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Neural organization of ventral white matter tracts parallels the initial steps of reading development: A DTI tractography study

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ABSTRACT

Insight in the developmental trajectory of the neuroanatomical reading correlates is important to understand related cognitive processes and disorders. In adults, a dual pathway model has been suggested encompassing a dorsal phonological and a ventral orthographic white matter system. This dichotomy seems not present in pre-readers, and the specific role of ventral white matter in reading remains unclear. Therefore, the present longitudinal study investigated the relation between ventral white matter and cognitive processes underlying reading in children with a broad range of reading skills (n = 61). Ventral pathways of the reading network were manually traced using diffusion tractography: the inferior fronto-occipital fasciculus (IFOF), inferior longitudinal fasciculus (ILF) and uncinate fasciculus (UF). Pathways were examined pre-reading (5–6 years) and after two years of reading acquisition (7–8 years). Dimension reduction for the cognitive measures resulted in one component for pre-reading cognitive measures and a separate phonological and orthographic component for the early reading measures. Regression analyses revealed a relation between the pre-reading cognitive component and bilateral IFOF and left ILF. Interestingly, exclusively the left IFOF was related to the orthographic component, whereas none of the pathways was related to the phonological component. Hence, the left IFOF seems to serve as the lexical reading route, already in the earliest reading stages.

1. Introduction

Reading is a complex skill that children acquire through formal instruction in primary school and practice at home. Learning to read begins with the awareness that words can be subdivided into sound segments (i.e. phonemes), which can be linked to a restricted set of visual symbols (i.e. graphemes) by applying grapheme-phoneme conversion rules. According to a reading model by Frith (1985), initial reading relies upon grapheme-phoneme decoding, that is achieved through formal reading instruction. Reading according to this strategy is represented by the phonological route for reading of the dual route cascaded (DRC) model (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). Mastering of reading through grapheme-phoneme conversion is later complemented by the emergence of a second reading route in which words are directly read through the direct recognition of the visual word form. This is the lexical reading route (Coltheart et al., 2001; Frith, 1985). The phonological route for reading is in advanced reading stages mainly applied for reading novel or infrequent words, while the lexical stream sustains reading of frequent or irregular words (Coltheart et al., 2001).

In the adult brain, neural correlates have been proposed for the phonological and the lexical reading routes (Jobard, Crivello, & Tzourio-Mazoyer, 2003). The phonological reading route is suggested to be sustained by left dorsal regions connected by the arcuate fasciculus (AF), while the lexical reading route has been suggested to be sustained by the left inferior fronto-occipital fasciculus (IFOF) (Vandermosten et al., 2012). This dichotomy at the neuroanatomical level reported in adults has been suggested not to be present in pre-reading children. Vandermosten et al. (2015) reported that in pre-reading children, where orthographic knowledge was not substantially developed, both dorsal and ventral white matter networks were involved in phonological processes. Hence, the pre-reading brain differs from the adult brain and the dynamic organization of the reading network should take place during the early stages of reading

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acquisition.

Understanding the process of reading acquisition requires investigation of the involved white matter pathways throughout reading development. The role of the dorsal AF in phonological processing has to date consistently been shown, both prior to reading instruction onset and at more advanced reading stages (Saygin et al., 2013; Vandermosten et al., 2012, 2015; Wang et al., 2016; Yeatman et al., 2011). The pathway has also been related to grapheme-phoneme conversion (Gullick & Booth, 2014) and a deficit in this pathway prior to reading onset has been associated with the development of dyslexia later on (Vanderauwera, Wouters, Vandermosten, & Ghesquière, 2017). Furthermore, a lesion in this pathway resulted in a phonological deficit (Rolheiser, Stamatakis, & Tyler, 2011). The specific role of ventral white matter in reading, and more broadly in language, has been less thoroughly investigated (Dick & Tremblay, 2012). A ventral specialization has been reported in adults, sustaining the lexical reading route, however this specialization was not retrieved in pre-reading children (Vandermosten et al., 2015). It is thus of special interest to investigate the developmental trajectory of ventral white matter. The ventral white matter network consists of the inferior fronto-occipital fasciculus (IFOF), the inferior longitudinal fasciculus (ILF) and the uncinate fasciculus (UF), and has been related to reading processes, although a clear specialization for the semantic and/or orthographic processes of reading has not been consistently found (Dick & Tremblay, 2012).

The IFOF connects the inferior frontal gyrus to inferior and medial occipital regions, around the visual word form area (VFWA) (Catani & Thiebaut de Schotten, 2012; Dehaene & Cohen, 2011; Forkel et al., 2014; Martino, Brogna, Robles, Vergani, & Duffau, 2010; McCandliss, Cohen, & Dehaene, 2003; but see Yeatman, Rauschecker, & Wandell, 2013), and presumably a small part of the medial parietal lobe (Catani, Howard, Pajevic, & Jones, 2002; Martino et al., 2010). At the level of the external capsule the fasciculus is narrow, while at the endpoints the fibers are more diffuse (Catani & Thiebaut de Schotten, 2012; Forkel et al., 2014). White matter organization in the IFOF has been reported to sustain orthographic knowledge in adults (Vandermosten et al., 2012), while prior to reading onset, this pathway has been suggested to sustain phonological processing (Vandermosten et al., 2015).

