

Atypical neural activation and age-related patterns in dyslexia

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This magnetoencephalography study investigated the spatiotemporal neural responses during single-word reading. We used a silent reading task with linguistic stimuli varying in lexicality and frequency (high- and low-frequency words, and pseudowords), and tested typically developing (TD) and dyslexic developing (DD) children (aged 7 to 12). We observed no significant sensitivity to word frequency or lexicality either within or between the groups, likely reflecting the constraints of the silent reading paradigm. Direct comparisons between the groups revealed significant amplitude reductions in the DD group across the bilateral occipito-temporal and left superior temporal cortices. Despite these reduced signal amplitudes, the inter-hemispheric relationship of peak latencies (PLs) in the DD group remained consistent with the TD pattern. Furthermore, within the TD group, we identified a clear relationship between age and PL: older typical readers exhibited decreased latencies in the left hemisphere, pointing to the age-related automatization of the reading network. In contrast, we did not observe this age-related pattern in the DD group, which highlights a functional atypicality that remains evident across the investigated age range. Overall, these findings indicate that the core neural atypicality in dyslexia involves reduced activation strength and an absence of typical age-related PL decreases, rather than a fundamental overall shift in PL.

Keywords magnetoencephalography (MEG), single word reading, reading development, word frequency, developmental dyslexia

Introduction

Reading acquisition is 1 of the most critical aspects of a child's development. Despite constant access to print and standard education, children with developmental dyslexia (DD) fail to develop sufficient literacy skills. Uncovering the neural mechanisms of atypical reading development will help to advance early identification and intervention (Shaywitz et al. 2006; Noordenbos et al. 2013). While behavioral tests capture the end-product of reading, neurophysiological methods like magnetoencephalography (MEG) track the ongoing neural processes with high spatial and temporal precision (Salmelin 2007). By analyzing Event-Related Fields (ERFs), 1 can compare typically developing (TD) children and those with DD to identify specific neural markers of the reading disorder.

Drawing on a foundational cognitive model of reading, the dual-route cascaded model (Coltheart et al. 2001), MEG studies have established a consistent spatiotemporal framework of reading (Tarkiainen et al. 1999; Salmelin 2007). According to this neurophysiological framework, the cortical dynamics involve a sequence of 3 functional components: visual feature analysis, letter-string analysis, and lexical-semantic analysis.

The first component, visual feature analysis, consistently appears during reading in adults as an early component peaking

approximately 100 ms after stimulus onset in the midline occipital cortex (Tarkiainen et al. 1999; Cornelissen et al. 2003). Functionally, this neural response in the occipital cortex reflects the pre-lexical analysis of basic visual features and is insensitive to the lexical or semantic properties of the stimulus (Wyddell et al. 2003; Salmelin 2007). When comparing adult readers with DD to TD controls, the early waveform generally exhibits comparable morphological patterns across both groups during the processing of high-frequency words (HFW) and low-frequency words (LFW) stimuli (Johannes et al. 1995). Specifically, the overall P1/P100 amplitude lacks significant between-group differences and group-by-stimulus interactions. Stimulus effects, however, vary. Araújo et al. (2015) reported greater right-hemisphere positivity for real words in both TD and DD groups. Conversely, Silva et al. (2022) found greater bilateral P100 amplitudes for pseudowords (PW) in DD, whereas TD showed greater left-hemisphere amplitudes for PW and right-hemisphere amplitudes for quasi-words. Neural lateralization findings are equally mixed. Araújo et al. (2015) observed an atypical rightward activity shift in DD and bilateral asymmetry in TD. In contrast, Silva et al. (2022) reported higher right-hemisphere P100 amplitudes across both groups. Turning to developmental studies, this early activation is approximately 1.4 times stronger in TD children than the amplitude observed

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in adults (Helenius 1999; Tarkiainen et al. 1999), while response latencies remain comparable (Parviainen et al. 2006). Notably, studies comparing children with DD to TD controls have consistently reported no significant group differences in this early component across various paradigms, including implicit reading (Araújo et al. 2012) and reading aloud tasks (Trauzettel-Klosinski et al. 2006). This suggests that while the overall early extraction of visual features is unimpaired in children with DD, atypical patterns of neural lateralization may already be present prior to the more pronounced reading deficits that emerge at later stages of processing.

The second component, letter-string analysis, typically maximizes over the lateral parieto-occipital sites at approximately 150 to 170 ms and is sensitive to the orthographic and morphological properties of letter strings (Bentin et al. 1999; Salmelin 2007). Supposedly localized in the Visual Word Form Area, the functional role of this component remains a subject of debate. While some adult studies suggested that this component discriminates solely between orthographic and non-orthographic stimuli without showing sensitivity to lexicality (Bentin et al. 1999; Tarkiainen et al. 1999; Cornelissen et al. 2003), others reported distinct sensitivity to both lexicality and word frequency. For instance, neural responses are modulated by word frequency. HFW elicit weaker responses than LFW (Assadollahi and Pulvermüller 2003; Hauk et al. 2006). Furthermore, amplitude modulations occur when comparing real words to PW. PW typically elicit stronger responses than real words (Hauk et al. 2006; Araújo et al. 2015). When comparing adult readers with DD to TD adults, early between-group differences remain heterogeneous. Some research indicates that early waveforms up to 250 ms do not differentiate between groups based on word frequency (Johannes et al. 1995). Additionally, both groups can exhibit similar left-occipital lexicality effects (Araújo et al. 2015). Conversely, other studies report distinct lateralization patterns. TD adults demonstrate a left-lateralized N170 effect for both lexicality and word frequency, but adults with DD do not show this left-hemispheric asymmetry (Mahé et al. 2013). Instead, the DD response profile is characterized by a right-lateralized frequency effect. Furthermore, Silva et al. (2022) reported a general reduction of N170 amplitudes in the left occipitotemporal region for adults with DD compared to TD adults, accompanied by atypical right-hemisphere lateralization across all stimulus types. Turning to studies involving children, in TD children, this component similarly distinguished letter strings from symbols or false fonts, showing higher amplitudes for word-like stimuli during implicit reading (Maurer et al. 2007; Araújo et al. 2012; Gonzalez et al. 2014) and phonological lexical decision tasks (Hasko et al. 2013). However, regarding within-group condition effects, unlike the findings in adults, these same studies demonstrated that both TD children and those with reading difficulties often showed no significant amplitude difference between real words and PW. Turning to between-group comparisons (TD vs. DD), overall activation during the reading of these stimuli has yielded inconsistent results. While some studies reported no significant overall activation differences between TD and DD children employing an implicit reading paradigm (Araújo et al. 2012; Kemény et al. 2018), phonological lexical decision (Hasko et al. 2013), semantic judgment (Sun et al. 2023), and reading aloud tasks (Trauzettel-Klosinski et al. 2006), others have found reduced overall activation in the DD group compared to TD. Crucially, this reduction has been reported as a general main effect of group across all orthographic stimuli, lacking a group-by-stimulus interaction, during standard and phonological lexical decision tasks (Kast et al. 2010; Bakos et al. 2018). Consequently, the extent to which

early orthographic processing is disrupted in dyslexia remains an open question, highlighting the need for further investigation into the interaction between stimulus features and group differences at this processing component.

The third major reading component involves lexical-semantic analysis, which typically reaches maximal activation around 400 ms in the superior temporal cortex and reflects the integration of lexical, semantic, phonological, and morphosyntactic information (Helenius 1998; Halgren et al. 2002; Salmelin 2007). In adult studies, this component has been shown to exhibit sensitivity not only to lexicality (real words vs. PW) (Salmelin et al. 1996; Wydell et al. 2003; Wilson et al. 2005) but also to word frequency (HFW vs. LFW). Specifically, research demonstrated an inverse relationship between frequency and signal strength: LFW elicited higher amplitudes, while HFW modulated lower amplitudes (Barber et al. 2004; Hauk and Pulvermüller 2004; Kutas and Federmeier 2011; Vergara-Martínez et al. 2020; Silva et al. 2022; Samoylov et al. 2025). When comparing adult readers with DD to TD controls, overall N400 response amplitudes are generally comparable (Johannes et al. 1995; Rüsseler et al. 2003). However, neural responses to specific stimulus properties diverge significantly. While TD readers show the standard greater negativity for PW, adults with DD display an inverted lexicality effect, eliciting more negative amplitudes for real words (Silva et al. 2022). Furthermore, adults with DD exhibit altered frequency modulations, including an absent old/new effect for HFW (Johannes et al. 1995). Turning to studies involving children, findings regarding TD cohorts are less consistent. While some studies reported no significant amplitude differences between real words and PW in lexical decision (Hasko et al. 2013; Bakos et al. 2018), letter identification (Mehlhase et al. 2020), and reading aloud tasks (Trauzettel-Klosinski et al. 2006), others observed higher amplitudes for PW compared to real words during implicit reading (Kemény et al. 2018) and semantic judgment (Sun et al. 2023). Turning to between-group comparisons (TD vs. DD), evidence on overall activation differences during reading is also contradictory: whereas some researchers found no significant overall difference between TD and DD children during phonological lexical decisions (Bakos et al. 2018) or letter identification (Mehlhase et al. 2020), others reported abnormal activation patterns in the dyslexic group when employing phonological lexical decision (Hasko et al. 2013), implicit reading (Kemény et al. 2018), rhyme-matching (Simos et al. 2000b), word recognition (Simos et al. 2000a), or semantic judgment tasks (Sun et al. 2023). Thus, despite increasing interest, results remain inconclusive (for an overview of key parameters and findings from these studies, see Table 1). Moreover, to the best of our knowledge, no study has yet systematically investigated the modulation of word frequency within this component specifically in both TD and DD children.

