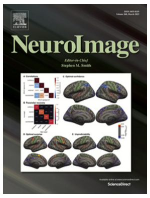
NeuroImage 268 (2023) 119869

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage



Disentangling influences of dyslexia, development, and reading experience on effective brain connectivity in children

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ARTICLE INFO

Keywords:
Reading network
Developmental dyslexia
Dynamic causal modeling (DCM)
Effective connectivity
fMRI
Visual Word Forma Area (VWFA)
Inferior parietal lobule
Development

ABSTRACT

Altered brain connectivity between regions of the reading network has been associated with reading difficulties. However, it remains unclear whether connectivity differences between children with dyslexia (DYS) and those with typical reading skills (TR) are specific to reading impairments or to reading experience. In this functional MRI study, 132 children ($M = 10.06$ y, SD = 1.46) performed a phonological lexical decision task. We aimed to disentangle (1) disorder-specific from (2) experience-related differences in effective connectivity and to (3) characterize the development of DYS and TR. We applied dynamic causal modeling to age-matched ($n_{dys} = 25$, $n_{TR} = 35$) and reading-level-matched ($n_{dys} = 25$, $n_{TR} = 22$) groups. Developmental effects were assessed in beginning and advanced readers (TR: $n_{beg} = 48$, $n_{adv} = 35$, DYS: $n_{beg} = 24$, $n_{adv} = 25$). We show that altered feedback connectivity between the inferior parietal lobule and the visual word form area (VWFA) during print processing can be specifically attributed to reading impairments, because these alterations were found in DYS compared to both the age-matched and reading-level-matched TR. In contrast, feedforward connectivity from the VWFA to parietal and frontal regions characterized experience in TR and increased with age and reading skill. These directed connectivity findings pinpoint disorder-specific and experience-dependent alterations in the brain's reading network.

1. Introduction

Learning to read is essential to everyday life. However, despite appropriate schooling and reading instruction, around 5–10% of children experience severe difficulties learning this skill (Snowling, 2013) and are diagnosed with developmental dyslexia (henceforth dyslexia). There is considerable evidence for deviations in brain structure, function, and more recently, the connectivity of the reading network in children (Brem et al., 2020; Maurer et al., 2010; Morken et al., 2017; Pleisch et al., 2019; Wise Younger et al., 2017), adolescents (Kronschnabel et al., 2014), and adults (Achal et al., 2016; Martin et al., 2015; Reis et al., 2020; Richlan, 2020) with dyslexia. However, insights into aberrant brain network structure and function are often limited because individuals with dyslexia usually have less expertise in reading than do their peers with typical reading skills. Differences found between children with typical and poor reading skills are presumably a combination of dyslexia-specific effects and the effects of reading experience. Whether the reported brain differences are specific to the reading disorder or a consequence of less reading experience and print exposure (Maughan et al., 2009; Peterson et al., 2013) has only rarely been addressed in neuroimaging studies with chronological-age-matched and reading-level-matched designs (Cao et al., 2018; Chyl et al., 2019; Hoeft et al., 2007; Krafnick et al., 2014; Schulz et al., 2009; Xia et al., 2016). Unraveling differential contributions to poor reading therefore remains a challenge that has a high potential for directing novel therapeutic approaches.

Abbreviations: DCM, dynamic causal modelling; fMRI, functional manetic resonance imaging; VWFA, visual word form area; DYS, developmental dyslexia; TR, typical reading skills.

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https://doi.org/10.1016/j.neuroimage.2023.119869.
Received 11 May 2022; Received in revised form 29 December 2022; Accepted 9 January 2023

One of the core regions within the reading network (Richlan, 2012) is the visual word form area (VWFA) in the ventral occipitotemporal cortex (vOT). This region responds preferentially to written words and orthographic stimuli compared to non-orthographic control stimuli (Cohen et al., 2000; Wang et al., 2019) and is critically involved in fluent reading (Dehaene and Cohen, 2011; Vinckier et al., 2007). Initial studies suggested a posterior-to-anterior vOT gradient of higher activation to words than to letter strings (Brem et al., 2009; James et al., 2005; Vinckier et al., 2007). More recent studies have elaborated on this concept and propose a subdivision of the VWFA's function with more posterior regions implicated in perceptual aspects of visual word form processing and more anterior regions in lexical ones (Caffarra et al., 2021; Lerma-Usabiaga et al., 2018; Taylor et al., 2019; Thesen et al., 2012; White et al., 2019). Studies examining functional connectivity during rest in preschool children (Saygin et al., 2016) and neonates (Li et al., 2020) indicate that connectivity within the language network shapes the functional development of the VWFA, meaning that the VWFA develops as a language region because of its connections with other regions of the language network, for example with frontotemporal regions. Functional activation studies in development show a rapid increase in VWFA sensitivity to print in the first phase of learning to read (Ben-Shachar et al., 2011; Brem et al., 2010; Caffarra et al., 2021; Centanni et al., 2017; Dehaene-Lambertz et al., 2018; Fraga-González et al., 2021; Maurer et al., 2006; Nordt et al., 2021) and after relative short training in children (James, 2010; Pleisch et al., 2019) and adults (Brem et al., 2018; Hashimoto and Sakai, 2004; Xue et al., 2006). Additionally, more advanced reading skills have been linked to a stronger VWFA response (Richlan et al., 2009), especially in individuals with dyslexia (Brem et al., 2020). According to the interactive account model of occipitotemporal specialization (Price and Devlin, 2011), the strength of the VWFA response in the initial learning stages may reflect the integration of emerging top-down and bottom-up predictions resulting in high prediction error signals (Friston et al., 2006; Zhao et al., 2019). Feedforward connections from the VWFA represent the conveyance of sensory inputs. By contrast, feedback connections to the VWFA are used to transfer information about nonvisual stimulus attributes, such as phonological and orthographic information about the print stimulus (Price and Devlin, 2011). This view emphasizes the close interaction of the VWFA with other regions of the reading network, such as the inferior frontal gyrus (IFG) (Bouhali et al., 2014; Whaley et al., 2016), the inferior parietal lobule (IPL) (Moulton et al., 2019; Yu et al., 2018), and the precentral gyrus (PreG) (Morken et al., 2017). Both the IPL and the PreG are part of the dorsal stream of the reading network, which is especially active in younger children and poor readers due to their effortful letter-by-letter reading strategy (Pugh et al., 2001; Sandak et al., 2004). The ventral stream of the reading network, involved in automatic word recognition, becomes more important with age and expertise (K. R. Pugh, Mencl, Jenner, et al., 2000; Sandak et al., 2004; Wise Younger et al., 2017). This may lead to decreased responses in the dorsal stream in more skilled readers during print processing (Sandak et al., 2004; Wise Younger et al., 2017).