Next to the IFOF, involvement of the inferior longitudinal fasciculus (ILF) in reading processes has been suggested. The ILF runs parallel and lateral to the IFOF (Catani & Thiebaut de Schotten, 2012), but contrary to the IFOF, the ILF anteriorly projects to the temporal cortex. An involvement of the ILF in reading is plausible since its posterior projections, which are intermingled with the posterior projections of the IFOF, terminate around the VWFA (Wandell, 2011; Yeatman, Dougherty, Ben-Shachar, & Wandell, 2012). However, results on the involvement of this pathway are inconclusive. Whereas Yeatman et al. (2012) did report a relation between reading and the ILF, no relation to reading processes was reported by other studies (Cummine et al., 2015; Saygin et al., 2013).

Moreover, a potential role of the ventral UF in reading has been suggested recently. The UF connects the anterior part of the temporal lobe with the medial and lateral orbitofrontal cortex (Catani et al., 2002), and is considered part of the limbic system (Catani, Dell'acqua, & Thiebaut De Schotten, 2013; Feldman, Lee, Yeatman, & Yeom, 2012; Ross, 2008). The frontal fibers branch into ventral projections to the lateral orbitofrontal cortex and in the anterior insula and medial projections towards the frontal pole and cingulate gyrus (Catani & Thiebaut de Schotten, 2012; Dejerine, 1895). These frontal projections terminate ventrally in close proximity to the anterior frontal projections of the IFOF (Forkel et al., 2014). Within the temporal lobe the UF streamlines project medially and merge with anterior projections of the ILF (Catani & Thiebaut de Schotten, 2012). In adults, word reading has been positively associated with FA in a cluster of the left UF (Zhang et al., 2014). In line with these results, FA in the left UF has also been related to reading irregular words in adults (Cummine et al., 2015). In reading children the right UF has been related to non-word reading, a measure that relies on the phonological decoding ability (Odegard, Farris, Ring, McColl, & Black, 2009), and increased FA in the right UF has been demonstrated in reading children compared to pre-readers (Travis, Adams, Kovachy, & Feldman, 2016).

The present longitudinal study investigates the development of the ventral white matter network and its involvement in reading development in children throughout the very first reading stages. Therefore, we will investigate the structural organization of the left and right IFOF, UF and ILF at two different stages in reading development, i.e. prior to formal reading instruction (pre-reading children) and after two years of reading instruction (early reading children). We will study the developmental trajectory of ventral white matter pathways and their involvement in most prevalent underlying cognitive processes. Based on previous research in school-aged children and adults, we hypothesize that the role of ventral white matter in reading might differentiate according to the stage of reading development with an involvement of the IFOF in phonological processes prior to reading onset (Vandermosten et al., 2015) that reduces in later stages and develops towards an involvement in orthographic knowledge (Vandermosten et al., 2012). For the UF, based on previous research an involvement of the right pathway in phonological processing can be expected in children (Odegard et al., 2009). For the ILF, no firm hypothesis can be formulated given its inconclusive role in reading.

2. Methods

2.1. Participants

The data presented here are part of a longitudinal study on the development of the reading network through the course of reading acquisition, in which originally 87 Dutch-speaking children participated (Vanvooren, Poelmans, Hofmann, Ghesquière, & Wouters, 2014). The children that initially participated in the MRI study at the end of last year of kindergarten (n = 75), were selected based on willingness to participate in the MRI investigation. MRI data were acquired in 75 children at the end of last year of kindergarten (5–6 years old) and 65 of these children were scanned again after two years of reading acquisition (7–8 years old). Four children were excluded due to motion artefacts in their diffusion-weighted imaging (DWI) scans or inadequate scan acquisitions. The present study thus includes 61 children (39 male, 22 female). This sample covers a broad range of literacy skills as 34 participants have a familial risk for dyslexia (FRD$^+$) based on a first degree relative with dyslexia, which elevates the chance to develop dyslexia up to 50% (Gilger, Pennington, & Defries, 1991). The remaining 27 children have no familial risk for dyslexia (FDR$^-$) and represent the general population with a 3–7% chance to develop dyslexia (Peterson and Pennington, 2015; Snowling, 2000). The FRD$^+$ and FRD$^-$ groups do not differ in age (pre-reading MRI: $t_{(59)} = .258$, $p = .797$; early reading MRI: $t_{(59)} = .334$, $p = .739$), sex (Chi-square = .157, $p = .692$), non-verbal intelligence ($t_{(59)} = .1.065$, $p = .291$) and parent's socioeconomic status (SES) ($t_{(59)} = -.082$, $p = .935$). At the start of the longitudinal study, five inclusion criteria were used ensuring that all children had: (1) a non-verbal IQ above 80, (2) normal hearing (i.e. a Fletcher index of less than 20 dB HL), (3) Dutch mother tongue, (4) no history of brain damage, vision deficits, or articulatory problems, and (5) no high risk for developing attention deficit/hyperactivity disorder (ADHD) (for more information see Vanvooren, et al., 2014). Fifteen of the participants included in this study can be retrospectively classified as dyslexic readers (DR) based on word reading, pseudoword reading and spelling scores administered at the start of the second and third grade (for more information see Vanderauwera et al., 2016). One child diagnosed with ADHD was included in the final analysis as removing this participant from the analyses did not change the results. At the early reading stage, one participant had one year of reading experience and another child had three years of reading experience. Results did not change when removing these participants.

In kindergarten, the children that participated in this study did not receive formal reading and writing instruction, conform the guidelines of the Flemish government (http://www.ond.vlaanderen.be/). Hence, at the time of the first MRI acquisition, all children except one were illiterate. By including a longitudinal sample covering a broad range of literacy skills, we aim at addressing reading as a continuous skill. This study was approved by the ethics committee at the University Hospital of Leuven. All parents of the participants gave their written consent for the children to participate in the study in line with the Declaration of Helsinki.

