fsleves/flseves/userdoc/). dMRI data quality was assessed using the EDDY QUAD tool (Bastiani et al., 2019), and scans with average relative motion exceeding .7 mm and/or total outliers exceeding 10 % were excluded from further processing (n = 3). One additional scan was excluded because motion artifacts were apparent in the preprocessed image (these datasets were excluded prior to selection of data for analysis based on the criteria described above). Next, single-shell 3-tissue constrained spherical deconvolution (SS3T-CSD) was performed via MRtrix3Tissue (https://3Tissue.github.io, a fork of MRTrix3) using group average response functions. This method was chosen to optimize the fiber orientation distribution modelling by reducing the influence of gray matter-like and cerebrospinal fluid-like signal contributions and enhance sensitivity to intra-axonal signal by excluding a lower b-value shell (Dimond et al., 2020). Multi-tissue informed log-domain intensity normalization (*mtnormalise*; (Dhollander et al., 2021; Raffelt, Dhollander, et al., 2017) was performed on the resulting fiber orientation distribution (FOD) maps for each tissue compartment. Fixel-based metrics were derived following the fixel-based analysis pipeline in MRtrix3 (Tournier et al., 2019); 'fixel' is defined as an individual fiber population within a voxel. A study-specific FOD template was generated using FOD maps from 30 randomly selected sessions (all from different individuals, age range: 3.76-11.59 years) (Raffelt et al., 2011), as recommended in the MRTrix3 fixel-based analysis pipeline (https://mrtrix.readthedocs.io/). This template is required to register data across sessions and individuals into a common space and match fixels between sessions and participants, ensuring comparable data over time and among individuals. A template mask was generated as the intersection of all participants' brain masks in template space and a corresponding fixel mask was generated. All participants' FOD images were registered to template space, FOD lobes were segmented to estimate fixels, and apparent fiber density of each fixel was calculated. Each participants' fixels were then reoriented in template space based on the local transformation at each voxel and assigned to template fixels.

2.3. Tractography

Automated tractography was performed on the FOD template via TractSeg (Wasserthal et al., 2018) to ensure that tract streamlines (and their underlying fixels) would be consistent within and between participants, similar to our prior study (Dimond et al., 2020). The following tracts were segmented bilaterally: arcuate fasciculi (AF), ventral superior longitudinal fasciculi (SLF-III; this branch was selected because of its terminations in temporo-parietal and inferior frontal cortices), inferior longitudinal fasciculi (ILF), and inferior fronto-occipital fasciculi (IFOF). Each tract was converted to a fixel map, which was thresholded to include only fixels with ≥ 5 streamlines passing through and then binarized to create a fixel mask. Mean fiber density of each tract was calculated as the mean fiber density of fixels included in the tract-specific fixel mask for each participant. Segmented tracts are

Developmental Cognitive Neuroscience 72 (2025) 101537

shown in Fig. 2. Code used for dMRI data processing and tractography is available here: https://github.com/developmental-neuroimaging-lab/mrtrix/tree/main/ss3tCSD_scripts

2.4. Reading assessment

Reading ability was assessed at 6 years and older using the Woodcock Reading Mastery Tests 3rd Edition (Woodcock, 2011) using the Word Identification and Word Attack subtests. We report descriptive statistics for both subtests in Supplementary Table 1. Our brain-behavior analyses focused on Word Attack because this assessment targets phonological decoding skills. The Word Attack subtest requires children to read aloud a series of pseudowords (spelled according to English conventions) of increasing difficulty. The test is not timed. We expected this subtest to be more sensitive and specific to individual differences in phonological decoding abilities than Word Identification, which is an untimed test that requires the child to sight read English words, and can reflect phonological decoding and/or automatic lexical retrieval. Raw Word Attack scores were converted to age-normed standard scores, which have a population mean of 100 (SD = 15); higher scores indicate better performance. Standard scores of reading ability are expected to be stable over time in typically developing children, and are best described as a trait, rather than a variable skill (Woodcock, 2011; Yeatman et al., 2012). We confirmed that the Word Attack Standard Scores in our sample did not show age-related changes by running a linear mixed effects model with time-varying Word Attack Standard Scores as the dependent variable, age as a fixed effect and participant as a random effect. Word Attack Standard Scores were not associated with age (*beta*=-0.198, p = .628).¹ Accordingly, we calculated an average "decoding ability" score for each participant, which was the mean of their standard Word Attack scores across all available time points, excluding outlier scores (defined as a \geq 30-point [2 SDs] difference between standardized scores of consecutive time points. Outlier scores were checked for scoring errors (none found) and removed for three individuals before computing their average decoding scores.