To address the revealed gaps, the present MEG study examined the spatiotemporal dynamics of word frequency and lexicality processing during silent single-word reading in 2 groups of school-aged children: TD and DD. Stimuli comprised HFW, LFW, and PW, enabling us to probe frequency-sensitive lexical access effects without articulatory confounds. Guided by the established spatiotemporal framework of reading and based on prior research in adults and children, we hypothesized that: (i) word frequency and lexicality would modulate neural activity in both groups, particularly in later processing stages; (ii) the DD group would exhibit distinct neural dynamics compared to TD peers, manifesting as reduced signal amplitude, delayed peak latency (PL), or atypical hemispheric lateralization; (iii) these effects

Table 1 Overview of key parameters and findings from neurophysiological studies on reading in TD and DD children.

Study	Sample (<i>n</i> , mean age)	Experimental paradigm and linguistic stimuli	Target components (time windows)	Key findings
Araújo et al. 2012	TD: 20 (10.7 yr) DD: 20 (10.6 yr)	Task: Implicit reading (repetition detection) Stimuli: High- and LFW, PW	P1 (110 to 160 ms) N1 (180 to 260 ms) N320 (290 to 360 ms)	No significant relevant between-group differences for word/pseudoword processing
Maurer et al. 2007	TD: 22 (6.47 and 8.25 yr) DD: 15 (6.53 and 8.29 yr)	Task: Implicit reading (repetition detection) Stimuli: Words, PW	P1 (55 to 163 ms) N1 (164 to 272 ms)	P1: DD exhibited reduced amplitudes compared to controls across all conditions at occipito-temporal sites Component 3: DD showed delayed latencies
Trauzettel-Klosinski et al. 2006	TD: 13 (114.8 m) DD: 9 (115.7 m)	Task: Reading aloud Stimuli: High- and LFW	Component 1 (130 to 140 ms) Component 2 (170 to 220 ms) Component 3 (235 to 285 ms) Component 4 (360 to 420 ms) Late complex (430 to 530 ms)	
Hasko et al. 2013	TD: 29 (8.15 yr) DD: 52 (8.30 yr)	Task: Phonological lexical decision Stimuli: Words, pseudohomophones, and PW	N170 (170 to 290 ms) N400 (330 to 460 ms) LPC (600 to 900 ms)	N400: TD showed more negative mean peak amplitudes than DD across all conditions LPC: TD (but not DD) exhibited greater activation for words and pseudohomophones compared to PW
Kemény et al. 2018	TD: 18 (9.49 yr) iSD: 11 (9.91 yr) iRD: 6 (9.66 yr) RSD: 8 (9.28 yr)	Task: Implicit reading (catch-trial identity) Stimuli: Words, pseudohomophones, legal and illegal PW	N1 (180 to 230 ms) N400 (310 to 430 ms) LPC (500 to 700 ms; 700 to 900 ms)	N400: Good spellers (TD and iRD) showed significantly higher amplitudes for meaningless (PW) than for meaningful stimuli (words/pseudohomophones). This effect was absent in poor spellers (iSD and cRSD) N400: Nonwords elicited significantly larger negative amplitudes than real words in TD; this effect was absent in DD LPC: TD exhibited significantly smaller amplitudes for nonwords compared to real words
Sun et al. 2023	TD: 29 (9.54 yr) DD: 18 (9.01 yr)	Task: Semantic judgment (target detection) Stimuli: Words, nonwords (target: animal words)	N1 (170 to 270 ms) N400 (250 to 550 ms) LPC (500 to 800 ms)	N400: Nonwords elicited significantly larger negative amplitudes than real words in TD; this effect was absent in DD LPC: TD exhibited significantly smaller amplitudes for nonwords compared to real words
Bakos et al. 2018	TD: 36 (113.94 m) cRSD: 33 (114.21 m) iRD: 21 (115.10 m) iSD: 21 (115.71 m)	Task: Phonological lexical decision Stimuli: Words, pseudohomophones, legal and illegal PW	N170 (130 to 280 ms) N400 (300 to 450 ms) LPC (600 to 1100 ms)	N170: Higher amplitudes in the TD group compared to all affected subgroups (iRD, iSD, cRSD) LPC: TD and iRD showed higher amplitudes for words than pseudohomophones in early time windows (600 to 976 ms). This lexicality effect was delayed (850 to 1100 ms) in cRSD and shortened (600 to 850 ms) in iSD
Kast et al. 2010	TD: 24 (9.92 yr) DD: 36 (10.27 yr)	Task: Lexical decision Stimuli: Words, PW	N170 (220 to 236 ms)	N170: TD exhibited significantly enhanced amplitudes compared to DD when reading PW (bilaterally) and words (left hemisphere)
Mehlhase et al. 2020	TD: 35 (123.29 m) cRSD: 35 (123.80 m) iRD: 17 (123.71 m) iSD: 20 (125.80 m)	Task: Letter identification Stimuli: Words, legal and illegal PW, and nonwords	N200 (160 to 260 ms) N400 (280 to 440 ms)	No significant relevant between-group differences for word/pseudoword processing
Simos et al. 2000b	TD: 10 (8 to 16 yr range) DD: 11 (10 to 17 yr range)	Task: Rhyme-matching Stimuli: PW	Regional activation onsets: Basal temporal cortex (BTC) (~200 to 260 ms) and temporoparietal (TMP) (~270 to 470 ms)	Regional activation: DD showed significantly less activation in the left TMP region and greater activation in the right TMP region compared to TD. DD also displayed significantly delayed onset latencies in the left TMP and right BTC.

(continued)

Table 1 Continued.

Study	Sample (n, mean age)	Experimental paradigm and linguistic stimuli	Target components (time windows)	Key findings
Simos et al. 2000a	TD: 8 (12.9 yr) DD: 10 (12.6 yr)	Task: Word recognition (target detection) Stimuli: Words	Regional activation onsets: BTC (~200 to 260 ms) and TMP (~270 to 470 ms)	Regional activation: TD showed greater left lateralization for TMP and BTC activation. DD exhibited the opposite pattern for the TMP region (greater right activation) but maintained left lateralization for the BTC. The timing of right TMP activity in DD was comparable to left TMP activity in TD
Gonzalez et al. 2014	TD: 20 (8.78 yr) DD: 19 (8.97 yr)	Task: Implicit reading (repetition detection) Stimuli: Words	P1 (50 to 180 ms) N1 (175 to 300 ms) P2 (250 to 400 ms)	N1: TD showed reduced word amplitudes in the left hemisphere compared to the right; this hemispheric difference was absent in DD

Note. The summary of key findings is restricted strictly to results relevant to the processing of linguistic stimuli (eg words, PW, and pseudohomophones). Findings related to nonlinguistic control conditions (eg false fonts, symbol strings) reported in the original studies are omitted from this table to maintain relevance to the current research question.

would localize primarily to occipito-temporal and temporo-parietal regions in both hemispheres, consistent with the established spatiotemporal cascade; and (iv) age and behavioral measures (such as intelligence and language skills) would modulate ERF responses, revealing the developmental trajectory of the reading network in TD and its corresponding variations in DD. By leveraging MEG’s millisecond resolution and high spatial resolution, our goal was to delineate precisely where and when group differences arise along the reading cascade.

Materials and methods

Participants

The study’s final dataset comprised 2 groups: 30 TD children (12 female; mean age=9.7 yr, SD=1.3, range=7.2 to 12; mean grade=3.2, SD=1.6, range=1 to 6) and 27 children diagnosed with DD (10 female; mean age=9.9 yr, SD=1.17, range=7.2 to 12; mean grade=3.1, SD=1.0, range=1 to 5). All children were native speakers of Russian.

General exclusion criteria for all participants was: any diagnosed learning disability (other than DD for the dyslexia group), any known neurological or psychiatric disorders, or the presence of nonremovable magnetic metal implants. Initially, 38 TD and 33 DD children were recruited for participation. Eight participants from the TD group were excluded based on excessive in-scanner movement artifacts (n=2), compromised data quality due to external noise (n=2), contraindications for Magnetic Resonance Imaging (MRI) scanning (n=2), obscured screen visibility from improper MEG helmet positioning (n=1), or substandard performance on the engagement monitoring task (n=1). Similarly, 6 children from the DD group were excluded, 1 due to technical failures during MEG acquisition and 5 due to poor data quality from external noise.