Previous studies have shown increasing connectivity within the reading network, encompassing occipitotemporal, parietal, and inferior frontal regions, with advancing reading skills (Cao et al., 2008; Hampson et al., 2006; Horwitz et al., 1998; Quaglino et al., 2008). Others have reported aberrant functional connectivity within the reading network in poor readers (Finn et al., 2014; Hampson et al., 2006; Horwitz et al., 1998; K. R. Pugh, Mencl, Shaywitz, et al., 2000; van der Mark et al., 2011; Wang et al., 2020), and indicated prospective associations of functional connectivity in infancy and toddlers with subsequent language and literacy precursor skills (Yu et al., 2021). Few studies have examined the development of effective connectivity in the reading network, a method for studying which brain region's (de)activation influences other brain regions' (de)activation, or how these influences are modulated by task parameters. These studies showed that connectivity within the reading network is dependent on reading skills and development (e.g. (Siok et al., 2020)). For example, delayed development of effective connectivity was reported for children with dyslexia (Morken et al., 2017): The connections between the brain regions of the reading network differed significantly between children with poor and typical reading skills at an early stage (age 8) but were indistinguishable at a later stage (age 12). In addition to delayed development of connectivity within the reading network, Wise Younger et al. (2017) reported that connectivity development in children with low reading progress differed substantially from that in children with typical reading progress. However, the study designs used did not allow the dyslexia-specific effects to be disentangled from those related to a lack of reading experience. A valid approach for disentangling these effects is a reading-level-matched design that compares older children with dyslexia and younger typically reading children with the same reading skills (Chyl et al., 2019; Hoeft et al., 2006; Krafnick et al., 2014; Schulz et al., 2009; but see Zoccolotti, 2020).

Here, we compared effective connectivity in the reading network of children with typical reading skills (TR) and children with dyslexia (DYS) in the middle and at the end of formal reading instruction in a chronological-age-matched and reading-level-matched design during a functional magnetic resonance imaging (fMRI) phonological lexical decision task (Kronbichler et al., 2007; van der Mark et al., 2009). We used a dynamic causal modeling (DCM) approach (Friston et al., 2015) to examine the coupling of left-lateralized brain regions: the VWFA, IPL, PreG, and IFG. If deviations in effective connectivity are dyslexia-specific, we expected to observe them when comparing children with dyslexia not only to age-matched controls but also to reading-level-matched controls. If the differences are not dyslexia-specific but mediated by lower reading experience, the differences between DYS and their age-matched controls should diverge from those between DYS and their reading-level-matched controls. From previous research, we expected beginning readers and DYS to rely on the dorsal pathway and advanced readers to shift towards a predominant reliance on the ventral pathway (Pugh et al., 2001; Wise Younger et al., 2017). For DYS, we hypothesized a delay in the development of part of the reading network (e.g. Morken et al., 2017), in particular in connections to and from frontal regions (Chyl et al., 2019; Levy et al., 2009). We expected feedforward connections from the VWFA to frontal areas to depend on reading experience rather than skill level (Yan et al., 2021) but connections to and from parietal areas to be specific to the disorder (Hoeft et al., 2007; van der Mark et al., 2011). Finally, our developmental analyses provide additional insights into the changes of connectivity within the reading network in TR and DYS.

2. Materials and methods

2.1. Participants

In total, 181 German-speaking subjects participated in the fMRI session. The following reasons led to exclusion of data from the final analysis: Not meeting our stringent fMRI data quality criteria as described below ($n = 7$), technical problems during fMRI session ($n = 1$), artifacts due to non-removable dental braces ($n = 4$), missing time series for DCM analysis ($n = 7$), threshold criteria for assignment to the groups as described below ($n = 30$), leaving a final sample of 132 subjects for analysis (age: 10.06 ± 1.46; 63 female; for a more detailed view of the demographics, see Table 1). All participants had nonverbal IQ scores > 85, normal or corrected to normal vision and no neurological or psychiatric impairment, with the exception of ADHD/ADD ($n = 8$). The few cases with ADHD were either unmedicated or were required to discontinue medical treatment at least 24 h before the fMRI and behavioral sessions. The participants were recruited from two different studies, one conducted in older children in 5th grade, and one in younger children in grades 1 to 4. All children and their parents gave oral and written informed consent and received vouchers and presents for participation. The studies were approved by the local ethics com-

Table 1
Demographic characteristics of study participants.

	TR adv.	DYS adv.	TR beg. (RL)	TR beg. (Dev)	DYS beg.
n	35	25	22	48	24
Age (years),	11.46 (0.31),	11.55 (0.40),	8.54 (0.61),	8.68 (0.75),	9.22 (0.75),
range (min-max)	10.76–12.09	10.70–12.16	7.36–9.64	6.88–10.15	7.67–10.79
Risk score,	.37 (0.12),	.55 (0.11),	.39 (0.14),	.35 (0.13),	.38 (0.13),
range (min-max)	.15-0.62	.36-0.80	.18-0.64	.09-0.64	.17-0.69
Sex (females), No. (%)	17 (49%)	15 (60%)	13 (59%)	23 (48%)	8 (33%)
Handedness (right), No. (%)	33 (94%)	22 (88%)	21 (96%)	43 (90%)	23 (96%)
Reading fluency score,	67.36 (20.79),	5.20 (4.62),	44.14 (16.10),	59.40 (22.80),	4.50 (4.23),
range (min-max)	30.25–96.50	1.00–15.50	25.50–87.50	25.50–98.00	1.00–14.50
Reading fluency raw,	73.66 (11.19),	32.44 (7.36),	33.43 (7.93),	45.10 (18.33),	21.25 (6.80),
range (min-max)	56.00–104.50	21.00–44.50	20.50–45.00	9.50–86.50	7.50–33.00
Nonverbal IQ,	105.74 (7.30),	101.64 (7.55),	104.86 (6.81),	106.77 (7.67),	103.83 (6.26),
range (min-max)	93–123	88–119	90–116	89–123	90–113
fMRI task global ACC (%)	86.91 (6.68)	80.87 (7.56)	78.18 (9.04)	80.00 (11.11)	68.75 (12.35)
fMRI task global RT (ms)	1484 (184)	1687 (261)	1744 (255)	1662 (298)	2065 (413)

	Age-matched		Reading-level-matched	
	Test statistic	*p* value	Test statistic	*p* value
Age	$t(58) = -1.03$	.309	$t(35.08) = -19.69$	<0.001
Risk score[a]	$t(55.02) = -5.85$	<0.001	$t(36.96) = -4.20$	<0.001
Sex	$\chi^2(1) = 0.77$	.382	$\chi^2(1) = 0.004$	.949
Handedness[b]	$\chi^2(1) = 0.75$	.385	$\chi^2(1) = 0.83$	.361
Reading fluency score	$U < 0.001$	<0.001	$U < 0.001$	<0.001
Reading fluency raw value	$t(58) = 16.08$	<0.001	$t(45) = 0.44$	.659
Nonverbal IQ	$U = 301.00$	.040	$t(44) = 1.51$[c]	.139
fMRI task global ACC	$U = 202.50$[d]	.001	$t(45) = -1.11$	.274
fMRI task global RT	$t(40.78) = -3.31$[d]	.002	$t(45) = 0.76$	.453