2.5. Statistical analysis

We modelled the fiber density of each tract as a function of age and decoding ability using linear mixed effects regression with the lme4 and ImerTest packages (Bates et al., 2015; Kuznetsova et al., 2017) in RStudio (RStudio Team, 2020). Given prior evidence of tract-specific associations between phonological decoding and white matter microstructure (e.g., Broce et al., 2019, Cross et al., 2023), we ran separate models for each tract to test our hypotheses. Mixed effects regression enabled us to model a time-varying dependent variable (fiber density) as a function of both time varying (age) and time invariant (decoding ability) fixed factors while accounting for repeated measures within participants by including subject-specific intercepts as a random effect. Mean fiber density values were scaled x100 to bring them to a closer scale to the other measures. We examined main effects of age and decoding ability on fiber density, and we tested whether rate of fiber density development was associated with decoding ability as the interaction between age and decoding score. Interaction terms were dropped from models when they did not show a significant effect. Models for each tract were defined as follows:

$$Y_{ij} = B_1 \cdot a_{ij} + B_2 \cdot d_i + (B_3 \cdot a_{ij} \cdot d_i) + B_{0i} + \epsilon_{ij}$$

¹ We ran a similar model using Word ID Standard Scores as the dependent variable, and found a significant positive association with age (*beta*=2.503, p < .001), indicating that participants' Word ID Standard Scores improved with age. Thus, averaging Word ID Standard Scores to obtain an overall sight word recognition score would not be a valid representation of word reading ability because it would be biased by the age at assessment.





Where Y_{ij} = fiber density of a given tract for the *i*th subject at the time of the *j*th scan, B_1 = coefficient for age, a_{ij} = *i*th subject's age at time of *j*th scan, B_2 = the coefficient for decoding ability, d_i = the *i*th subject's decoding ability (time invariant), B_3 = the coefficient for the interaction between age and decoding ability, B_{0i} = subject-specific y-intercept, and e_{ij} = random error.

We initially ran models that included an additional fixed effect of participant sex; however including sex as a factor only improved model fit in the right SLF model, and was not significantly associated with fiber density in any other tracts. Therefore, we selected the more parsimonious models excluding sex. Model summaries including sex are presented in the Supplementary Materials (Tables S2 & S3).

False-discovery rate (FDR; (Benjamini and Hochberg, 1995) was used to correct for multiple comparisons over eight tracts and two effects of interest (age and decoding ability). We report both uncorrected *p*-values and FDR-corrected *q*-values in the results.

Post-hoc analysis was performed to examine asymmetry of the AF as a function of age and decoding score. Asymmetry indices for fiber density of the AF were calculated as:

$$AI = \frac{(AF_l - AF_r)}{(AF_l + AF_r)} \bullet 100$$

Where AI = asymmetry index of fiber density of the AF, AF_l = mean fiber density of the left AF, and AF_r = mean fiber density of the right AF. Greater values indicate stronger leftward asymmetry.

Asymmetry was modelled as a function of age and reading ability using the linear mixed effects model described above, substituting *AI* for *Y*.

3. Results

Descriptive statistics for age, reading ability, and fiber density are reported in Table 1.

3.1. Reading ability

Overall, our sample had significantly higher Word Attack standard scores (mean=107.66, SD=14.21) relative to the normative sample (mean 100, SD = 15; z = 4.15, 95 % CI of the mean [104.04, 111.28], p < .001); however, variability in reading scores was similar. Our sample included 6 children (9 %) with poor decoding abilities (Word Attack Mean Standardized Scores \leq 85; at least 1 standard deviation below the mean of the normative sample), which is consistent with the population prevalence of reading disability (or developmental dyslexia) for which estimates range from ~5–20 % with recent estimates centering around 7 % (Lyon et al., 2003; Peterson and Pennington, 2015; Yang et al., 2022). Descriptive statistics are reported in Table 1. Descriptive statistics for individual reading sub-tests are provided in Supplementary

Table 1

Descriptive statistics. Means reported across all included observations (*exception: Word Attack Mean Standardized Scores reported per individual participant).