All experimental procedures received ethical approval from the Higher School of Economics University Committee on Interuniversity Surveys and Ethical Assessment of Empirical Research. The study was conducted in compliance with the ethical standards for human experimentation outlined in the Declaration of Helsinki (World Medical

Association). Written informed consent was obtained from the parents or legal guardians of all participants before the data collection.

A summary of these demographic and behavioral measures is provided in Table 2.

Behavioral assessment

Nonverbal intelligence was measured for all participants using the Raven’s Colored Progressive Matrices (Raven 2000). Language abilities were comprehensively evaluated with the Russian Child Language Assessment Battery (Arutiunian et al. 2022). This standardized instrument assesses multiple linguistic domains, including phonology, vocabulary, morphosyntax, and discourse, across both comprehension and production. Composite scores for mean language comprehension and mean language production were computed for each participant. Crucially, all participants, including those in the DD group, scored within the normal, age-appropriate range for both nonverbal intelligence and general language abilities. This ensures that any observed group differences in neural activation are specific to reading deficits rather than generalized cognitive or linguistic impairments.

Stimuli

The stimulus set consisted of 3 conditions, each containing 65 words (nouns): HFW, LFW, and PW. The selection criteria of words included length in letters, frequency, and familiarity to children of 7 to 11 yr old. Initially, a pool of 100 high-frequency and 100 low-frequency nouns was sourced from the frequency dictionary of the modern Russian language (Lyashevskaya and Sharov 2009). Because extensive age-of-acquisition databases are lacking for Russian, we empirically validated the familiarity of these words. A separate sample of 149 children (age range: 7 to 11 yr; mean=9.3, SD=1.58) evaluated their subjective familiarity with each individual word via an online questionnaire. The children were asked to rate how well they knew each noun on a 5-point scale: 1 (completely unfamiliar), 2 (poorly familiar), 3 (moderately familiar), 4 (well familiar), and 5 (very familiar). Based on these ratings, we selected the final 65 nouns for each condition. The final HFW list consisted of highly familiar words (mean=4.94,

Table 2 Descriptive statistics and between-group comparisons for demographic and cognitive-linguistic measures.

Variable	TD mean (SD)	DD mean (SD)	Statistic (t)	P-value	Effect size (Cohen's d)	95% CI [lower, upper]
Age (years)	9.74 (1.28)	9.96 (1.28)	$t(55) = -0.66$	0.514	0.17	[-0.35, 0.69]
IQ	32.57 (2.42)	30.15 (2.42)	$t(55) = 3.78$	<0.001	1.00	[0.44, 1.55]
Language comprehension	0.96 (0.06)	0.91 (0.06)	$t(55) = 3.34$	0.001	0.89	[0.34, 1.43]
Language production	0.94 (0.04)	0.96 (0.04)	$t(55) = -2.17$	0.035	0.57	[0.04, 1.10]

Note. SD = Standard deviation (calculated from residual standard error of the models). IQ = Intelligence quotient, based on Raven's Colored Progressive Matrices. Language comprehension and production scores are based on the Russian Child Language Assessment Battery (RuCLAB).

SD = 0.05), whereas the final LFW list comprised fewer familiar words (mean = 2.23, SD = 0.51).

PW stimuli were created using the multilingual word generator (Keuleers and Brysbaert 2010). Their generation was based on Russian real-word seeds spanning a wide frequency spectrum (ipm = instances per million): 2.6 to 7.8 ipm, 50 to 200 ipm, 250 to 709 ipm, and 500 to 35,801 ipm (Lyashevskaya and Sharov 2009). This resulted in a final list of 65 PW stimuli, 32 derived from LFW seeds (2.6 to 7.8 ipm) and 33 from HFW seeds (50 to 35,801 ipm). To maintain orthographic and phonotactic legality, nearly half of the PW (31 out of 65) preserved consonant clusters identical to their real-word counterparts (eg real word: книга [kniga; book] → pseudoword: кница [knitsa]).

Stimulus length was strictly controlled. Each of the 3 stimulus conditions contained exactly 24 5-letter words, 22 6-letter words, and 19 7-letter words. The full corpus of 195 stimuli, detailing their Russian orthography (Stimulus), English translation (Gloss), and International Phonetic Alphabet (IPA) transcription, is available in the Supplementary Materials (Table S1).

Experiment design

Participants performed a silent single-word reading task, which was implemented using PsychoPy (Peirce et al. 2019). Participants were seated at a viewing distance of approximately 135 cm from the projection screen (44.5 × 35 cm). Stimuli appeared as white text (Arial font) on a black background, centered on the screen. The presented words (5 to 7 letters in length) subtended a vertical visual angle of 1.49° and a horizontal visual angle ranging from approximately 4.9° to 6.8°. Each trial consisted of a 3,000 ms stimulus presentation followed by a 1,000 ms inter-stimulus interval, during which a central fixation cross was shown to maintain gaze.

The 195 stimuli were distributed across 3 balanced blocks (65 stimuli each). Within each block, the presentation order was fully randomized for every participant. A pseudorandomization constraint was applied to minimize adaptation effects: no more than 3 consecutive trials could be from the same stimulus category (HFW, LFW, or PW). Note that each specific item was presented only once. This procedure resulted in ~71% of trials being non-repeated (ie following a different stimulus type), ~22% repeating (stimulus type) twice, and ~7% repeating 3 times.

Participant engagement was monitored using catch trials. A question mark would occasionally appear, prompting the child to vocalize the preceding word. An experimenter, monitoring via a video feed and microphone from outside the MEG chamber, manually scored each response as correct (+) or incorrect (−). Responses were evaluated under a strict accuracy criterion: an answer was classified as incorrect

if the participant misread or altered even a single letter in the target word. These engagement checks were presented 16 times per block (48 total), distributed pseudorandomly and balanced across the stimulus conditions (16 HFW, 16 LFW, 16 PW). Each experimental block lasted approximately 5 min (306 s). The presentation order of the 3 blocks was counterbalanced across participants.

MRI data acquisition and preprocessing

High-resolution structural T1-weighted MRI scans were obtained using a 1.5 T Siemens Avanto scanner. Acquisition parameters were: Repetition Time (TR) = 1,900 ms, Echo Time (TE) = 3.37 ms, flip angle = 15°, matrix = 256 × 256 × 176, yielding an isotropic voxel size of 1.0 mm³.

Cortical surface reconstruction and segmentation of the MRIs were processed using FreeSurfer. Co-registration between the structural MRI data and the functional MEG data was accomplished within the Brainstorm toolbox (Tadel et al. 2011). This alignment utilized 6 fiducial points (nasion, left/right preauricular points, anterior/posterior commissure, and interhemispheric point) and approximately 150 supplemental digitized head points.

MEG data analysis

MEG data were acquired with a 306-channel (Vectorview, Elekta Neuromag) cryogenic system, sampling continuously at 1,000 Hz. Head position inside the MEG helmet was tracked throughout the experiment using 4 head position indicator coils, which were digitized along with fiducial points using a “Fastrak” 3D digitizer (Polhemus). Position was monitored at 4 ms intervals. External interference and head-movement artifacts were addressed using the temporal signal space separation method (Taulu and Simola 2006) and movement compensation, as implemented in MaxFilter software (Elekta Neuromag). Physiological artifacts were monitored concurrently. Four Electrooculography (EOG) electrodes were used to record ocular activity (vertical blinks: above/below left eye; horizontal movements: left/right outer canthi). Cardiac artifacts were monitored using Electrocardiography (ECG) electrodes.

The continuous 1,000 Hz MEG data were offline band-pass filtered between 0.1 and 40 Hz. A 2-stage artifact rejection procedure was then applied. First, independent component analysis was employed to identify and remove physiological artifacts. Components were rejected if they exhibited high temporal correlation with EOG or ECG channels, displayed typical ocular or cardiac topographies, and had corresponding artifactual power spectra. Second, all epochs underwent manual visual inspection in Brainstorm. Any epoch was discarded if its peak-to-peak amplitude on gradiometers surpassed ±3,000 fT/cm or if it

contained other clear artifacts, such as Superconducting Quantum Interference Device (SQUID) jumps, muscle activity, or flatlined data. The filtered continuous data were epoched from $-1,000$ to $3,500$ ms relative to stimulus onset ($4,500$ ms total duration). A Direct Current (DC) offset correction was applied using the pre-stimulus baseline period of -100 to -2 ms.

This preprocessing pipeline resulted in a high trial retention rate. The TD group retained (mean $\pm$ SD): 63.3 ± 2.55 (97%) HFW, 63.4 ± 2.58 (98%) LFW, and 62.8 ± 3.42 (97%) PW trials. The DD group retained: 63.2 ± 4.42 (97%) HFW, 62.8 ± 5.25 (96%) LFW, and 62.8 ± 5.48 (96%) PW trials.