	Developmental effect TR		Developmental effect DYS	
	Test statistic	*p* value	Test statistic	*p* value
Age	$t(66.50) = 23.10$	<0.001	$t(34.65) = 13.57$	<0.001
Risk score[a]	$t(75.44) = 0.65$	.515	$t(46) = 4.91$	<0.001
Sex	$\chi^2(1) = 0.003$	.953	$\chi^2(1) = 3.50$	.062
Handedness[b]	$\chi^2(1) = 0.58$	.446	$\chi^2(1) = 1.00$	.317
Reading fluency score	$U = 661.00$	.099	$U = 259.50$	.417
Reading fluency raw value	$t(78.85) = 8.78$	<0.001	$t(47) = 5.52$	<0.001
Nonverbal IQ	$U = 722.00$	.345	$t(47) = -1.11$	.275
fMRI task global ACC	$U = 437.00$[d]	.001	$t(47) = 4.16$	<0.001
fMRI task global RT	$t(75.89) = -3.28$[d]	.002	$t(47) = -3.85$	<0.001

Notes. Data are presented as mean (SD) if not indicated otherwise. Reading fluency score (percentiles) and raw values (number of correctly reads items/minute) measured with Salzburger Lese- und Rechtschreibtest II, nonverbal IQ measured with Reynolds Intellectual Assessment Scales, risk score measured with adult reading history questionnaire ARHQ (Lefly and Pennington, 2000). In case of non-normally distributed data, Mann-Whitney-U tests were used as test statistic. Handedness based on Edinburgh handedness scale (Oldfield, 1971); in case of ambidexterity, the writing hand is reported. [a] Risk score missing for two participants. [b] Handedness for one ambidextrous subject declared here as right-handed. [c] Nonverbal IQ scores are missing for one participant due to early termination of the study. [d] FMRI task performance data missing for one advanced and two beginning TR. Global fMRI task performance measures (ACC and RT) reflect the mean performance across all four conditions. Significance threshold $p<.05$. Abbreviations: TR, children with typical reading skills; DYS, children with dyslexia; RL, reading-level matched design; ACC, accuracy; RT, reaction time; beg., beginning; adv., advanced; Dev, developmental design.

mittee of the Canton of Zurich and neighboring Cantons in Switzerland.

2.2. Group matching

To disentangle the effects of reading skills, reading experience and developmental effects on the connectivity between regions of the reading network, four different analyses were conducted: one with an age-matched design, one with a reading-level-matched design and two with developmental designs. For the four analyses, the matching was done as follows. Based on a combined score of word and pseudoword reading fluency, measured with the Salzburger Lese- und Rechtschreibtest II (SLRT-II, (Moll and Landerl, 2010)), participants were grouped into TR (>25th percentile) and DYS (<16th percentile) readers. In a first step, all DYS 5th graders ($n = 25$) were matched to TR 5th graders based on their age range and mean age. The age-matched control group ($n = 35$) thus included all TR in fifth grade within the age range of the youngest to the oldest DYS participant. In a second step, the same DYS 5th graders were matched to younger, beginning TR based on their mean raw SLRT-II word and pseudoword reading score to form the reading-level-matched group. Congruent to the age-matching, the raw SLRT-II score of the DYS defined the range for the reading-level-matched control group ($n = 22$) and the two groups were matched based on their mean values. All beginning TR irrespectively of their raw reading fluency score ($n = 48$; beginning TR of the reading-level-matched group enlarged with additional children) and the advanced TR from the age-matched design formed the TR developmental groups. Lastly, all beginning DYS irrespectively of their raw reading fluency score ($n = 24$; not in any of the other groups) and the advanced DYS from the age-matched design formed the DYS developmental groups. Our analyses were thus based on the following groups: 60 subjects (25 DYS, 35 TR) for the age-matched design, 47 subjects (25 DYS, 22 TR) for the reading-level-matched design, 83 subjects

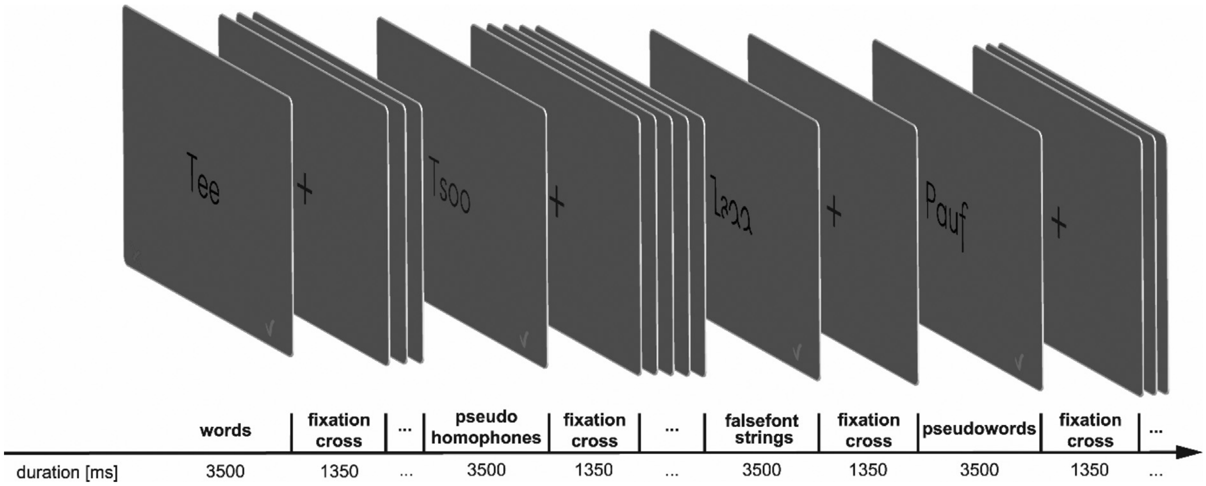

Fig. 1. Phonological lexical decision task with the conditions words, pseudohomophones, falsefont strings and pseudowords, left to right. Mini blocks depicted in figure, but durations shown for singular events. Tee: German for tea, Tsoo: Pseudohomophone for German word “Zoo” (English “zoo”).

(TR, 35 advanced, 48 beginning) for the developmental design with TR, and 49 subjects (DYS, 25 advanced, 24 beginning) for the developmental design with DYS. Of the 49 DYS, 29 received an official dyslexia diagnosis by a psychologist, doctor or speech therapist (9/24 in the beginning reading group, 20/25 in the advanced reading group). It is important to note that there is a large regional heterogeneity of whether children do or do not receive official dyslexia diagnoses during their elementary school years in Switzerland, and if so, then such diagnoses are often given towards the end of elementary school. The discrepancy between official diagnosis and categorization as dyslexic in the current study is therefore unsurprising, especially for the younger children. All children without official diagnosis, however, performed below the 10th percentile in at least one of the two reading measures (word or pseudoword reading fluency) and thus would qualify for a dyslexia diagnosis. Group characteristics and matching parameters can be found in Table 1.