2.2. Cognitive assessment

Assessments were conducted each year at the start of the school year. For the purpose of the present study, cognitive measurements of phonological awareness, letter knowledge and orthographic knowledge were included. In addition, reading measures at the early reading stage are included as well. In the pre-reading children, phonological awareness was measured based on an end-phoneme and end-rhyme identification task administered at the start of last year of kindergarten (Boets et al., 2010; de Jong, Seveke, & van Veen, 2000). The end-phoneme identification task consisted of two practice items followed by 10 test items. A target word was visually presented to the child by a picture of the object on paper, and the child was asked to choose the word that had the same end sound from four alternatives. These four alternatives, also represented by pictures of the object, were visually separated from the target word by a vertical line. All pictures were named for the child and represented highly frequent monosyllabic Dutch words. The maximum score was 10. The end-rhyme identification task was constructed similar to the end-phoneme identification task and consisted of two practices items and 12 test items. Again, a target word was visually presented and named to the child. The child was asked which of the four visually presented and named alternatives had the same end rhyme as the given word.

Letter knowledge was measured by a productive and receptive subtest (Boets, Wouters, van Wieringen, De Smedt, & Ghesquière, 2008) conducted at the start of the first grade. For both subtests 16 letters that are frequent in Dutch language were visually presented. For the productive subtest the child was asked to name all letters while in the receptive subtest the child had to point to the letter that was spoken to the child. For each test the score was defined as the number of correctly answered items.

In third grade phonological awareness was assessed by a phoneme deletion and spoonerisms task (Boets et al., 2010). In both tasks the stimuli are bilaterally presented through headphones at 70 dB sound pressure level. In the phoneme deletion task the child is asked to delete a particular phoneme from a non-existing word (e.g. ‘bijlf’ without ‘f’, an equivalent English example would be ‘spoonk’ without ‘k’). Twenty-eight items are presented in two sections, each preceded by two practice items that are orally presented to the child. The spoonerisms task consisted of 3 sections of each 10 items. For the first section the participant has to swap the initial phoneme of a (pseudo)word with a given phoneme (e.g. ‘kat’ with a ‘m’, an equivalent English example would be ‘cat’ with a ‘b’). For the second section the child has to swap the initial phoneme of two presented (pseudo)words (e.g. ‘saai’ and ‘hok’, equivalent English example is ‘cat’ and ‘book’) in order to create two new words (‘haai’ and ‘sok’, or ‘bat’ and ‘cook’ in English). For the final section the child has to swap the first two phonemes of two (non-existing) words. In both tasks the score is defined as the number of correct answered items. Orthographic knowledge was measured by a pseudo-homophones task administered at the start of grade 3 (Bekebrede, van der Leij, Plakas, Share, & Morfidi, 2010). In these test two practice items and 70 test items were visually presented to the child. Each item consisted of three answer alternatives that were orthographically different, although they were phonologically related (e.g. ‘voet – voed – foet’, an English equivalent would be ‘fox – phox – focks’) . The child had to determine which answer alternative was orthographically correct. The orthographic knowledge score was defined based on the accuracy, there was no time limit. This pseudo-homophones task has been confirmed to represent a correct operationalization of the theoretical concept. The task was composed based on the six categories of spelling difficulty in Dutch, as defined by Assink and Kattenberg (1994), i.e. analogy, congruence, etymology, double vowels or consonants, pronunciation options and spelling of loan words. The task showed differentiating value amongst good and poor readers (Horsley, 2005). For Grade 3, internal consistency (Cronbach’s α) was found to be .91 (Bekebrede, 2011). Reading skills were quantified by standardized achievement tests, i.e. two word reading tasks (Brus & Voeten, 1973; Dudal, 1997) and one pseudoword reading test (Van den Bos, Spelberg, Scheepstra, & De Vries, 1994). The child was asked to read the items as accurate and fast as possible, during one minute for the word reading tasks and two minutes for the pseudoword reading task. The word reading task by Brus & Voeten (1973) and the pseudoword reading task (Van den Bos et al., 1994) have an increasing word complexity level between items whereas the word reading task by Dudal (1997) consists of three different one minute reading tasks, of which the first and second tasks can be assumed to be read with a lexical reading strategy, as the words consist of CVC and CVCC/CCVC words. The third task is not included for the aims of the present study, as we were especially interested in the two subtests that are being read through a lexical reading strategy. For all tests, the score was defined as the number of correct read items.

2.3. Neuroimaging assessment

Diffusion-weighted images (DWI) were acquired on a 3T MRI scanner (Philips, Best, The Netherlands) using a 32-channel head coil and a single shot EPI with SENSE (parallel) acquisition. Sagittal diffusion volumes slices were obtained using the following parameters: repetition time 7600 ms, echo time 65 ms, isotropic voxel size 2.5 × 2.5 × 2.5 mm, b-value 1300 s/mm^2, 60 non-collinear directions, and 6 non-diffusion-weighted images. The scan acquisition time was 10:32 min. All children underwent this DWI scan twice, at the pre-reading and early reading time point, on the same scanner.

All data were pre-processed using ExploreDTI (version 4.8.3; Leemans & Jones, 2009). Diffusion volumes were corrected for eddy current-induced distortions and subject motion. The diffusion tensor model was fitted to the data and whole-brain tractography was conducted using the following parameters: fractional anisotropy (FA) threshold = 0.2, maximum turning angle between voxels = 40°, step length between calculations = 1 mm. TrackVis (www.trackvis.org) was used to perform virtual in vivo dissections of bilateral ventral IFOF, UF and ILF (see Fig. 1, right upper panel). All Regions of interest (ROIs) were defined in frontal, temporal and occipital regions as described by Catani and Thiebaut de Schotten (2008). Tract-specific measurements, quantified by the FA index were extracted for statistical analyses.