MEG source processing

Source reconstruction was performed using gradiometer data only. This decision was data-driven, as initial quality checks revealed significantly higher noise levels in the magnetometer channels, a frequent issue in children MEG recordings often linked to head motion (Gross et al. 2013). This approach was deemed optimal for our focus in cortically-generated reading activity, as gradiometers are less susceptible to distant environmental noise and typically yield a better signal-to-noise ratio for the superficial neocortical sources relevant to our hypotheses (Baillet 2017). Forward modeling was accomplished by constructing individual head models via the overlapping spheres method (Huang et al. 1999), wherein a unique sphere is fitted for each sensor. We solved the ill-posed inverse problem by applying a depth-weighted linear L2-minimum norm estimation (Lin et al. 2006). Dipole orientations were constrained to be perpendicular to the cortical surface. Regularization was applied during the computation of the inverse operator to ensure numerical stability and reduce the impact of measurement noise (Hämäläinen and Ilmoniemi 1994). The regularization parameter (λ) was fixed at 0.33, which corresponds to an estimated signal-to-noise ratio of 3 derived from the pre-stimulus baseline (-100 to -2 ms) of the averaged ERF data.

For each participant, a single, common imaging kernel was computed and then applied to all individual epochs to reconstruct trial-by-trial source activity. The source estimation process utilized a noise covariance matrix calculated from a 2-min empty-room recording taken immediately following each child's experimental session.

To enable group-level analyses, all individual cortical source estimates were spatially normalized (projected) to the standard International Consortium for Brain Mapping 152 (ICBM152) brain template. This normalization utilized the surface-based registration calculated during the FreeSurfer segmentation process, allowing for the interpolation of individual source activity estimates onto the ICBM152 template vertices. Subsequent ERF analysis was conducted in source space. For each of the $\sim 15,000$ vertices on the template surface, epochs were averaged to compute a mean time course. Finally, cortical activation maps were normalized by applying a z-score transformation relative to the -100 to -2 ms pre-stimulus baseline.

Region of interest analysis

Based on the previous studies on the neurobiology of reading (Tarkiainen et al. 1999; Parviainen et al. 2006; Salmelin 2007; Vartiainen et al. 2011), 3 sets of regions of interest (ROIs) were anatomically defined using the Desikan–Killiany atlas in Brainstorm; they corresponded to key functional components in both hemispheres involved in single-word reading. To extract ROI-level time courses from the vertex-wise source estimates, we took the absolute amplitude of the

z-score normalized source signal for each vertex. This crucial transformation yielded nonnegative values, effectively preventing signal cancelation across opposite dipole orientations. These nonnegative values were then spatially averaged across all vertices within each predefined ROI to produce a single representative, cancelation-free time course per participant and condition. For each ROI, the time window of maximal peak activity was identified. “The first set” (ROI 1), corresponding to the initial functional component, consisted of the lateral occipital cortex. The peak activity in this region was identified within the 70 to 130 ms time window. “The second set” (ROI 2) represented the second functional component and included the fusiform gyrus and the inferior temporal gyrus. The maximal signal for this component was observed between 160 and 240 ms. “The third set” (ROI 3), mapping to the third functional component, comprised the superior temporal gyrus and the transverse temporal gyrus. Its peak activity typically occurred within the 380 to 680 ms time window.

Mean ERF amplitudes were extracted from strictly symmetrical, predefined time windows across both hemispheres (eg 380 to 680 ms for ROI 3 in both the left and right hemispheres) to ensure an unbiased inter-hemispheric comparison of overall activation strength.

However, for the extraction of PL, a data-driven approach was prioritized to capture the true timing of maximal cortical engagement. The peak identification process was designed to capture the most prominent neurophysiological event within the ROI. Consequently, while the left hemisphere of ROI 3 peaked as expected within the late 380 to 680 ms window, the massive early peak (~ 200 ms) consistently observed in the right hemisphere of ROI 3 was deliberately captured. Forcing the extraction of a nonphysiological local maximum from the flatter 380 to 680 ms time window in the right hemisphere would have compromised the validity of the latency analysis.

Statistical analysis

All statistical analyses were performed using R Studio. Key packages included “lme4” for linear mixed-effects models (LMM), “lmerTest” for *P*-value estimation using Satterthwaite's approximation, “emmeans” (including the “emtrends” function) for post hoc comparisons and trend analyses, “effectsize” for computing standardized effect sizes, and the “tidyverse” suite for data manipulation.

Analysis of task performance

To evaluate participants' engagement during the MEG acquisition, the LMM was constructed with accuracy percentage as the continuous dependent variable. Group (TD, DD) and Stimulus type (HFW, LFW, PW) were entered as interacting fixed effects. To account for the nonindependence of repeated measures across different stimulus conditions within the same participant, subject Identifier (ID) was included as a random intercept. The model formula was specified as:

$$\text{lmer}(\text{Accuracy} \sim \text{Group} * \text{Stim} + (1 | \text{ID}))$$

The statistical significance of the fixed effects was evaluated via type III Analysis of Variance (ANOVA) using Satterthwaite's method for degrees of freedom approximation. The significant Group $\times$ Stimulus interaction was decomposed using post hoc pairwise comparisons via the “emmeans” package, applying a Tukey adjustment (adjust = “tukey”) to correct for multiple comparisons and to extract the exact magnitude of accuracy differences (with 95% CIs) between the groups across varying levels of stimulus complexity.

Analysis of behavioral data

To compare the demographic and cognitive-linguistic profiles between the TD and DD groups, linear regression models (*lm*) were utilized to estimate group differences. This approach allowed for the extraction of *t*-statistics, *P*-values, and Cohen's *d* effect sizes with 95% CIs for all behavioral measures (age, intelligence quotient [IQ], language comprehension, and language production).

Linear mixed-effects modeling of MEG data

Given the non-normal, right-skewed distribution of the raw ERF amplitude and PL data, both dependent variables were log-transformed to meet the assumptions of normality for parametric testing. To assess differences in neurophysiological responses (logERF and logPL), we implemented LMMs.

The current analysis rigorously controlled for behavioral variance by incorporating centered cognitive and linguistic scores (Age_c, IQ_c, Language Comprehension_c, and Language Production_c) directly into the models. The fixed effects structure included Group (TD, DD), Region (ROI 1, ROI 2, ROI 3), Stimuli (HFW, LFW, PW), Hemisphere (left, right), and Age_c as interacting factors, with the remaining centered behavioral scores acting as covariates.

Crucially, to account for inter-individual topographic variability and avoid the inflation of type I errors, the random effect structure was maximized. It included not only random intercepts for participants but also random slopes for Region and Hemisphere. The core inter-group model formula was defined as follows:

$$\begin{aligned} \text{lmer}(\text{Dependent_Variable} \sim \text{Group} * \text{Region} * \text{Stimuli} * \text{Hemisphere} * \\ \text{Age_c} + \text{IQ_c} + \text{Language Comprehension_c} + \text{Language Production_c} \\ + (1 + \text{Region} + \text{Hemisphere} | \text{ID})) \end{aligned}$$

Furthermore, to investigate the specific neurodevelopmental dynamics and topographic patterns within each child group, identical LMMs were subsequently applied to the TD and DD data separately. For these within-group analyses, the Group factor and its associated interactions were omitted, while all other fixed covariates and the complex random effects structure were strictly maintained:

$$\begin{aligned} \text{lmer}(\text{Dependent_Variable} \sim \text{Region} * \text{Stimuli} * \text{Hemisphere} * \text{Age_c} \\ + \text{IQ_c} + \text{Language Comprehension_c} + \text{Language Production_c} \\ + (1 + \text{Region} + \text{Hemisphere} | \text{ID})) \end{aligned}$$

Significance of the fixed effects was evaluated using type III ANOVA with Satterthwaite's method for degrees of freedom. Partial eta-squared (η_p^2) was calculated to report the effect sizes for all main effects and interactions. Significant and most relevant interactions were decomposed using post hoc comparisons via the "emmeans" package, applying a Tukey adjustment (adjust = "tukey") for multiple comparisons and 95% CIs for all contrast estimates.

Brain-behavior interaction analysis

To investigate whether the modulatory effect of cognitive and linguistic resources on brain activity differed between the 2 groups, we specifically tested the interactions between the Group factor and the behavioral covariates (IQ_c, Language Comprehension_c, and Language Production_c) in predicting logERF and logPL within the unified

LMMs. This approach resulted in 6 targeted brain-behavior interaction tests (3 behavioral predictors $\times$ 2 MEG metrics).

To strictly control the family-wise error rate across these specific interaction tests, a conservative Bonferroni correction was applied, setting the adjusted significance threshold at $\alpha = 0.0083$. Effects that survived this rigorous threshold were subsequently decomposed using the "emtrends" function to estimate, compare, and extract the 95% CIs of the marginal linear trends (regression slopes) between the behavioral predictors and neural responses.