2.3. Experimental design

During fMRI acquisition, participants completed a 6-min phonological lexical decision task (Fig. 1), similar to the tasks used by Kronbichler et al. (2007) and van der Mark et al. (2009). The task consisted of four conditions: Words (W, e.g. “Tee”), pseudowords (PW, e.g. “Pauf”), pseudo-homophones (PH, e.g. “Tsoo”, the pseudohomophone for the German word “Zoo” (English “zoo”); note that pseudohomophones sound like real words, but are written differently) and falsefont strings (FF, e.g. “lɘɑɑ”). Stimuli were all based on German monosyllabic, highly frequent concrete words with three or four letters (type-frequency absolute based on ChildLex (Schroeder et al., 2015): 1161.2 (2690.6), range 4–10,472). For the PH condition, the words from the W condition were changed in a way that they still sounded like the same real word, but were spelled differently. All conditions were matched based on the number of letters ($t(14) < 0.001$ and $p = 1.0$ for all paired t-tests). W and PH conditions were matched in terms of summated bigram frequency ($t(14) = 1.057$, $p = .308$). PW were created by rearranging either the letters of a W or a PH stimulus to obtain a nonexistent pseudoword matched in summated bigram frequency to W ($t(14) = 1.666$, $p = .118$) and PH ($t(14) = 0.061$, $p = .953$). Lastly, the FF condition was written in a font created out of letters of the Latin alphabet (with parts of the letter rearranged to create the falsefont) and contained a balanced number of W, PW and PH. For the task, participants were instructed to press one button whenever the stimulus sounded like a real word (W, PH) and another when it did not (PW, FF). Participants did not receive feedback concerning their responses. We presented 15 trials per condition. They were structured in mini blocks of one to three trials of the same condition, which were presented in a fixed pseudo-randomized order, with condition order and response button mapping balanced between participants. After 15 trials (respectively eight mini blocks), a resting period of 5000 ms was inserted. Stimuli were presented in black in the middle of a gray background (RGB 128, 128, 128) using goggles (VisuaStimDigital, Resonance Technology, Northride, CA) and the presentation software Presentation® (Version 16.4, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). The participants practiced the task outside of the scanner before the fMRI session and were reminded of the task once again directly before the task itself via intercom.

2.4. FMRI data acquisition and preprocessing

MRI recordings took place in a Philips Achieva 3T scanner (Best, The Netherlands) using a 32-channel head coil. Functional images were acquired with a T2* weighted whole-brain gradient echoplanar image (EPI) sequence (5 dummy scans followed by 366 dynamic scans, repetition time TR = 1 s, echo time TE = 30 ms, 36 slices, voxel size = $3.0 \times 3.0 \times 3.5$ mm^3, matrix size 64×62 px, flip angle 65°, no gap, multiband-factor = 2, SENSE-factor = 2). T1 weighted images used for coregistration were recorded using a magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence with the following parameters: TR = 6.8 ms, TE = 3.2 ms, aligned at AC-PC, flip angle = 9°, voxel size = $1.0 \times 1.0 \times 1.0$ mm^3, field of view = 270×255 mm^2, number of slices = 176.

For preprocessing and analysis, the MATLAB (version R2017a) toolbox SPM12 (v7219) was used. Preprocessing included slice-time correction, realignment, coregistration and segmentation. For normalization, a pediatric template was created using Template-O-Matic toolbox (average structural data with the mean age of 10.0 years; (Wilke et al., 2008)). After the described preprocessing steps, we applied smoothing with an 8-mm full width at half maximum (FWHM) Gaussian kernel and resampled to isometric $3 \times 3 \times 3$ mm^3 voxels. Using linear interpolation between the nearest unrepaired scans of the ArtRepair toolbox (Mazaika et al., 2007), we repaired volumes with scan-to-scan motion exceeding 1.5 mm. Head movement, measured with framewise displacement, did not differ between the groups within the four designs (see Supplementary Information, subsection 8.1 for details). Volumes without movement surrounded by bad scans (motion > 1.5 mm) were flagged. Data sets containing more than 10% repaired and flagged volumes were not considered for further analysis ($n = 7$).

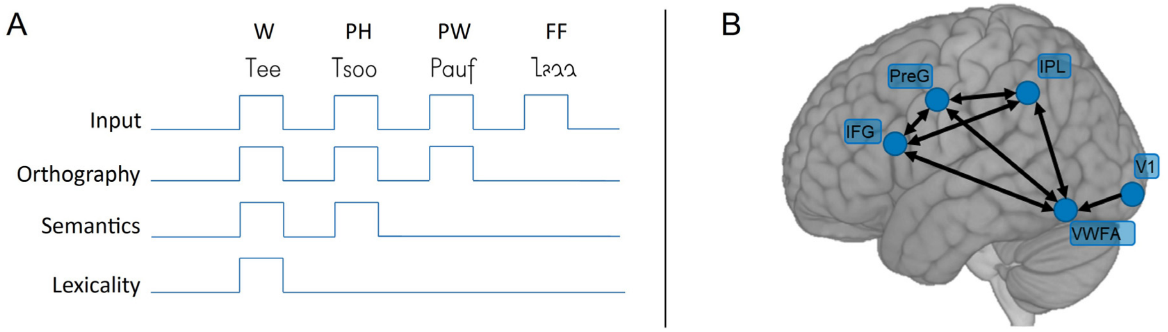

Fig. 2. A) Parametrization of modulatory input of the DCM model (B-matrix). Abbreviations: W, words; PH, pseudohomophones; PW, pseudowords; FF, falsefont strings. B) Effective connectivity model. Anatomical localization of the investigated brain regions in the left hemisphere. Abbreviations: IFG, inferior frontal gyrus; PreG, precentral gyrus; IPL, inferior parietal lobule; VWFA, visual word form area; V1, primary visual cortex.

2.5. Task performance

Task performance in the MR scanner was assessed by measuring average response-time (RT) and accuracy (ACC) per condition. Due to technical problems, behavioral data is not available for three TR. Unpaired t-tests and Mann-Whitney-U tests (in case of non-normally distributed data) were used to analyze performance differences with SPSS (Version 24.0, Armonk, NY: IBM Corp.).

2.6. Dynamic causal modeling (DCM)

For the current study, we performed a dynamic causal modeling (DCM) analysis to investigate effective connectivity differences between TR and DYS in the reading network. For the DCM analysis, the four conditions were combined for the first-level analysis to reflect four different levels of the reading process (see also Fig. 2A): W, PH, PW and FF formed the input condition. The condition “orthography” included all readable stimuli, i.e. W, PH and PW. Next, the stimuli with phonological representations matching a lexical entry were combined as “semantic” condition and included W and PH. Lastly, the condition “lexicality” was formed by the orthographically accurate word stimuli.

Regions of the reading network in the left hemisphere were chosen based on previous studies (Cao et al., 2008; Morken et al., 2017; Wise Younger et al., 2017) and included V1 (−17, −93, −6 mm [MNI]) as input region, the VWFA (−38, −48, −18 mm [MNI]), the IFG (−56, 12, 15 mm [MNI]), the PreG (−44, 6, 30 mm [MNI]) and the IPL (−40, −48, 42 mm [MNI]), see Fig. 2B. To extract the individual time series, a threshold of $p<.05$ was administered, and the data were extracted within an 8 mm radius extraction sphere in a 12 mm radius spherical search volume around the participants maxima from the word>baseline contrast (V1), and the pseudohomophone>baseline contrast (VWFA, IFG, IPL, PreG), based on activations from a group-level one-sample *t*-test. The input condition, comprised of all four stimulus-types, was the driving input for the primary visual cortex (V1; C matrix). From the V1, direct forward connections were modelled to the VWFA only. For all other regions, we modelled feedforward as well as feedback connections (A matrix). Lastly, we included orthography, semantics and lexicality as modulators on all feedforward and feedback connections in the model (B matrix).