2.4. Statistical analyses

One extreme FA-value ($>$ 1.5 interquartile range) was removed from the early reading left IFOF. There were no other outliers. Repeated measures analyses of variance were run for FA in each hemisphere with developmental stage (pre-reading and early reading) and pathway (IFOF, UF and ILF) as within subject factors. For these models normal distribution of the residuals was confirmed. Significant interaction effects were further explored by post-hoc analyses applying Bonferroni correction. Next, given that the different cognitive skills at one developmental stage are mutually related, dimension reduction analyses have been performed by means of a principal component analysis (PCA) with Varimax rotation for the pre-reading and early reading cognitive measurements related to phonological processing and orthographic

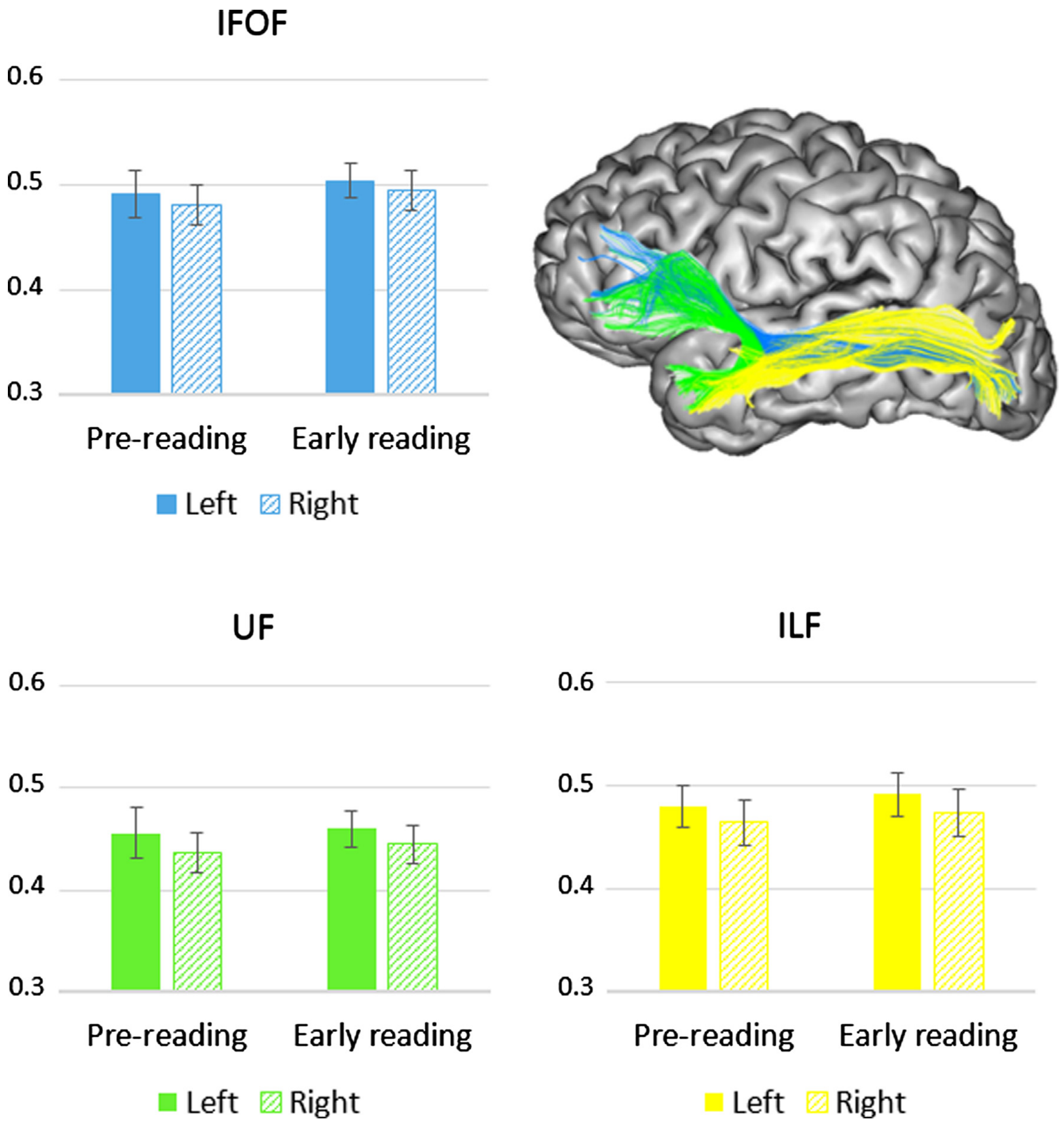

Fig. 1. Visualization and white matter properties (mean FA-values and SD) of the three investigated ventral white matter pathways, i.e. the inferior fronto-occipital fasciculus (IFOF) in *blue*, the uncinate fasciculus (UF) in *green* and the inferior longitudinal fasciculus (ILF) in *yellow*, prior to reading onset and at the early reading stage.

knowledge. For the pre-reading PCA, end-rhyme identification, end-phoneme identification, productive and receptive letter knowledge were included. For the early reading measurements, the two subtests of the phoneme deletion task and the three subtests of the spoonerisms task were included, as well as the pseudohomophones task and two reading tasks that are read by means of a lexical reading strategy. Note that each phonological awareness subtest requires a different instruction and thereby differently loads on working memory. PCA grants the advantage of investigating whether all subtest equally measure phonological awareness, despite their working memory load. Small coefficients were suppressed in the PCA. The relation between the principal components and FA of different white matter pathways was investigated with a regression analysis for each white matter pathway, including FA of the tract, the interaction between tract and developmental stage (pre-reading and early reading) as predictors and sex and whole brain FA as covariates. A correction for multiple comparisons was reported for the regression analyses, by means of False Discovery Rate (FDR) correction. In order to decrease the chance of over-correction and increment of type II errors, the FDR correction was applied separately for each white matter pathway, correcting for the three regression analyses within each pathway. The FDR correction was applied according to the Benjamini and Hochberg's procedure, as described in the version of Benjamini and Yekutieli (2001), with the constant c(N) = 1.