Results

Task performance

The TD group performed with high accuracy across all conditions: HFW ($M = 15.79$, $SD = 0.62$; 98.7% accuracy), LFW ($M = 14.93$, $SD = 0.96$; 93.3% accuracy), and PW ($M = 14.79$, $SD = 0.94$; 92.5% accuracy). The DD group exhibited significantly lower overall accuracy ($F(1, 54) = 36.41$, $P < 0.001$), yielding 90.3% ($M = 14.44$, $SD = 1.62$) for HFW, 80.8% ($M = 12.93$, $SD = 2.43$) for LFW, and 74.1% ($M = 11.85$, $SD = 2.43$) for PW.

A significant Group $\times$ Stimulus interaction ($F(2, 108) = 8.37$, $P < 0.001$) indicated that the difference in accuracy between the groups varied depending on the stimulus type. Post hoc comparisons revealed that the DD group scored lower than the TD group across all conditions. The difference in accuracy between the groups was smallest for HFW (Estimate = -8.64% , 95% CI [-14.10 , -3.23]), increased for LFW (Estimate = -13.39% , 95% CI [-18.80 , -7.98]), and was largest for PW (Estimate = -19.24% , 95% CI [-24.70 , -13.83]). Importantly, performance in the DD group remained above chance level across all conditions (all conditions $\geq 74\%$).

Behavioral data

The groups were perfectly matched by age, with no significant differences observed ($t(55) = -0.66$, $P = 0.514$, $d = 0.17$, 95% CI [-0.35 , 0.69]).

Regarding cognitive and language profiles, the TD group showed relatively higher scores than the DD group in IQ ($t(55) = 3.78$, $P < 0.001$, $d = 1.00$, 95% CI [0.44 , 1.55]) and language comprehension ($t(55) = 3.34$, $P = 0.001$, $d = 0.89$, 95% CI [0.34 , 1.43]). Conversely, the DD group exhibited slightly higher performance in language production ($t(55) = -2.17$, $P = 0.035$, $d = 0.57$, 95% CI [0.04 , 1.10]).

Although these between-group differences were statistically significant, the performance of all participants remained within the age-appropriate normative range across all standardized tests. Full statistical comparisons and descriptive data are summarized in Table 2.

MEG data group differences

Comparison of ERF data

The LMM analysis revealed a significant main effect of Group ($F(1, 50.86) = 4.62$, $P = 0.036$, $\eta_p^2 = 0.08$, 95% CI [0.00 , 1.00]), indicating generally lower ERF amplitudes in the DD group.

Crucially, the analysis demonstrated a highly significant Group $\times$ Region $\times$ Hemisphere interaction ($F(2, 714) = 10.17$, $P < 0.001$, $\eta_p^2 = 0.03$, 95% CI [0.01 , 1.00]). Post hoc comparisons revealed that the TD group exhibited significantly greater ERF amplitudes than the DD group in ROI 3 of the left hemisphere (Estimate = -0.44 , $P < 0.001$, 95% CI [-0.67 , -0.21]). Additionally, a significant difference was observed in ROI 2 of the right hemisphere (Estimate = -0.23 , $P = 0.03$, 95% CI

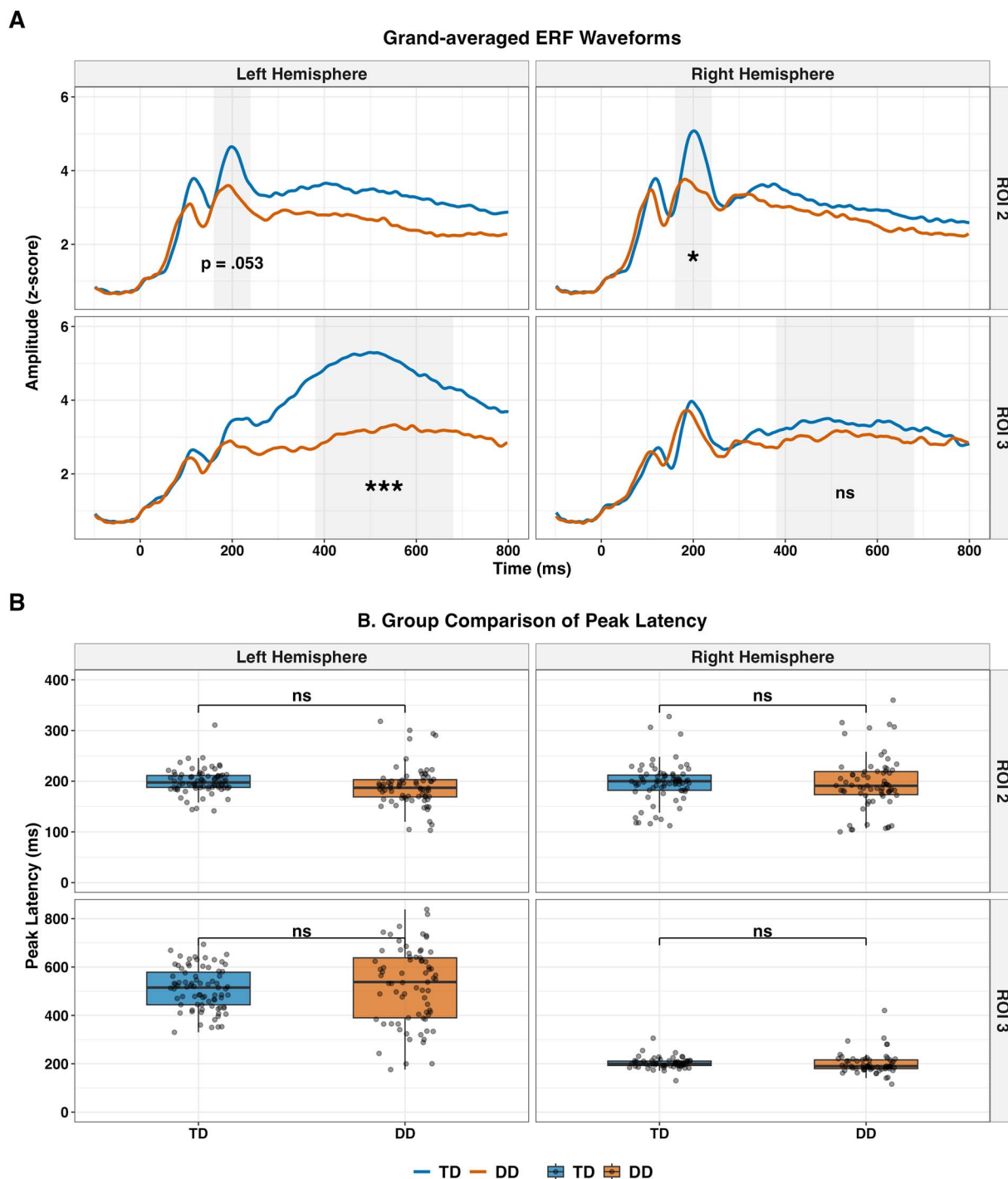


Figure 1 Group differences in neural activation and PL. a) Grand-averaged ERF waveforms comparing TD and DD groups in ROI 2 and ROI 3. The shaded areas indicate the time windows for analysis: 160 to 240 ms for ROI 2 and 380 to 680 ms for ROI 3. Significant group differences are marked with asterisks located below the waveforms (* $P < 0.05$, *** $P < 0.001$, ns = not significant). b) Direct comparison of PL between TD and DD groups in ROI 2 and ROI 3. Note the different Y-axis scales (0 to 400 ms for ROI 2 and 0 to 850 ms for ROI 3), reflecting the temporal progression of reading processing from “letter-string analysis” (ROI 2) to “lexical-semantic analysis” (ROI 3).

[−0.43, −0.02]), while ROI 2 of the left hemisphere showed a marginal trend (Estimate = −0.21, $P = 0.053$, 95% CI [−0.43, 0.00]) (Fig. 1a; for grand average waveforms and topographic maps, see Figs S2 and S3).

The variance components of the random effects justified the model structure, showing substantial inter-individual variability in baseline amplitude (Intercept SD = 0.41) and in the sensitivity of

specific regions (ROI 3 SD = 0.38) and hemispheres (right hemisphere SD = 0.15).