The group comparisons of the DCM analysis were conducted within the Parametric Empirical Bayes (PEB) framework (Zeidman et al., 2019, 2019). The second-level PEB model comprised of the individual first-level DCM parameters, and was used to identify differences between TR and DYS in a) the age-matched design, b) the reading-level-matched design and between advanced and beginning TR in c) the developmental design within TR and d) the developmental design within DYS. For all four designs, analyses were performed for intrinsic connections (A matrix), as well as modulatory influences on these connections (B matrix). After setting up the model, Bayesian model reduction was used to discard the model parameters not contributing to the model evidence. After this, a Bayesian Model Average (BMA) was calculated over all models, the average of the parameters weighted by the models’ posterior probabilities. Each PEB model parameter exceeding a 95% posterior probability based on the model evidence was deemed significant. Since the inference is about an effect being greater than a specified size instead of it being significantly different from zero, as is the case with classical inference, there are no false positives. This means that the posterior probability for each connection is the same, irrespective of whether all the connections are analyzed or not, and it is therefore not necessary to adjust the p values (Friston et al., 2003; Friston and Penny, 2003).

3. Results

Behavioural performance in the task was in general high across all groups and conditions (cf. Table 1 and Table S1), and did not differ between groups for the reading-level-matched design for either accuracy or reaction time. Beginning readers did perform worse than their respective advanced peers in both accuracy and reaction time, as did DYS compared to TR of the same age. More detailed behavioral task performance analyses per condition can be found in Table S1.

For the effective connectivity analyses, we first analyzed the connectivity within the reading network independent of the groups. These average connectivity analyses across groups mainly showed a general positive connectivity and thus an excitatory influence between the VWFA and all other regions of the reading network, while the connections from the IPL had an inhibitory influence to the other regions of the reading network. The results of this analysis can be found in Table S2 and Figure S1. Second, we analyzed the group effect in those four designs separately. We analyzed the effect of a) reading ability in the same age group (age-matched design), of b) reading experience independent reading ability in reading matched participants (reading-level-matched design), of c) TRs’ development (Developmental TR) and of d) DYSs development (Developmental DYS) with the same second-level PEB model. Furthermore, we performed an exploratory analysis and included orthography, semantics and lexicality as modulators on all feedforward and feedback connections in the model (B matrix). Last, we investigated the group effects on the connectivity in the right hemispheric equivalents to the chosen regions in exploratory analyses. The analyses mainly showed group differences in the self-inhibitions, a stronger feedforward connectivity between the IPL and the PreG for DYS compared to TR in the age-matched design and a stronger connection from the PreG to the IFG in advanced compared to beginning DYS. The results can be found in the Supplement (chapter 8.5).

3.1. Group effects on the effective connectivity in the reading network

The intrinsic connections (A matrix) were analyzed for all four designs across all conditions. In the age-matched design (cf. Fig. 3A,

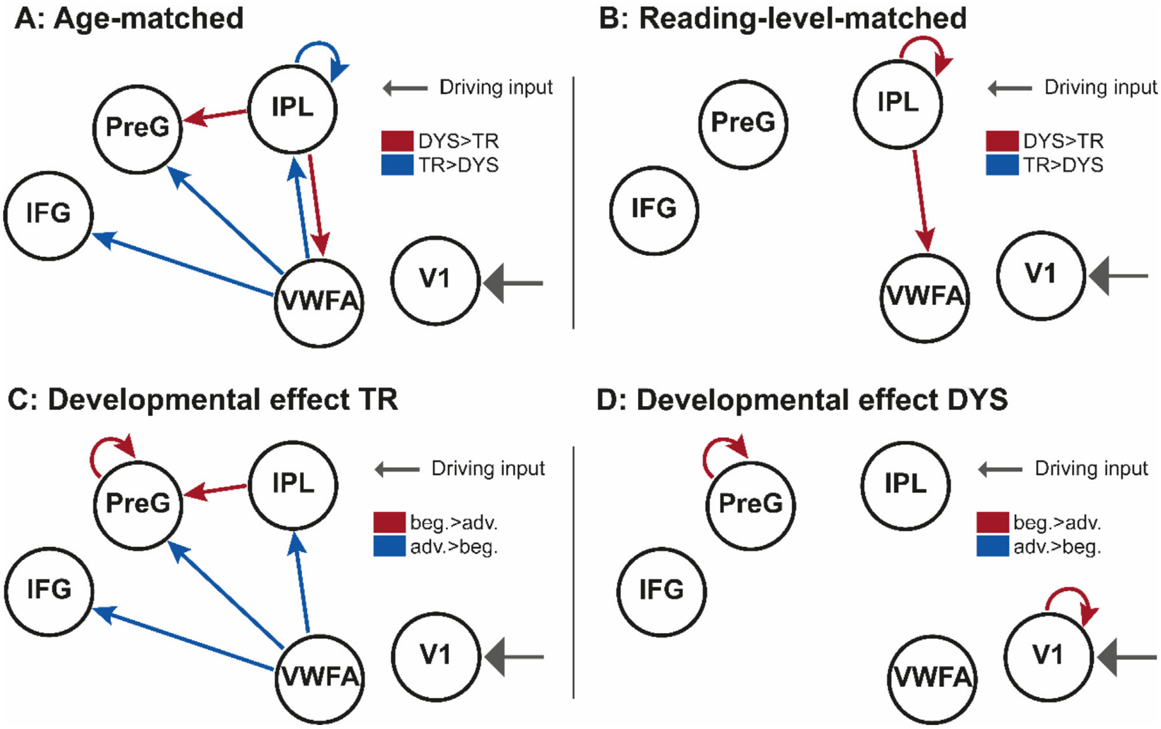

Fig. 3. Results of the DCM analysis within the A) age-matched design, B) reading-level-matched design, C) of the developmental effect in a group of TR, and D) of the developmental effect in a group of DYS. Abbreviations: PreG, precentral gyrus; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; VWFA, visual word form area; V1, primary visual cortex; TR, children with typical reading skills; DYS, children with dyslexia.

Table 2
Influence of group on connectivity obtained by Bayesian model averaging of PEB model parameters.

	Age-matched		Reading-level-matched		Developmental effect TR		Developmental effect DYS	
	Effect size	PP	Effect size	PP	Effect size	PP	Effect size	PP
VWFA → IFG	0.106	1			0.113	1		
VWFA → IPL	0.103	1			0.097	1		
VWFA → PreG	0.157	1			0.146	1		
IPL → PreG	−0.124	1			−0.117	1		
IPL → VWFA	−0.124	0.96	−0.067	0.99				
IPL → IPL	0.140	1	−0.096	1				
PreG → PreG					−0.126	0.98	−0.164	1
V1 → V1							−0.132	1

Notes. n = 60 for age-matched design, n = 47 for reading-level-matched design, n = 83 for developmental effect of TR, n = 49 for developmental effect of DYS. VWFA, visual word form area; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; PreG, precentral gyrus; V1, primary visual cortex; PP, posterior probability; TR, children with typical reading skills; DYS, children with dyslexia.

Table 2), Bayesian model averaging revealed stronger feedforward connectivity from the VWFA to all three other regions, IPL, PreG, and IFG, for TR compared to DYS. Additionally, the results showed stronger, less inhibitory feedback connectivity from the IPL to the VWFA for DYS than for TR, and stronger feedforward connectivity between the IPL and the PreG for DYS compared to TR. Lastly, there was a stronger self-inhibition of the IPL for TR compared to DYS of the same age.