3. Results

The characteristics of the participants and the results on the neurocognitive tests are presented in Table 1. In the table the raw scores for phonological awareness and letter knowledge are presented. Composite scores for these cognitive variables are defined as the mean of the standardized scores of two subtests. Concerning the manual DTI tractography, bilateral IFOF, bilateral ILF and the right UF were traceable in all brains at both reading stages, whereas the left UF was not visible in two brains at both reading stages.

Table 1
Descriptive statistics of the participants and cognitive skills. Mean, standard deviation (SD), minimum and maximum scores are presented. Composite scores are calculated as the mean of the standardized scores of each subtest.

	Mean (SD)	Range/maximum score*
Participant characteristics		
Sex (male/female)	39/22	
SES	5.4 (1.6)	2–8
Age at pre-reading MRI scan (months)	73.6 (3.0)	68–80
Age at early reading MRI scan (months)	95.3 (3.0)	90–101
Pre-reading cognitive skills		
Phonological awareness		
End-rhyme identification	8.5 (2.4)	2–12/12
End-phoneme identification	4.1 (2.3)	0–10/10
Letter knowledge		
Receptive	10.4 (3.7)	3–16/16
Productive	9.4 (4.1)	0–16/16
Early reading cognitive and reading skills		
Phonological awareness		
Phoneme deletion	18.1 (5.9)	3–26/28
Spoonerisms	30.2 (11.4)	3–48/50
Orthographic knowledge (Pseudohomophones)	40.4 (10.1)	17–62/70
Reading skills		
Word reading (Brus & Voeten, 1973)	36.8 (15.9)	7–77
Word reading CVC (Dudal, 1997)	62.0 (21.6)	21–113
Word reading CVCC/CCVC (Dudal, 1997)	48.3 (26.4)	7–108
Pseudoword reading	27.5 (13.0)	4–66

* A maximum score is presented for those tasks where the score is exclusively based on accuracy, and not on speed.

Table 2
Component loading for the pre-reading PCA.

	Pre-reading PC
Pre-reading measurements	
End-rhyme identification	.620
End-phoneme identification	.572
Receptive letter knowledge	.916
Productive letter knowledge	.913

Table 3
Component loading for the early reading PCA. For all cognitive measurements, the highest load has been marked in bold.

	Early reading PC1	*Early reading PC2*
Early reading measurements		
Phoneme deletion subtest 1	**.830**	.192
Phoneme deletion subtest 2	**.793**	.338
Spoonerisms subtest 1	**.743**	.275
Spoonerisms subtest 2	**.855**	.312
Spoonerisms subtest 3	**.834**	.307
Pseudohomophones	.504	**.754**
Lexical reading task 1	.249	**.943**
Lexical reading task 2	.281	**.941**

3.1. White matter development

The development of ventral white matter in each hemisphere was investigated by a repeated measures analysis of variance with pathway (IFOF, UF and ILF) and developmental stage (pre-reading and early reading) as within subject factors. Mean FA indices for each pathway at both reading stages are presented in Fig. 1. In the left hemisphere, a main effect of developmental stage was present ($F_{(1,57)} = 28.560$, $p < .001$), as well as a main effect of pathway ($F_{(1,57)} = 149.512$, $p < .001$). In addition, a developmental stage by pathway interaction was observed ($F_{(1,57)} = 7.151$, $p = .002$). Post-hoc pairwise comparisons with Bonferroni correction revealed that the interaction effect was driven by significant development in the left IFOF ($p < .001$) and the left ILF ($p < .001$), but not in the left UF ($p = .066$). In the right hemisphere, significant development was present in all white matter pathways ($F_{(1,60)} = 47.208$, $p < .001$), as well as a significant main effect of pathway ($F_{(1,60)} = 208.623$, $p < .001$). No developmental stage by pathway interaction was present ($F_{(1,60)} = 2.591$, $p = .092$).

3.2. Principal component analyses

Two principal component analyses (PCA) were run. PCA for the pre-reading cognitive measurements resulted in one principal component (PC). The pre-reading PC explained 59.6% of the total variability in the data. All four components loaded on the pre-reading PC, as presented in Table 2. PCA for the early reading cognitive measurements resulted in two components, explaining 80.7% of the total variability in the data. The first component (PC1) was mainly loaded on by all subtests measuring phonological awareness, regardless of working memory load, and will therefore be further referred to as the phonological awareness component (PC_PA; Table 3). The second component (PC2) was mainly loaded on by the measurements of orthographic knowledge and lexical reading and will therefore be referred to as the orthographical component (PC_OK; Table 3).