Comparison of PL data

For PL, the LMM analysis showed no significant main effect of Group ($F(1, 47.12) = 0.18$, $P = 0.675$, $\eta_p^2 < 0.01$), and no significant Group $\times$

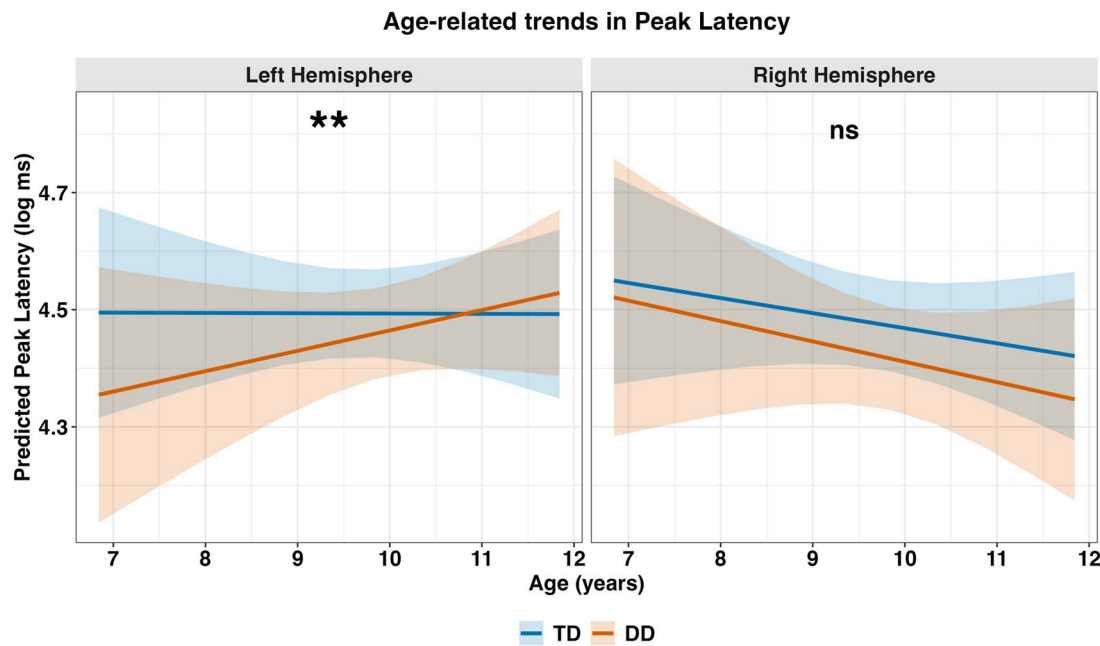


Figure 2 The left panel illustrates the distinct age-related trends in the left hemisphere, where PL decreases with age in the TD group but increases in the DD group. The right panel displays the corresponding trends for the right hemisphere. Shaded areas represent 95% CIs. Significance markers explicitly denote the between-group differences in these age-related slopes: The double asterisks (**) indicate that the age-related patterns significantly differ between the groups in the left hemisphere ($P=0.002$), whereas “ns” (not significant) indicates that the group trends do not significantly differ in the right hemisphere.

Region $\times$ Hemisphere interaction ($F(2, 585.44)=0.09$, $P=0.915$, $\eta_p^2 < 0.01$, 95% CI [0.00, 1.00]) (Fig. 1b).

However, the analysis revealed a significant Group $\times$ Hemisphere $\times$ Age interaction ($F(1, 50.09)=10.07$, $P=0.003$, $\eta_p^2=0.17$, 95% CI [0.04, 1.00]). Post hoc trend analysis revealed that in the left hemisphere, the TD group showed a significant age-related decrease in latency (Slope = -0.032 , $P=0.017$), whereas the DD group exhibited a marginally significant age-related increase (Slope = 0.033 , $P=0.054$). The direct comparison of these slopes confirmed that the age-related patterns significantly differed between the groups in this hemisphere (Difference = 0.065 , $P=0.002$, 95% CI [0.024, 0.105]). In the right hemisphere, the DD group demonstrated an age-related decrease in latency (Slope = -0.042 , $P=0.049$), whereas the TD group showed no significant age-related change (Slope = -0.020 , $P=0.197$). Importantly, the direct comparison confirmed that these age-related patterns did not significantly differ between the groups in this hemisphere (Difference = -0.021 , $P=0.4$, 95% CI [-0.072 , 0.029]) (Fig. 2).

The variance components of the random effects indicated inter-individual variability in regional latency (ROI 3 SD = 0.12) and hemispheric asymmetry (SD = 0.07).

Brain-behavior analysis

To investigate whether the relationship between behavioral performance and neural processing differed between the groups, we analyzed the Group $\times$ Behavior interactions for each cognitive measure.

The LMM analysis did not reveal any significant interactions between Group and behavioral scores for ERF amplitudes (Group $\times$ IQ: $F(1, 50.32)=0.15$, $P=0.696$, $\eta_p^2 < 0.01$; Group $\times$ Language Comprehension: $F(1, 50.30) < 0.01$, $P=0.962$, $\eta_p^2 < 0.01$; Group $\times$ Language Production: $F(1, 50.96)=0.56$, $P=0.459$, $\eta_p^2=0.01$).

Similarly, no significant group interactions were observed for PL (Group $\times$ IQ: $F(1, 47.70)=1.61$, $P=0.211$, $\eta_p^2=0.03$; Group $\times$ Language Comprehension: $F(1, 49.77)=0.01$, $P=0.924$, $\eta_p^2 < 0.01$; Group $\times$ Language Production: $F(1, 47.94)=1.09$, $P=0.301$, $\eta_p^2=0.02$). These results indicate that the associations between cognitive-linguistic abilities and neural activation patterns did not significantly differ between TD and DD children.

The inclusion of random intercepts for participants and random slopes for Region and Hemisphere was strictly justified by the variance components, which demonstrated substantial inter-individual variability in baseline neural responses (ERF Intercept SD = 0.40 ; PL Intercept SD = 0.10) and regional sensitivity (ERF ROI 3 SD = 0.37 ; PL ROI 3 SD = 0.12).

MEG data analysis in TD group

ERF data analysis

For the TD group, the LMM analysis revealed a significant main effect of Hemisphere ($F(1, 28)=9.74$, $P=0.004$, $\eta_p^2=0.26$, 95% CI [0.06, 1.00]) and a significant Region $\times$ Hemisphere interaction ($F(2, 392)=38.00$, $P < 0.001$, $\eta_p^2=0.16$, 95% CI [0.11, 1.00]). Post hoc comparisons showed that in ROI 3, the ERF amplitude in the left hemisphere was significantly greater than in the right (Estimate = 0.36 , $P < 0.001$, 95% CI [0.27, 0.44]). No significant hemispheric differences were observed in ROI 1 or ROI 2 (all $P > 0.1$) (Fig. 3a).

A 3-way Region $\times$ Hemisphere $\times$ Age interaction was also significant ($F(2, 392)=5.82$, $P=0.003$, $\eta_p^2=0.03$, 95% CI [0.01, 1.00]). Trend analysis revealed an age-related increase in amplitude in the right hemisphere of ROI 3 (Slope = 0.18 , $P < 0.001$, 95% CI [0.10, 0.26]), whereas the left hemisphere showed a much smaller, nonsignificant trend (Slope = 0.07 , $P=0.101$, 95% CI [-0.01 , 0.15]). Crucially,