	N obs.	Mean	SD	Min.	Max.
Age at MRI	279	7.24	2.43	2.41	12.92
Age at Reading Assessment	159	8.50	1.82	6	12.71
Word Attack (Decoding)	66 *	107.66	14.21	71	143
Mean Standardized Score					
L. AF Fiber density	279	0.45	0.02	0.39	0.51
R. AF Fiber density	279	0.44	0.02	0.38	0.50
L. SLF Fiber density	279	0.41	0.02	0.34	0.46
R. SLF Fiber density	279	0.41	0.03	0.32	0.46
L. ILF Fiber density	279	0.51	0.03	0.44	0.57
R. ILF Fiber density	279	0.49	0.03	0.41	0.55
L. IFOF Fiber density	279	0.55	0.03	0.49	0.60
R. IFOF Fiber density	279	0.53	0.02	0.46	0.59

Materials Table S1.

3.2. Age-related changes in fiber density of reading network tracts

Fiber density increased significantly with age in all tracts, model statistics reported in Table 2.

3.3. Associations between fiber density and decoding ability

We observed a main effect of decoding ability on fiber density in the left AF, such that better decoders had higher initial fiber density that remained higher over time compared to poorer decoders (*beta*=.041, 95 % CI[.005,.077], p = .028, q=.05) (Table 2; Fig. 3). The interaction between age and decoding ability was not significant (p = .875) and was thus dropped from the model. Decoding ability was not significantly associated with fiber density in any other tract.

3.4. Associations between fiber density asymmetry and decoding ability

We conducted post-hoc analysis to examine microstructural asymmetry of fiber density in the AF as a function of age and decoding ability. The model showed significant main effects of age and decoding ability on AF asymmetry, such that leftward asymmetry increased with age and decoding ability (*beta*_{age}=.393, 95 %CI[.03,.75], *p*_{age}=.032; *beta*_{decoding}=.041, 95 %CI[0,.08], *p*_{decoding}=.027). In addition, we observed a marginal interaction effect (*beta*_{ageXdecoding}=-.003, 95 %CI [-.01, 0], *p* = .05) showing that better decoders had initial leftward asymmetry of the AF with little-to-no change over time, while poorer decoders had lower asymmetry of AF microstructure initially, which shifted toward more leftward asymmetry with age (Fig. 4).

4. Discussion

In this study, we show a specific association between decoding ability and fiber density of the left AF across development of phonological decoding skills. The rate of fiber density development was not moderated by decoding ability, with good and poor decoders showing similar age-related changes. In contrast, microstructural asymmetry of the AF was associated with decoding ability, and a marginal moderation effect by decoding ability was found (p = .05): good decoders had stable leftward asymmetry across the age range, while poorer decoders had increasing leftward asymmetry of AF fiber density with age. These findings distinguish fiber density as a key microstructural feature driving associations between white matter and reading abilities and highlight the left AF as an important tract for developing and sustaining reading skills.

The main effect linking left AF fiber density and phonological decoding ability (in the absence of an age-by-decoding ability interaction) indicates that better decoders had higher fiber density than poorer decoders across the whole age range. The effect we observed in the left AF corresponds to a recent study in which reading ability was strongly associated with a composite measure of fiber density and fiber bundle cross-sectional area in left temporo-parietal white matter (Meisler and Gabrieli, 2022b), as well as prior DTI research showing associations between diffusivity metrics in the left AF and reading and phonological processing abilities (Borchers et al., 2019; Broce et al., 2019; Cross et al., 2023; Vandermosten et al., 2012b). Our finding is also consistent with prior evidence linking white matter microstructure in infancy and early childhood to later language and reading skills (Manning et al., 2022; Van Der Auwera et al., 2021; Zuk et al., 2021). Together with earlier findings, our results show that dense, coherent white matter connections in the left hemisphere reading network (here, the AF) in early childhood provide a neural foundation for learning to read and precede reading difficulties. The continued refinement of these fibers throughout childhood may reflect a reciprocal relationship with reading experience, as ongoing practice further strengthens white matter pathways.

Table 2

Model summaries showing age and decoding ability effects on fiber density of each tract. Age-by-decoding ability interactions were not significant, and were thus excluded from the final models. Unstandardized beta values 95 % confidence intervals, uncorrected p-values, and FDR-corrected q-values are shown. R=Right, L=left.