In line with the results of the age-matched design, Bayesian model averaging in the reading-level-matched design (cf. Fig. 3B, Table 2) showed stronger, less inhibitory feedback connectivity from IPL to the VWFA for advanced DYS compared to beginning TR. In contrast to the age-matched design, the self-inhibition of the IPL was stronger for advanced DYS than for beginning TR.

The feedforward connectivity between the VWFA and all three other regions, IPL, PreG and IFG, was stronger for advanced compared to beginning TR (cf. Fig. 3C, Table 2). Moreover, the feedforward connectivity between the IPL and the PreG was stronger for beginning than for advanced TR. Additionally, there was a stronger self-inhibition of the PreG for beginning compared to advanced TR. For DYS, two self-inhibitions showed a significant developmental effect: The self-inhibition of the PreG and the V1 were stronger for beginning DYS than advanced DYS (cf. Fig. 3D, Table 2).

3.2. Modulatory effects of orthography, semantics and lexicality on the connectivity in the reading network

For the age-matched and reading-level-matched design and the developmental design of TR, we found a significant modulation of orthography on several connections between the reading network regions (see Fig. 4, Table 3). The modulatory influence of orthography on the connection between the PreG and the IPL was stronger for DYS than TR in the age-matched design. In the same design, the modulatory effect of orthography on the connection between the IPL and the VWFA was stronger for TR than DYS. Lastly, there was a stronger modulatory ef-

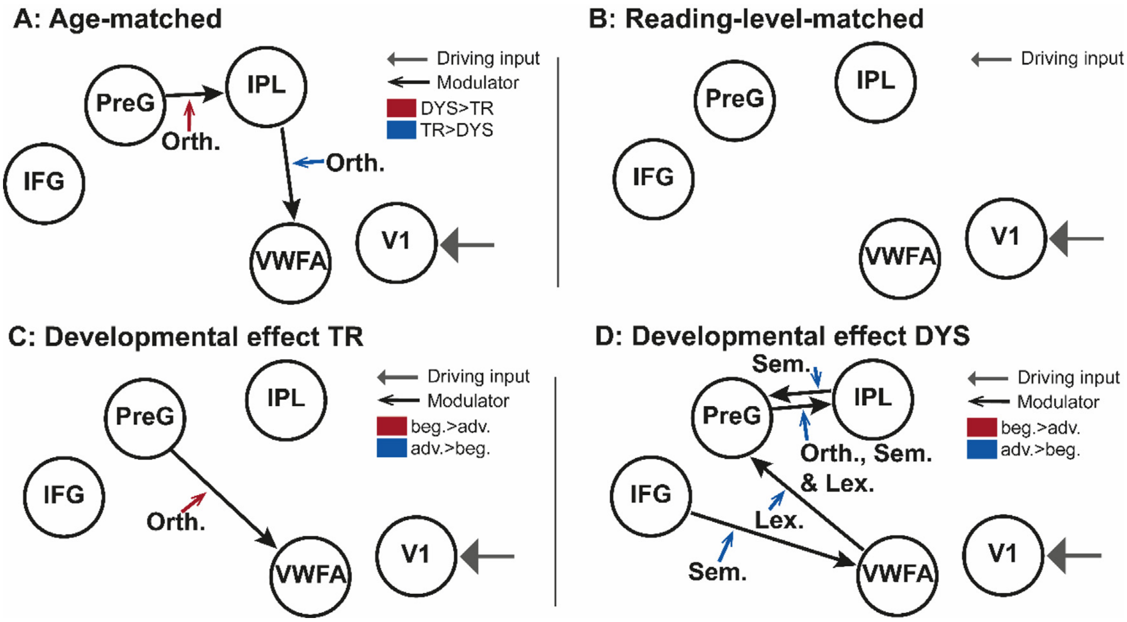

Fig. 4. Modulatory effect of task on the connections of the reading network in the A) age-matched design, B) reading-level-matched design, C) of the developmental effect in a group of TR and D) developmental effect of DYS. Abbreviations: PreG, precentral gyrus; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; VWFA, visual word form area; V1, primary visual cortex; TR, children with typical reading skills; DYS, children with dyslexia; sem., semantics; orth., orthography; lex., lexicality.

Table 3
Modulatory effects.

	Age-matched		Reading-level-matched		Dev effect TR		Dev effect DYS	
	Effect size	PP	Effect size	PP	Effect size	PP	Effect size	PP
Modulatory effect of orthography								
PreG → IPL	−0.484	1					0.414	1
IPL → VWFA	0.493	0.99						
PreG → VWFA					−0.541	1		
Modulatory effect of lexicality								
PreG → IPL							0.219	1
VWFA → PreG							0.215	1
Modulatory effect of semantics								
IPL → PreG							0.226	1
PreG → IPL							0.310	1
IFG → VWFA							0.437	1

Notes. n = 60 for age-matched design, n = 47 for reading-level-matched design, n = 83 for developmental effect of TR, n = 49 for developmental effect of DYS. VWFA, visual word form area; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; PreG, precentral gyrus; V1, primary visual cortex; PP, posterior probability; TR, children with typical reading skills; DYS, children with dyslexia; dev, developmental.

fect of orthography on the connection between the PreG and the VWFA for beginning than for advanced TR in the developmental design. No modulation was found by semantics or lexicality. For the developmental effect in DYS, there was a stronger modulatory effect for advanced readers than for beginning readers in the following connections: Between the PreG and the IPL for orthography, lexicality and semantics, between the VWFA and the PreG for lexicality and between the IPL and the PreG, and the IFG and the VWFA for semantics.

4. Discussion

In this study, we examined the effective connectivity of the reading network during an explicit phonological lexical decision task. Using age-matched, reading-level-matched, and developmental designs, we were able to disentangle the effects of dyslexia from those of reading experience and age on connectivity. The study revealed two main findings: dyslexia-specific differences in the feedback connection from the IPL to the VWFA, and age-dependent and reading-experience-dependent feedforward connectivity from the VWFA to other areas of the reading network. All findings are discussed in detail in the next sections.