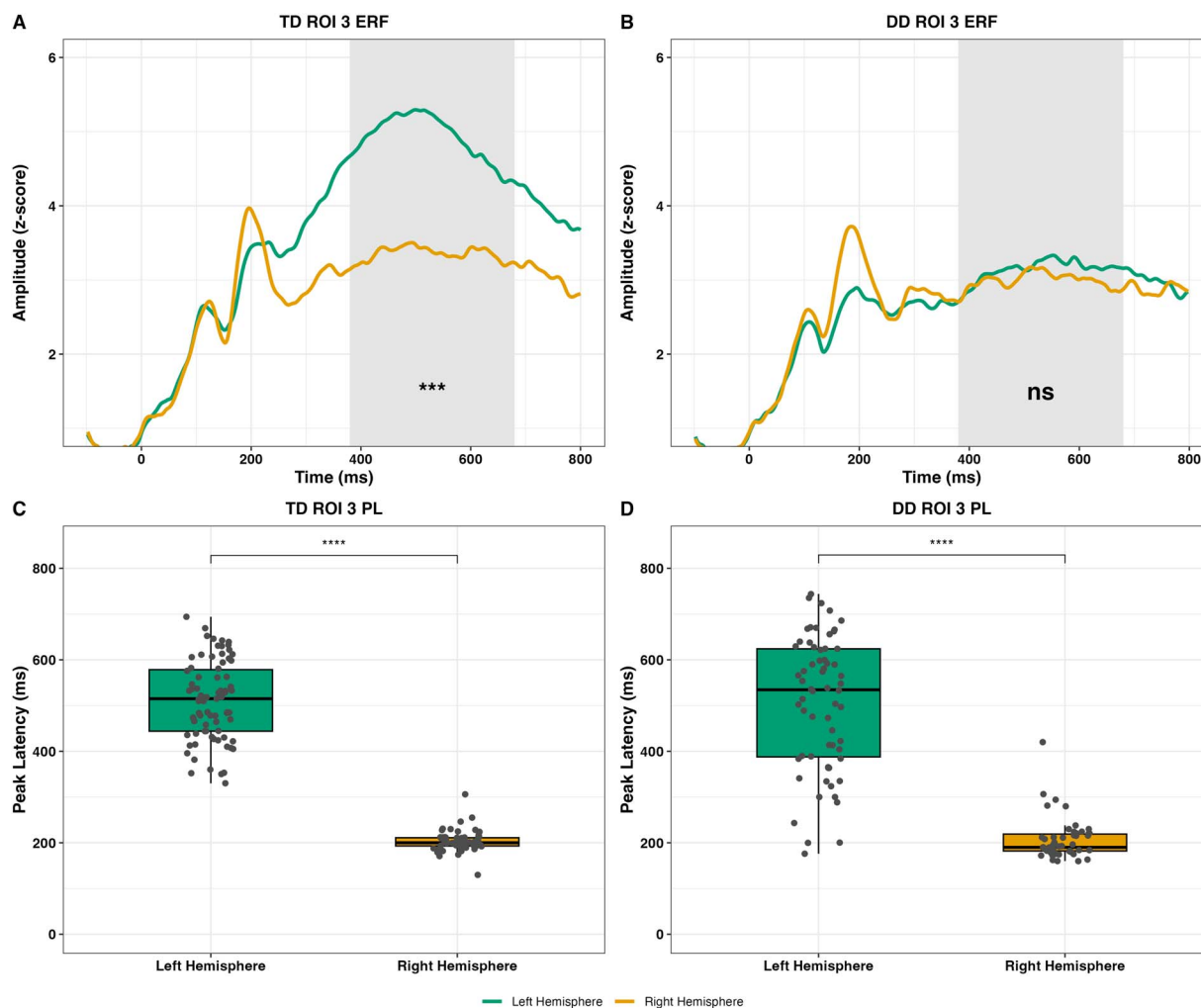


Figure 3 Hemispheric asymmetry and temporal dynamics of reading in TD and DD groups. a and b) Grand-averaged ERF waveforms for the TD and DD groups in ROI 3. The shaded area (380 to 680 ms) indicates the time window used for the analysis of the lexical-semantic component. Asterisks indicate significant hemispheric differences in amplitude (*** $P < 0.001$, ns = not significant). c and d) PL of the response in ROI 3 for TD and DD groups, respectively. Boxplots represent the distribution of latency values. Note the preserved right-hemisphere precedence (shorter latency) in both groups.

the direct comparison of these slopes confirmed that the age-related increase was significantly steeper in the right hemisphere compared to the left (Difference = 0.11, $P = 0.002$, 95% CI [0.04, 0.18]) (Fig. 4a).

The variance components of the random effects showed inter-individual variability in ROI 3 (SD = 0.39) and ROI 2 (SD = 0.28).

PL data analysis

For PL, the LMM analysis in the TD group revealed a Region $\times$ Hemisphere interaction ($F(2, 354.96) = 496.90$, $P < 0.001$, $\eta_p^2 = 0.74$, 95% CI [0.70, 1.00]). Post hoc comparisons showed that in ROI 3, PL was significantly shorter in the right hemisphere compared to the left (Estimate = 0.92, $P < 0.001$, 95% CI [0.87, 0.97]) (Fig. 3c). Importantly, following our data-driven peak selection approach, this inter-hemispheric comparison reflects differences between the dominant PLs within the respective ROI waveforms, rather than the timing of the same late functional component across hemispheres.

Although the Hemisphere $\times$ Age interaction was not significant ($F(1, 25.5) = 0.64$, $P = 0.430$, $\eta_p^2 = 0.02$, 95% CI [0.00, 1.00]) (Fig. 4c), the LMM revealed a significant Region $\times$ Stimulus $\times$ Age interaction ($F(4, 342.62) = 3.94$, $P = 0.003$, $\eta_p^2 = 0.04$, 95% CI [0.01, 1.00]). Post

hoc trend analysis demonstrated significant age-related decreases in latency in ROI 3 for HFW (Slope = -0.052 , $P = 0.003$, 95% CI [-0.086 , -0.017]) and PW (Slope = -0.041 , $P = 0.028$, 95% CI [-0.077 , -0.004]). Conversely, in ROI 2, a robust age-related decrease in latency was observed specifically for LFW (Slope = -0.071 , $P < 0.001$, 95% CI [-0.110 , -0.032]). No significant age-related trends were found in ROI 1 (all $P > 0.05$).

MEG data analysis in DD group

ERF data analysis

In contrast to the TD group, the DD group demonstrated no significant main effect of Hemisphere ($F(1, 23.0) = 0.59$, $P = 0.45$, $\eta_p^2 = 0.02$) and no significant Region $\times$ Hemisphere interaction ($F(2, 322.0) = 1.98$, $P = 0.14$, $\eta_p^2 = 0.01$) (Fig. 3b). Furthermore, the 3-way Region $\times$ Hemisphere $\times$ Age interaction was also not significant ($F(2, 322.0) = 1.60$, $P = 0.204$, $\eta_p^2 = 0.01$, 95% CI [0.00, 1.00]) (Fig. 4b).

PL data analysis

For PL, the LMM analysis in the DD group revealed a significant Region $\times$ Hemisphere interaction ($F(2, 247.4) = 174.70$, $P < 0.001$, $\eta_p^2 = 0.59$,

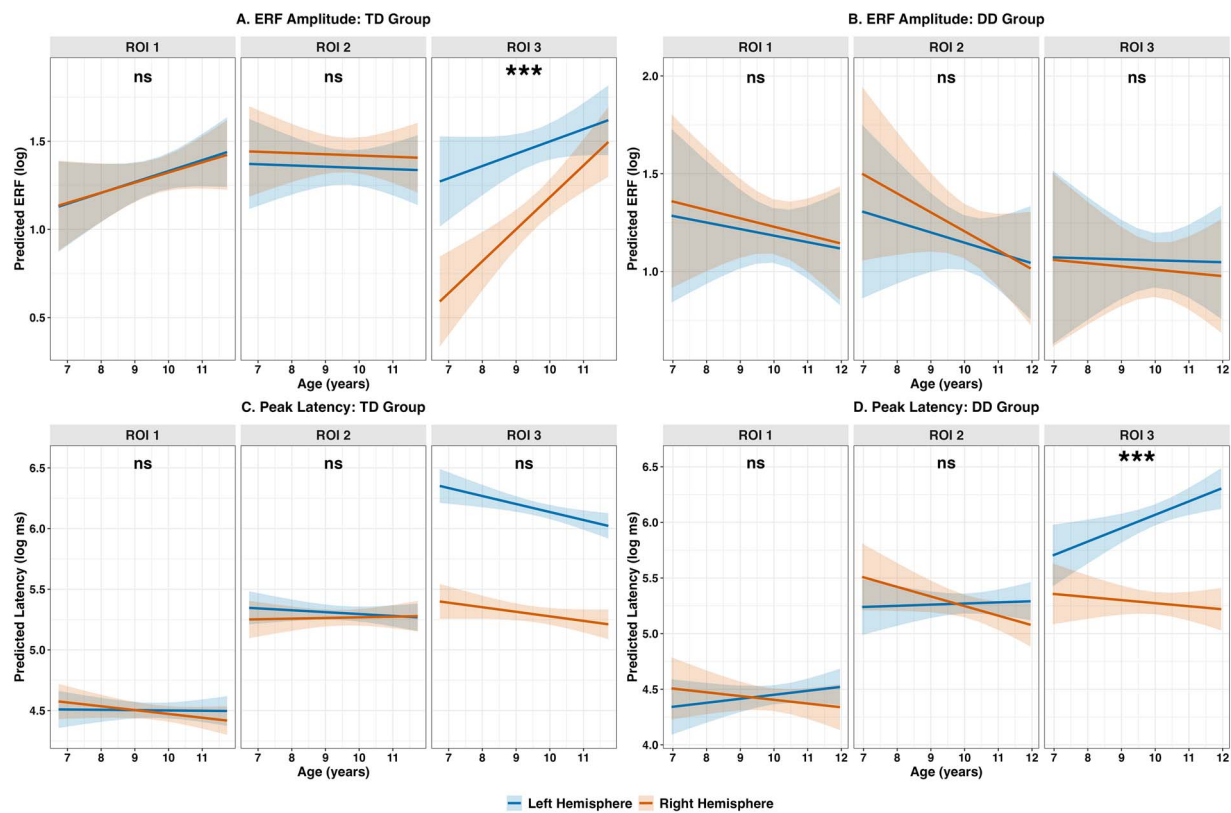


Figure 4 Predicted age-related trends of neuromagnetic responses. LMM predictions for ERF amplitude and PL as a function of age. The top row displays predicted log-transformed ERF amplitudes for the TD (panel a) and DD (panel b) groups. The bottom row displays predicted log-transformed PLs for the TD (panel c) and DD (panel d) groups. Within each panel, developmental trends are separated by ROI (ROI 1, ROI 2, and ROI 3). Shaded areas denote the 95% CIs of the marginal predictions. Significance markers at the top of the facets denote the results of post hoc comparisons between the left and right hemispheres within the respective ROI: *** $P < 0.001$, whereas “ns” indicates no significant hemispheric difference.