Fixed Effect	Statistics	L. AF	R. AF	L. SLF	R. SLF	L. ILF	R. ILF	L. IFOF	R. IFOF
Age	beta	.303	.261	.321	.183	.431	.423	.486	.417
	95% CI	[.260, .346]	[.215, .307]	[.278364]	[.140, .226]	[.370, .491]	[.367, .479]	[.437, .534]	[.366, .468]
	p	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
Decoding Ability	р	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
	q	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
	beta	0.041	0.024	0.021	0.006	0.032	0.019	0.027	0.022
	95% СІ	[.005, .077]	[012, .061]	[017, .059]	[035, .047]	[009, .074]	[021, .059]	[011, .064]	[013, .057]
	р	.028	.190	.284	.775	.120	.349	.156	.215
	q	.05	.253	.325	.775	.192	.372	.227	.265
	R ² Cond.	.900	.877	.901	.907	.852	.864	.892	.860

Two previous studies showed that the rate of FA development in the left AF was associated with childrens' subsequent reading abilities, with faster FA increases in good readers compared to poor readers (Wang et al., 2017; Yeatman et al., 2012). In contrast, our findings show similar rates of AF fiber density across participants. This discrepancy in findings may be due to differences in sample characteristics between studies. Our study included mainly average-good readers, with 9 % performing in the below-average range, while the Wang et al., 2017 and Yeatman et al., 2012 studies recruited groups with and without reading disability (Yeatman) or familial risk of reading disability (Wang). Thus, those studies may have captured the altered developmental trajectories in poor readers that result from persistent reading difficulties and/or reliance on alternative pathways for reading, while our study represents the typical patterns of white matter development among children without reading disability or a familial history of reading problems.

Importantly, the present study enhances our understanding of the microstructural features that support skilled reading by showing a specific association between fiber density and decoding ability. This helps to clarify prior evidence that has shown associations between reading ability and tensor-based metrics such as FA (Lebel et al., 2013; Vandermosten et al., 2012a, 2012b; Wang et al., 2017; Yeatman et al., 2012). Our findings suggest that axon packing within the left AF is related to decoding skill; this architecture may reflect a greater capacity for efficient signalling between posterior and anterior reading network regions. The robustness of our CSD model to the influences of crossing fibers further enhances the specificity of these findings and provides confidence that fiber density, rather than the presence of crossing fibers, drives the observed brain-behavior associations.

Additional analyses showed that leftward asymmetry of AF fiber density increased with both age and decoding ability. A modest interaction effect indicated that children with better phonological decoding skills had leftward asymmetry of the AF in early childhood and showed little-to-no change with age, while poorer decoders exhibited increasing leftward asymmetry over time. Thus, along with overall greater fiber density of the left AF, early leftward asymmetry of the AF appears to predispose children to acquire strong reading skills. The overall tendency toward leftward asymmetry of the AF is consistent with prior evidence (Dubois et al., 2009; Langer et al., 2015; Reynolds et al., 2019), and leftward asymmetry of the AF and other reading network tracts has been associated with reading ability (Banfi et al., 2019; Broce et al., 2019; Niogi and McCandliss, 2006; Zhao et al., 2016). Regarding developmental changes in asymmetry, a previous study in an overlapping sample showed that macrostructural asymmetry of the AF is present by age two, but microstructural and functional asymmetry continue emerge into middle childhood (Reynolds et al., 2019). Here, we extend this finding to show that asymmetry of fiber density is established earlier in children who become strong readers. The leftward shift in AF asymmetry over childhood in poorer decoders may reflect experience-driven effects of learning to read on the micro-architecture of the left AF. Studies have shown mixed findings regarding changes in structural and functional asymmetry in response to reading intervention (Perdue et al., 2022), and further research is needed to disentangle practice-driven effects from maturational effects. Notably, the interaction effect in our study was modest and may be influenced by the inclusion of left-handed participants in the analysis (see Supplementary Table S4), who may exhibit different patterns of language lateralization (Ocklenburg et al., 2014). Six of the seven non-right-handed children in our sample had mean Word Attack Standard Scores above the sample mean (107.66), so poorer reading ability was not confounded with left-handedness in our sample.

We did not observe significant associations with decoding ability in any other tracts examined, highlighting the regional specificity of these relationships to the left AF. The left AF connects key hubs of the reading network (i.e., occipito-temporal, temporo-parietal, and inferior frontal cortices), and decoding ability relies explicitly on orthographic-tophonological mapping that is facilitated by the dorsal route *via* the temporo-parietal cortex (Jobard et al., 2003; Levy et al., 2009). Associations with ventral tracts may emerge when examining associations with reading skills that are more dependent on orthographic processing and rapid word recognition. For example, Vandermosten et al. (Vandermosten et al., 2012a) showed a dissociation between dorsal and ventral tracts in their associations with reading sub-skills in adults, such that dorsal tract microstructure was associated with phonological decoding while ventral tract microstructure was associated with rapid orthographic processing.