3.3. Relation between ventral white matter FA and reading-related skills

To investigate the relation between ventral white matter organization and reading-related skills throughout the initial course of reading development, regression analyses were run for the three principal components (Table 4). For the pre-reading principal component, the regression models revealed a relation with a broad network of ventral white matter pathways. There was a main effect of FA in the left IFOF ($F_{(1,116)} = 6.667$, $p = .011$, $\eta^2 = .054$), the right IFOF ($F_{(1,117)} = 14.809$, $p < .001$, $\eta^2 = .112$) and the left ILF ($F_{(1,117)} = 7.576$, $p = .007$, $\eta^2 = .061$). The prediction by the right ILF did not survive FDR correction ($F_{(1,117)} = 5.759$, $p = .018$, $\eta^2 = .047$). No significant developmental stage by tract interaction was present for bilateral IFOF and ILF, indicating that the relation between the pre-reading PC and white matter organization in these pathways was not dependent on the development of the pathway. For the model including the right UF pathway, a developmental stage by tract interaction was retrieved ($F_{(1,117)} = 4.448$, $p = .037$, $\eta^2 = .037$), as well as a main effect of whole brain FA ($F_{(1,117)} = 4.527$, $p = .035$, $\eta^2 = .037$), however both effects did not survive correction for multiple comparison. No effect on the pre-reading PC was found for the model including the left UF pathway (Table 4). In all models, no effect of sex was retrieved.

After two years of reading acquisition, dimension reduction analysis of reading-related cognitive skills resulted in two main components, i.e. a phonological based PC (PC_PA) and an orthographic based PC (PC_OK). For the PC_PA, no significant prediction was retrieved by the white matter tracts or the tract by developmental stage interaction, suggesting that the involvement of ventral white matter in reading processes was not driven by the phonological component. There was neither a significant effect of whole brain FA and sex. For the PC_OK, a significant prediction was found for the left IFOF ($\mathbf{F_{(1,116)} = 9.382}$, $\boldsymbol{p = .003}$, $\boldsymbol{\eta^2 = .075}$), in the absence of a significant developmental stage by tract interaction, a main effect of whole brain FA and sex (see Table 4). The prediction made by the right UF ($F_{(1,117)} = 4.864$, $p = .029$, $\eta^2 = .040$) did not survive FDR correction. Hence, ventral white matter organization in the left IFOF sustains orthographic processes of reading. Since no interaction effects were present, the relation

Table 4
Regression analyses for the three principal components (PC).

	IFOF		UF		ILF	
	Left	Right	Left	Right	Left	Right
Pre-reading PC						
ME pathway	**$F_{(1,116)} = 6.667$, $p = .011$, $\eta^2 = .054$**[*]	**$F_{(1,117)} = 14.809$, $p < .001$, $\eta^2 = .112$**[*]	$F_{(1,113)} = .606$, $p = .438$	$F_{(1,117)} = 1.353$, $p = .247$	**$F_{(1,117)} = 7.576$, $p = .007$, $\eta^2 = .061$**[*]	**$F_{(1,117)} = 5.759$, $p = .018$, $\eta^2 = .047$**
ME sex	$F_{(1,116)} = .181$, $p = .671$	$F_{(1,117)} = .006$, $p = .938$	$F_{(1,113)} = .803$, $p = .372$	$F_{(1,117)} = .128$, $p = .721$	$F_{(1,117)} = .408$, $p = .524$	$F_{(1,117)} = .152$, $p = .697$
ME whole brain FA	$F_{(1,116)} = .782$, $p = .378$	$F_{(1,117)} = 1.341$, $p = .249$	$F_{(1,113)} = 2.301$, $p = .132$	**$F_{(1,117)} = 4.527$, $p = .035$, $\eta^2 = .037$**	$F_{(1,117)} = 1.600$, $p = .208$	$F_{(1,117)} = 3.353$, $p = .070$
IE developmental stage x pathway	$F_{(1,116)} = 1.659$, $p = .200$	$F_{(1,117)} = 3.328$, $p = .071$	$F_{(1,113)} = 2.068$, $p = .153$	**$F_{(1,117)} = 4.448$, $p = .037$, $\eta^2 = .037$**	$F_{(1,117)} = 2.778$, $p = .098$	$F_{(1,117)} = 3.868$, $p = .052$
Early reading PC_PA						
ME pathway	$F_{(1,116)} = .004$, $p = .952$	$F_{(1,117)} = .148$, $p = .701$	$F_{(1,113)} = .305$, $p = .582$	$F_{(1,117)} = .370$, $p = .544$	$F_{(1,117)} = 1.949$, $p = .165$	$F_{(1,117)} = .078$, $p = .780$
ME sex	$F_{(1,116)} = .568$, $p = .453$	$F_{(1,117)} = .894$, $p = .346$	$F_{(1,113)} = 2.220$, $p = .139$	$F_{(1,117)} = 1.055$, $p = .306$	$F_{(1,117)} = 1.356$, $p = .247$	$F_{(1,117)} = .926$, $p = .338$
ME whole brain FA	$F_{(1,116)} = 1.013$, $p = .316$	$F_{(1,117)} = 1.054$, $p = .307$	$F_{(1,113)} = .105$, $p = .747$	$F_{(1,117)} = .804$, $p = .372$	$F_{(1,117)} = .218$, $p = .641$	$F_{(1,117)} = 1.427$, $p = .235$
IE developmental stage x pathway	$F_{(1,116)} = .857$, $p = .356$	$F_{(1,117)} = 1.037$, $p = .311$	$F_{(1,113)} = .102$, $p = .750$	$F_{(1,117)} = .785$, $p = .378$	$F_{(1,117)} = .448$, $p = .505$	$F_{(1,117)} = 1.296$, $p = .257$
Early reading PC_OK						
ME pathway	**$F_{(1,116)} = 9.382$, $p = .003$, $\eta^2 = .075$**[*]	$F_{(1,117)} = 1.587$, $p = .210$	$F_{(1,113)} = 1.466$, $p = .229$	**$F_{(1,117)} = 4.864$, $p = .029$, $\eta^2 = .040$**	$F_{(1,117)} = .940$, $p = .334$	$F_{(1,117)} = .025$, $p = .875$
ME sex	$F_{(1,116)} = 2.265$, $p = .135$	$F_{(1,117)} = .995$, $p = .321$	$F_{(1,113)} = 2.598$, $p = .110$	$F_{(1,117)} = 1.734$, $p = .191$	$F_{(1,117)} = .785$, $p = .377$	$F_{(1,117)} = 1.081$, $p = .301$
ME whole brain FA	$F_{(1,116)} = .328$, $p = .568$	$F_{(1,117)} = .782$, $p = .378$	$F_{(1,113)} = .031$, $p = .862$	$F_{(1,117)} = .112$, $p = .739$	$F_{(1,117)} = 3.643$, $p = .059$	$F_{(1,117)} = 2.012$, $p = .159$
IE developmental stage x pathway	$F_{(1,116)} = .001$, $p = .987$	$F_{(1,117)} = 1.163$, $p = .283$	$F_{(1,113)} = .045$, $p = .833$	$F_{(1,117)} = .302$, $p = .584$	$F_{(1,117)} = 2.796$, $p = .097$	$F_{(1,117)} = 1.780$, $p = .185$