4.1. Altered feedback connection from the IPL to the VWFA in children with dyslexia

First, we found dyslexia-specific differences in the feedback-connectivity between the IPL and the VWFA. This connection was less inhibitive in DYS than in TR, independently of age or reading experience. The IPL has been associated with general attentional processes (Vidyasagar, 1999), is recruited when linking letters with speech sounds (Blomert, 2011; Bonte et al., 2017; Xu et al., 2020) and therefore crucial for letter-by-letter reading (Pugh et al., 2001; Sandak et al., 2004). The dyslexia-specific top-down feedback connection from the IPL to the VWFA might represent altered reliance on input from the IPL during reading acquisition in DYS compared to TR. The average connectivity analyses (as detailed in the Supplement) indicated that the feedback connectivity from the IPL to the VWFA acts as an inhibitory connection. Increased connectivity between IPL and VWFA in children with dyslexia can therefore be interpreted as evidence of less inhibition of the VWFA upon activation of the IPL. This may support the hypothesis that these children rely on a more effortful serial, letter-by-letter processing strategy of written input, by guiding attention sequentially to the letters comprising the units of visual input for further decoding. Whether this alteration is part of an emerging compensatory process to support reading (Zhou et al., 2016) or may instead negatively affect the development of fluent sight word reading in children with dyslexia cannot be disentangled with the current study design and needs to be addressed in future studies. Interestingly, a recent study on white matter fiber tracts showed structural alterations in the vertical occipital fasciculus connecting the parietal lobule and ventral occipitotemporal regions in adults with dyslexia. The authors suggested that such structural alterations in the connectivity of this tract may impede the transformation of written information on both the ventral and the dorsal reading pathways (Sihvonen et al., 2021). This result may elicit the hypothesis that the altered effective connectivity in dyslexia, as measured in this study, could be explained by structural alterations in the corresponding fiber tracts. Previous studies have more generally shown increasing fractional anisotropy in some of the core white matter pathways connecting the regions of the reading network, such as the arcuate and the inferior longitudinal fasciculi, with growing age and reading experience and skills (Lebel et al., 2019; Vanderauwera et al., 2018; Wang et al., 2017). Importantly, experience-dependent changes in white matter properties can develop rapidly, within weeks, as a result of reading intervention in children (Huber et al., 2018). Interestingly, a recent study found no association between functional anisotropy and reading skills, but did find an association between poorer reading performance and greater myelination in pathways of the reading network, quantified by myelin water content (Economou et al., 2022). Taken together, these findings suggest the need for a more thorough investigation of the relation between reading, development and measures of structural and functional (including effective) connectivity.

Importantly, previous studies have shown that the functional selectivity of the VWFA is predetermined by earlier-developing connections with the rest of the brain (Saygin et al., 2016). Its coupling to language and attention networks allows top-down input from the dorsal attention network, which is especially important during effortful letter-by-letter processing (Chen et al., 2019; Vogel et al., 2012). However, findings on the quality of the connectivity between IPL and VWFA in individuals with dyslexia remain mixed. Some studies reported diminished functional connectivity to and from parietal regions, such as the angular gyrus, in individuals with dyslexia (Cao et al., 2008; Hampson et al., 2006; Horwitz et al., 1998; K. R. Pugh, Mencl, Shaywitz, et al., 2000; van der Mark et al., 2011). Others report a negative association between lexical processing and functional connectivity between the VWFA and inferior parietal regions, supporting the argument that proper word processing may necessitate the additional deployment of attentional control, especially in poor readers (Zhou et al., 2016). A compensatory mechanism in young DYS may support serial decoding by shifting attention from letter to letter within a string (Richlan, 2014), even though this strategy may not be the most efficient in terms of reading fluency. From this perspective, our findings may imply that the altered IPL-VWFA connectivity supports reading in children with dyslexia, but at the same time promotes a suboptimal strategy by constraining children's attentional focus to letter-by-letter processing and word decoding rather than the more efficient sight word reading. Alternatively, we may also argue that the altered IPL-VWFA connectivity is a consequence of deficient function in the dorsal and/or ventral pathways in dyslexia. The often-reported hypoactivation of the IPL may relate to impairments in mapping the letters onto phonological units, controlled by attention (Richlan et al., 2009) and consequently to deficient decoding abilities in children with dyslexia. Likewise, the consistent hypoactivation of the ventral pathway in dyslexia, and the VWFA in particular, is associated with inefficient sight word reading (Maisog et al., 2008; Richlan et al., 2009). Whether the reported alteration in connectivity is a potential cause for poor reading, a consequence of the decoding problems or a compensational mechanism in dyslexia remains to be examined in future studies. Importantly, these connections might additionally show a distinct developmental trajectory and thus depend on the age and reading stage. A recent review suggested that the endpoints of specific white-matter pathways may guide the emergence of functional specialization in either anterior or posterior parts of the VWFA (Caffarra et al., 2021). The posterior part of the VWFA, which is involved in perceptual aspects of print processing and therefore especially relevant at the beginning of reading acquisition, might be predefined by the left vertical occipital fasciculus connecting the vOT to parietal regions, while the anterior part of the VWFA, which is involved in linguistic processes and important especially in advanced reading stages, is guided by pathways such as the arcuate fasciculus connecting frontotemporal areas. With reading acquisition, gains in fluency, and a change from decoding to sight word reading, the reliance on posterior VWFA contributions may diminish, while the engagement of more anterior regions of the VWFA may increase. In children with dyslexia, however, this process may be delayed or impaired as they continue to rely on the less efficient decoding strategy based on letter-by-letter reading. Likewise, task demands might influence the connections between the VWFA and the dorsal attention network: The VWFA's activation may be modulated differently by top-down connections, depending on reading experience and on the current reading stage and strategy (Brem et al., 2020). Our exploratory analysis of the modulatory effects of orthography on brain connectivity confirms and extends this finding by showing a stronger influence on the IPL-VWFA feedback connectivity in TR when they are forced to use the dorsal decoding pathway to read pseudohomophones or pseudowords.

4.2. Feedforward connections from the VWFA to other areas in the reading network develop with age and reading skills

Second, we confirm previous studies showing reading performance-dependent differences in the connections between brain regions of the reading network, such as the VWFA, IFG, IPL, and PreG (Morken et al., 2017; Wise Younger et al., 2017) in children. More specifically, our data suggest that excitatory feedforward connections from the VWFA to other areas within the reading network are especially important for the efficient and fluent reading process: Children with poorer reading performance showed weaker connectivity, regardless of whether they were less experienced due to their younger age, as in the developmental design of TR, or due to specific reading impairments as in the age-matched design. Thus, a higher excitatory connectivity from the VWFA to other network regions might be associated with successful and more efficient word recognition processes as shown by the parallel increase in reading speed with expertise. This alteration in the feedforward connectivity from the VWFA to other language areas may thus also lay the base for a successful shift from the dorsal decoding to ventral sight word reading strategy. Our developmental design of TR demonstrates that this process appears to develop within the first few years of reading experience (McCandliss et al., 2003; Pugh et al., 2001).

Moreover, our results suggest that the reading impairments of the advanced DYS may be explained by an absent, reduced, or delayed shift from the dorsal to the more efficient ventral reading pathway; these children neither showed the same forward connectivity between the VWFA and other language regions, nor did they show major developmental differences in these connections compared to the TR controls. All modulators such as semantics, lexicality, and orthography had a stronger influence on specific connections between areas of the reading network in more advanced than in beginning DYS. This might indicate that the task requires more engagement from DYS due to suboptimal or delayed development of the connections within the reading network. A delay in the development of connectivity within the reading network has previously been suggested in a longitudinal study by Morken et al. (2017). In their study, similar age-groups of children were followed longitudinally. Children with and without reading difficulties showed different connectivity patterns mainly during the early years of reading instruction. However, these differences then disappeared between advanced readers, therefore suggesting only a delay in the development of connectivity.