4.1. Limitations

The relatively small proportion of poor readers in our sample (n = 6, 9 %) may explain the modest effect sizes relative to case-control samples with matched numbers of children with good and poor reading abilities. The lack of poor readers in our study could also explain the absence of a moderation effect of reading ability on rates of fiber density development. Altered rates of tract development and/or effects in right hemisphere tracts could possibly emerge in studies targeting children with reading disabilities. For example, Huber et al. (2019) showed altered patterns of white matter microstructural development in the left AF, left ILF, and posterior corpus callosum of children with reading disabilities undergoing intensive reading intervention. In addition, we did not exclude children from our study based on handedness, and report results from the full sample including both right- and left-handed children. Our main findings were preserved in a sensitivity analysis including only right-handed participants, but the inclusion of non-right-handed children may influence the observed asymmetry effects, which were no longer significant in the right-handed sub-sample (Model summaries are presented in the Supplementary Materials: Tables S3 & S4). Finally, the relatively high socioeconomic status of our sample limits generalizability of these findings to lower socioeconomic status populations. Notably, the proportion of poor readers in our sample (9%) and the proportion of non-right handed children in our sample (10.6 %) are consistent with population estimates of reading disability and left-handedness, respectively; thus, our findings represent effects that would be predicted from the general population. Our study demonstrates the sensitivity and specificity of CSD tractography and



Fig. 3. Scatterplots showing associations among age, fiber density and decoding ability. Dots are colored by decoding ability (mean Word Attack Standard Score per participant); darker colors indicate poorer decoding ability. Solid magenta lines show the overall fit for the age-fiber density association. Dashed fit lines for lower decoding ability (-1 SD from mean, dark purple long-dash) and higher decoding ability (+1 SD from mean, pink short-dash) are shown on the Left AF plot to illustrate main effect of decoding ability on fiber density: poorer readers (darker colors) had lower fiber density relative to better readers (lighter colors) overall, with similar slopes representing similar rates of fiber density development in readers of all abilities.



Fig. 4. Interaction plot showing associations among age, asymmetry index of fiber density in the AF, and decoding ability. Higher asymmetry values indicate more leftward asymmetry. Dots are colored by decoding ability (mean Word Attack standard score per participant); darker colors indicate poorer decoding ability. Solid magenta line shows the mean fit for the age-asymmetry association. Dashed fit lines for lower decoding ability (-1 SD from mean, dark purple long-dash) and higher decoding ability (+1 SD from mean, pink short-dash) are shown to illustrate the interaction effect whereby decoding ability moderated asymmetry index: children with lower decoding ability showed increasing leftward asymmetry with age, while children with average or above-average decoding ability showed little-to-no change in asymmetry with age.

fiber-specific microstructure measurement to individual differences in reading skills, supporting the extension of these methods to both typically developing readers and those with reading disabilities across all stages of reading acquisition.

5. Conclusion

Advanced dMRI modelling revealed a specific association between fiber density of the left AF and decoding ability over the course of reading acquisition. These findings highlight the left AF as a key tract supporting the acquisition of reading skills, especially phonological decoding. Fiber density of the left AF from early childhood (as young as age 2 years) through early adolescence was consistently associated with trait-level decoding abilities (measured at age 6 years and older), pointing to the architecture of this tract as a possible marker of later reading abilities. Ongoing tract microstructure changes and developmental shifts in asymmetry highlight the ongoing plasticity in reading network white matter. This protracted development points to the potential of the reading network to adapt in response to targeted reading interventions in children with reading difficulties.

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Data statement

Tabular data and code for statistical analyses are available here: htt ps://osf.io/wmvgc/?view_only=f11afec2ea774e28b90495b4e9ccf0b4

Raw dMRI data is available upon request to the corresponding author.

Code for dMRI preprocessing, CSD, and tractography is available here: https://github.com/developmental-neuroimaging-lab/mrtrix

CRediT authorship contribution statement

Perdue Meaghan Victoria: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data

curation, Conceptualization. Geeraert Bryce L: Writing – review & editing, Methodology. Manning Kathryn Y: Writing – review & editing, Methodology. Dewey Deborah: Writing – review & editing, Methodology. Lebel Catherine: Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

We have no competing interest to disclose.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2025.101537.

Data availability

Tabular data and code for statistical analyses are available here: https://osf.io/wmvgc/?

view_only=f11afec2ea774e28b90495b4e9ccf0b4. Raw dMRI data is available upon request to the corresponding author. Code for dMRI preprocessing, CSD, and tractography is available here: https://github. com/developmental-neuroimaging-lab/mrtrix

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