Significant effects are marked in bold. Significance levels of $p > .05$ have been referred to as non-significant (NS).
PA = phonological awareness, OK = orthographic knowledge, ME = main effect, IE = interaction effect.

[*] Remains significant after FDR correction.

between the orthographic PC and white matter was not dependent on the development of the pathway itself. In fact, by being able to separate principal components for phonology and orthography at the early reading stage, the role of ventral white matter organization in the left IFOF could be clarified.

4. Discussion

The present study investigates the development and the potential role of ventral white matter in reading-related processes at two stages of reading development, i.e. prior to reading instruction onset and after two years of reading acquisition. Our results suggest that (1) significant development takes place in important ventral white matter pathways during the first years of reading acquisition, (2) ventral white matter anatomy is associated with important reading-related processes, both at the pre-reading stage and at the early reading stage. While the pattern of relations between ventral white matter and important cognitive processes for reading was diffuse for the pre-reading cognitive measures, with many white matter pathways predicting the principal component that was loaded on by both phonological awareness and letter knowledge, the left IFOF demonstrated the strongest contributions to the early reading orthographic component, in the absence of significant predictions of the phonological component. By investigating the three ventral white matter pathways IFOF, UF and ILF in one longitudinal sample of young children with a broad range of reading skills, this study further elucidated insight on the specific involvement of ventral white in pre-reading cognitive measures, orthographic knowledge and phonological processing. and revealed that the left IFOF already sustained orthographic knowledge at the earliest reading stages, while none of the pathways sustained phonological processes.

In this study, we demonstrated positive FA development between the pre-reading (5–6 years) and early reading stage (7–8 years) in all but one ventral white matter pathway. No significant development was observed in the left UF ($p = .066$). Hence, these results indicate that the most important developmental stage in reading acquisition is paralleled by development in those ventral white matter pathways sustaining reading acquisition. Our results on age-related development are in line with the expected age-related development based on a large-scale cross-sectional study of white matter development by Lebel, Walker, Leemans, Phillips, and Beaulieu (2008). Lebel et al. reported a rapid increase in FA of the IFOF between the ages of 5 and 8. After the age of 8 FA in the IFOF further increased until early adulthood. The developmental curve of the UF reported by Lebel et al. was flatter than for the IFOF, although a slow increase remained present until adolescence. Hence, this supports our finding on the absence of a significant increase in the left UF while we did observe positive FA increase in the right UF, one of the pathways that related to the developing orthographic knowledge. Finally, rapid increase in FA of the ILF was reported by Lebel et al. between the ages of 5 and 8. In adolescence, the ILF did not significantly increase anymore.

The present study investigated the relation between ventral white matter and important cognitive reading-related processes throughout the initial steps of reading acquisition. Since cognitive measures of reading-related skills are interrelated, we first performed a dimension reduction analysis by means of principal component analyses. Interestingly, at the pre-reading stage, both measurements of phonological awareness and letter knowledge loaded on a single component, whereas at the early reading stage, two different components could be defined that were mainly loaded on by either orthographic knowledge or phonological skills. This presumably reflects that through development, both concepts are being further specialized. However, we cannot exclude an influence of the tasks that were used at the pre-reading stage. Either way, at the pre-reading level we were not able to make a distinction between two cognitive skills and therefore the relation with ventral white matter organization could only be defined for this one component, loaded on by both phonological awareness and letter knowledge measurements.