4.3. *Covert articulatory rehearsal may explain altered connectivity from and to the PreG in younger age and with lower reading skills*

Another difference between children with more and less reading experience across the typical developmental and age-matched designs was the altered connectivity between the IPL and the PreG for less experienced readers. In addition, orthography modulated the PreG-IPL connectivity more strongly in DYS than TR and more so in the advanced reading stage of DYS. It is important to note that the feedforward connectivity from the IPL to the PreG was again inhibitory, suggesting more activation in the PreG with less inhibition from the IPL. Activation in the PreG has previously been associated with covert articulatory processes (Hancock et al., 2017; Richlan, 2012), which seem especially important for beginning readers and reading-impaired individuals that are not yet able to recognize the stimuli without letter-to-letter reading (Brem et al., 2020; Richlan, 2014). In contrast to the aforementioned feedback connection between the IPL and the VWFA, the feedforward connection between the IPL and the PreG seems to depend on development and reading experience rather than being specific to a disorder. It is important to note that our task included the reading of pseudohomophones, pseudowords and words. Therefore, both the dorsal and the ventral pathways remain important for task performance and the developmental alterations in connectivity may not only lay the base for a shift to more fluently process words but also for decoding pseudowords. Levy et al. (2009) found that whether the reading strategy relies on the dorsal or the ventral stream is related to reading skill, suggesting that there is an optimal pathway for the task at hand, and reliance on the preferable pathway is related to more advanced reading skills. Moreover, because the IPL has been shown to be involved in the control of visual attention (Grainger and Ziegler, 2011; Pammer et al., 2006; Vidyasagar, 1999), it is especially relevant during the earliest reading stage, when children need attention to disambiguate letters (Dehaene et al., 2010) and focus on a text. It is therefore not surprising that feedforward connections between the IPL and PreG were stronger in beginning readers than in advanced readers and in DYS than in TR of the same age, suggesting stronger reliance on the dorsal stream and visual attention than the ventral stream of the reading network in beginning and struggling readers. Likewise, the higher modulation of the feedback connectivity between the PreG and the IPL in DYS may indicate the greater necessity to use subvocal rehearsal processes for task accomplishment. Finally, phonological demands also modulate the feedback connectivity of the PreG to the VWFA more strongly in beginning TR than advanced TR. Taken together, these results again indicate a prolonged dependence on the dorsal processing stream in children with dyslexia, whereas children with typical reading skills start relying on and benefitting from the ventral stream early during reading development. In tasks with high phonological demands, however, the top-down feedback from PreG to the VWFA may also support performance in young children with typical reading skills.

4.4. *Self-inhibitory connections in the IPL and the PreG*

Additional findings concern the self-inhibitory connections of the IPL and the PreG. Self-inhibition indicates a region's sensitivity to input from the network. The age-matched design showed that self-inhibition in the IPL increases with reading skill and the reading-level-matched design showed it to be stronger in more advanced DYS than in beginning TR. This finding suggests that the IPL in advanced readers with typical reading skills is the least sensitive to input from other regions of the reading network, followed by advanced readers with dyslexia, and that it is the most sensitive in beginning readers with typical reading skills. This stepwise decrease in sensitivity with increasing age and reading skill is another indication of a decline in reliance on the dorsal stream for print processing. With further expertise, the dorsal stream, and with it the IPL, becomes less important for the reading process (K. R. Pugh, Mencl, Jenner, et al., 2000; Pugh et al., 2001; Sandak et al., 2004) and might therefore become less sensitive to input from other brain regions. Surprisingly, the self-inhibition of the PreG was higher in beginning TR than in advanced TR. With a shift to reliance on the ventral stream from the dorsal stream with age, we would expect the self-inhibition of the PreG to increase with age, similarly to the IPL. Whether this unexpected shift in PreG self-inhibition may be explained by the task and potential changes in covert articulatory processes to perform phonological lexical decisions will need to be examined in future studies.

4.5. *Limitations and outlook*

Despite the fact that the total sample size in our study is large for a pediatric neuroimaging protocol, the complex matching process reduced the group sizes to between 22 and 48 children per group. As is common in pediatric studies with young children, the small final group sizes may limit the statistical power of the current study (Chyl et al., 2019; Morken et al., 2017; Schulz et al., 2009). Nonetheless, the effects observed in our study are strong enough to be detectable even with the rather limited sample size.

Future studies could combine a reading-level-matched design with a longitudinal design to better account for individual differences in developmental trajectories (Chyl et al., 2021; Goswami and Bryant, 1989). Our exploratory analysis of the modulatory effects of semantics, orthography, and lexicality on the various connections in our models adds interesting insights into how task demands influence the connectivity between regions across groups and with development. However, a limitation of these analyses is that the number of trials across the three modulators is not equal. This may also explain why modulatory effects were mainly detected for the orthographic decisions with most trials. Future studies should address this potential bias to better disentangle the specific contributions of semantics, lexicality, and orthography. Nonetheless, the present study combining age-matched with reading-level-matched and developmental analyses in both TR and DYS is unique and provides important evidence for connectivity differences in the reading network of children with dyslexia and for the development of the neural circuitry of reading in both children with dyslexia and children with typical reading skills.

Future studies working with interventions based on neuroscientific findings such as neurofeedback (Koush et al., 2013; Sulzer et al., 2013) should address the question of whether the training of specific regional circuits such as the connectivity between the IPL and the VWFA might actually support reading skills.

5. Conclusion

This is the first study to disentangle developmental and experience-based differences between children with typical reading skills and children with dyslexia concerning effective connectivity in the reading network. We were able to show that the connections from the VWFA to frontal and parietal regions of the reading network are strengthened with age and reading experience, whereas the feedback connection from the IPL to the VWFA reflects a dyslexia-specific difference in the reading network in children with dyslexia. This altered connection between IPL and VWFA for children with dyslexia is independent of their age and might therefore be a marker for dyslexia. Further studies should confirm this finding, which may also provide a target for neurotherapeutic interventions.

Data and code availability

The data and code supporting the conclusions of this article will be made available by the corresponding author upon reasonable request. Some restrictions may apply for data sharing due to the restricted consent of research participants.

Declaration of Competing Interest

None. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential competing interest.

Credit authorship contribution statement

Sarah V. Di Pietro: Conceptualization, Data curation, Formal analysis, Methodology, Investigation, Software, Writing – original draft. **David Willinger:** Methodology, Software, Writing – review & editing. **Nada Frei:** Investigation, Writing – review & editing. **Christina Lutz:** Conceptualization, Writing – review & editing. **Seline Coraj:** Conceptualization, Writing – review & editing. **Chiara Schneider:** Investigation, Writing – review & editing. **Philipp Stämpfli:** Methodology, Writing – review & editing. **Silvia Brem:** Conceptualization, Project administration, Supervision, Funding acquisition, Writing – original draft.

Data Availability

The data and code will be made available by the corresponding author upon reasonable request. Some restrictions may apply due to the restricted consent of research participants.

Funding

This work was supported by Fondation Botnar (grant: 6066) and the University Research Priority Program Adaptive Brain Circuits in Development and Learning at the University of Zurich (Project ChildBrainCircuits).

Acknowledgements

We thank all families and children for participating in this study. Additionally, we thank Rebecca Eva Hefti, David Tanner, Alexandra Brem, Jasmin Neuenschwander, Patrick Haller, Salome Häuselmann, Selina Schuehle, Iliana I. Karipidis, Gorka Fraga-González, Yu Jin Ressel, Carina Wick, Livia Haag and Sharon Schwarz for their contributions to recruitment, data collection, and their valuable input.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.119869.

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