The relation between ventral white matter and cognitive skills was investigated by means of regression models, that maximize the nature of the current longitudinal data. Results were corrected for multiple comparisons by means of FDR correction. In each model, one principal component was predicted by FA in the tract, developmental stage by tract interaction, and the covariates sex and whole brain FA were included as well. For the IFOF, both the left and right pathway significantly predicted the pre-reading cognitive component, represented by a main effect in both pathways. These results indicate that both the left and right IFOF sustain reading-related processes. A previous study suggested that the relation between pre-reading left and right IFOF was mainly driven by phonological processes and not by letter knowledge (Vandermosten et al., 2015). To interpret these findings it should be noted that letter knowledge is not a true measure of orthographic knowledge, as orthographic knowledge only develops with the emergence of reading skills. Another study in pre-readers showed that training grapheme–phoneme correspondences resulted in sensitivity for print in the left ventral occipito-temporal region in pre-readers (Brem et al., 2010). Previous research in adults, however, suggested that the left ventral IFOF would represent the lexical ventral stream for reading (Vandermosten et al., 2012). Interestingly, after two years of reading acquisition, when we were able to separate an orthographic and a phonological principal component, regression analyses revealed that the left IFOF significantly predicted the orthographic component, and not the phonological component. These results are of specific interest as the prediction of the left IFOF was represented by a main effect of FA in the pathway, in the absence of a developmental stage by pathway interaction effect. Hence, our results reveal that the left IFOF is related to orthographic processes, already prior to any formal reading instruction. Given that our brain is not pre-destined for reading, it cannot be assumed that the left IFOF is predestined for processing orthographic knowledge. However, it might be a consequence of early, although very limited, exposure to print. Hence, we can support the hypothesis by Brem et al. (2010) that early exposure to print might induce sensitivity for print in the ventral neural reading system. The left IFOF thus seems to serve as the lexical reading route, and sustains the development of orthographic knowledge. For the right IFOF, no relation was found with the orthographic or the phonological component. Hence, although the right IFOF predicted the pre-reading cognitive component, we were not able to further disentangle the specific role of this pathway in early reading processes. These results do confirm no significant contribution of the right IFOF as a ventral lexical reading route.

Next to the involvement of the IFOF, we observed a role of the ventral ILF in cognitive reading-related processes. The pre-reading cognitive component was significantly predicted by the left ILF, while the prediction by the right segment did not survive correction for multiple comparisons. Again, the relation between the left ILF and the pre-reading cognitive component was represented by a main effect of the pathway, in the absence of a significant developmental stage by pathway interaction. However, similar as for the right IFOF segment, the relation in the left ILF could not be further disentangled into a specific involvement in orthographic or phonological processes. Hence, the left ILF does not serve as a ventral lexical reading route. Given the relation between the left ILF and the pre-reading cognitive component, and the opposing findings of the involvement of this pathway in phonological processes (Yeatman et al., 2012 versus Cummine et al., 2015; Saygin et al., 2013), this pathway might serve a different role in reading, that was not captured by our early reading measures. Further research is required to understand the involvement of this pathway in early reading processes.

Next to the IFOF and the ILF, we also investigated the role of the UF in reading processes throughout the earliest reading stages. While no significant effects were found for the models including the left UF, the predictions made in the models including the right UF did not survive correction for multiple comparisons. To the best of our knowledge, only two studies directly investigated the relationship between white matter properties of the UF pathway and reading ability. The first study by Cummine et al. (2015) reported a relation between the left UF and irregular word reading in adults, suggesting that the left UF also sustains the lexical pathways for reading. Together with our results, this might imply that the involvement of the left UF develops throughout more advanced stages of reading development. The second study demonstrated an involvement of the right UF in reading in young children, as they showed increased FA in the right UF in young children who could read, relatively to pre-readers (Travis et al., 2016). Studies that used tract based spatial statistics (TBSS), a different method to analyze in vivo white matter (Smith et al., 2006), provide additional evidence for the role of the UF as a lexical pathway for reading. In adults, a relation was found between word reading and FA in a cluster of voxels that is part of the left UF (Zhang et al., 2014). However, this cluster was also part of the left IFOF, hence, the used TBSS method cannot disentangle the specific involvement of the ventral white matter pathways in reading. Another TBSS study in a small sample of 10–14 year old children also suggested an involvement of the right UF pathway in reading processes, showing a relation between FA in a cluster within the right UF and non-word reading (Odegard et al., 2009). Again, this relation was observed in a cluster within bilateral IFOF and right ILF as well. Finally, the role of the UF was suggested by a case study in a child with a missing bilateral AF and superior longitudinal fasciculus (Yeatman & Feldman, 2013). Hence, the relation between the UF and reading has been suggested by a few studies. However, the involvement of this pathway in reading needs to be further explored, especially by studies including measures that require different reading strategies, with different levels of complexity and frequency of the measured items. Nevertheless, an involvement of this pathway in some reading processes might not be unexpected. The frontal terminations have been related to phonological processing, especially within the left hemisphere (Katzir, Misra, & Poldrack, 2005; Welcome & Joanisse, 2012). In addition, this pathway sustains a connection between two regions that are adjacent to the anterior endpoints of the IFOF and the ILF. Hence, an involvement of the UF in different or later reading processes should be considered, but only in close interaction with other white matter pathways that have been shown to sustain reading, especially the left ventral IFOF.

In sum, our longitudinal ventral white matter analyses reveal the role of the left IFOF as a ventral lexical reading route, that is already specialized in the earliest stages of reading development. As orthographic knowledge is strongly related to reading ability and develops throughout the process of reading acquisition, we suggest that the development of orthographic knowledge might be sustained by the left IFOF in young children. Furthermore, the left ILF and right IFOF pathways seem to sustain early reading development as well, although this relation could not be attributed to either early reading phonological or orthographic reading processes. Hence, while our study demonstrated the specific role of the left IFOF in orthographic knowledge, in the absence of a role of ventral white matter in phonological processes, further research including a broader set of cognitive and behavioural measures, such as specific measures of different reading strategies, and follow up during later reading development is required to truly grasp the divergent roles of ventral white matter in reading development.

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