95% CI [0.52, 1.00]). Post hoc comparisons showed that in ROI 3, PL was significantly longer in the left hemisphere compared to the right (Estimate = 0.89, $P < 0.001$, 95% CI [0.81, 0.97]) (Fig. 3d). Consistent with the TD group, this inter-hemispheric difference reflects the timing of the dominant peaks within each hemisphere’s waveform, rather than a comparison of the same late component.

A significant Hemisphere $\times$ Age interaction was also observed ($F(1, 23.8) = 7.83$, $P = 0.01$, $\eta_p^2 = 0.25$, 95% CI [0.04, 1.00]). Trend analysis revealed a downward age-related trend in the right hemisphere (Slope = -0.043 , $P = 0.075$, 95% CI [-0.09 , 0.005]) and an upward trend in the left hemisphere (Slope = 0.03 , $P = 0.135$, 95% CI [-0.01 , 0.07]); however, both of these age-related trends were statistically nonsignificant (Fig. 4d).

Discussion

The present study investigated the neural mechanisms underlying silent single-word reading in DD children compared to TD peers. Contrary to our initial hypotheses, neither group showed significant modulation of ERF amplitude by word frequency or lexicality. However, the results revealed significant differences in ERF amplitude and hemispheric dominance between the groups. While TD children exhibited the expected left-lateralized profile in the superior temporal cortex, children with DD were characterized by bilateral reduced responses in occipito-temporal regions and reduced activation specifically in the left superior temporal cortex. Additionally, the

analysis identified different relationships between age and PL across the groups, potentially reflecting the progressive automatization associated with reading expertise specifically in TD.

Group comparisons

Regarding sensitivity to stimulus properties, a central finding was the absence of significant modulation by word frequency or lexicality across all 3 components in both groups. Regarding the first component, the present data showed no significant modulation by stimulus properties. This lack of differentiation is consistent with previous findings (Simos et al. 2000b; Trauzettel-Klosinski et al. 2006), which reported no stimulus-specific differentiation during this early processing stage. For the second component (160 to 240 ms), this lack of differentiation aligns with a broad consensus reporting that children generally do not show significant neural differentiation between real words and PW (Maurer et al. 2007; Kast et al. 2010; Araújo et al. 2012; Hasko et al. 2013; Gonzalez et al. 2014; Kemény et al. 2018; Mehlhase et al. 2020). Finally, for the third component (380 to 680 ms), the absence of lexicality effects observed in the current data underscores the ongoing inconsistencies in findings from studies involving children. While several studies demonstrate similar findings to the current results by reporting no significant amplitude differences between real words and PW during lexical decision (Hasko et al. 2013; Bakos et al. 2018), letter identification (Mehlhase et al. 2020), and reading aloud tasks (Trauzettel-Klosinski et al. 2006), conflicting

evidence exists. Other investigations have observed higher amplitudes for PW compared to real words during implicit reading (Kemény et al. 2018) and semantic judgment (Sun et al. 2023).

Importantly, the absence of significant stimulus-specific modulation in the current sample, as is generally observed in other studies, does not indicate an absolute lack of cognitive or neural differentiation. Instead, these discrepancies in findings across studies likely reflect specific methodological constraints and sample characteristics.

First, the experimental paradigm plays a critical role in eliciting stimulus-specific neural responses. The current study utilized a silent reading task, which is closely related to implicit reading tasks that also failed to show significant word/pseudoword differentiation in TD and DD children (Maurer et al. 2007; Araújo et al. 2012; Gonzalez et al. 2014). In contrast, studies reporting lexicality effects typically employ active paradigms, such as lexical decision (Hasko et al. 2013; Bakos et al. 2018) or semantic judgment (Sun et al. 2023). Active tasks explicitly force lexical access, engaging top-down feedback mechanisms from higher-order language regions, which enhances neural differentiation in the ventral stream (Twomey et al. 2011; Price 2012). Thus, silent or implicit reading tasks likely do not engage the lexical system sufficiently to trigger top-down semantic modulation.

Second, it is crucial to consider the specific time intervals analyzed. Evidence suggests that while stimulus-specific differentiation may be absent during the N400 time window, lexicality effects emerge during the Late Positive Complex (LPC, typically >500 ms). TD children exhibit LPC modulations that differentiate real words from PW (Hasko et al. 2013). Conversely, children with DD typically fail to show these late stimulus-specific LPC modulations (Hasko et al. 2013; Sun et al. 2023) or exhibit delayed effects (Bakos et al. 2018). This suggests that in children, lexical and frequency effects may become detectable at later processing intervals.

Finally, high inter-individual variability and group heterogeneity may have masked subtle frequency or lexicality effects. Dyslexia encompasses various cognitive profiles and reading deficit subtypes, such as combined reading and spelling deficits (cRSD), isolated reading deficits (iRD), and isolated spelling deficits (iSD). Previous research demonstrates that distinct reading profiles yield different neurophysiological patterns; for example, neural responses to words and PW vary depending on the specific spelling and reading abilities of the participants (Bakos et al. 2018; Kemény et al. 2018). Because the current study did not categorize the DD sample by specific reading deficit subtypes, opposing neural patterns within the group may have canceled each other out at the group average level, resulting in an overall lack of statistically significant stimulus modulation.

Turning to the global activation profiles, while stimulus-specific modulation was absent, the overall strength of the neural signal robustly differentiated the 2 groups. We first found no significant group differences in the early occipital component (~100 ms). This result agrees with the literature (Trauzettel-Klosinski et al. 2006; Maurer et al. 2007; Araújo et al. 2012), confirming that the reading deficit does not originate from a primary visual failure. We then found significantly reduced bilateral ERF amplitudes in the left and right occipito-temporal component (160 to 240 ms) in the DD group compared to TD children. This finding supports the idea that dyslexia involves deficits in early orthographic processing and aligns with studies showing reduced N170/M170 responses (Kast et al. 2010; Bakos et al. 2018). Critically, our results are in line with the specific pattern reported by Bakos et al. (2018), where significant group differences in global activation strength (DD < TD) were observed in the absence of detailed

lexicality effects within either group. This specific profile points to a deficit in neural activation rather than neural differentiation. Since both groups demonstrated comparable sensitivity, the impairment in the DD group appears to be a fundamental failure to engage the ventral stream neural resources to a sufficient level for print processing. However, this contrasts with reports finding no significant amplitude differences between groups (Araújo et al. 2012; Hasko et al. 2013; Kemény et al. 2018; Sun et al. 2023) in this component. This discrepancy is likely explained by variations in the functional engagement of the ventral stream across different samples. The degree of reduced activation in the occipito-temporal cortex likely acts as a marker of dysfunction severity. In studies where no group differences were found, participants may have engaged compensatory processing routes or possessed a milder deficit.

Another finding was the significant reduction in the ERF amplitude of the left superior temporal cortex in the DD group. This result is consistent with studies identifying atypical activation in temporo-parietal regions during late processing stages (Simos et al. 2000a, 2000b; Hasko et al. 2013; Sun et al. 2023). Functionally, these studies interpreted such profiles as a marker of an impaired lexico-semantic network. Simos et al. (2000b) described this as an “aberrant activation” where the specialized left-hemisphere regions required for phonological and semantic conversion fail to engage.

Importantly, we found no significant group differences in PL. This finding suggests that the behavioral slowness often observed in dyslexia may result from atypical neural processing dynamics rather than a fundamental delay in the timing of peak cortical engagement. Specifically, PL measurements alone may not capture the full duration of the underlying processing cascade. It is possible that atypical neural signals necessitate a prolonged integration period to accumulate sufficient information for successful word recognition, even if the maximum neural response is reached at a typical time. Furthermore, brain-behavior interaction analyses revealed that cognitive and linguistic capacities (IQ, language comprehension, and production) did not differentially modulate neural responses between the groups. This lack of interaction underscores that the observed spatiotemporal deficits represent a core neural signature of DD rather than a secondary artifact of broader cognitive variance.

Age-related effects

The current study revealed significantly different age-related patterns in PL between the TD and DD groups in the left hemisphere. Specifically, older TD children exhibited a significantly decreased PL in the left superior temporal cortex compared to younger TD children. In contrast, children with DD did not demonstrate this typical age-related decrease, resulting in a statistically significant difference in the age-related slopes between the 2 groups. Additionally, within the TD group, we observed an age-related increase in ERF amplitude specifically in the right hemisphere.

These findings shed light on the critical role of reading experience and the automatization of the reading network. Reading development between the ages of 7 and 12 is a period of substantial qualitative change. This developmental stage is characterized by the transition from slow, effortful decoding to rapid, automatized word recognition, which is conceptually linked to the “fourth-grade shift” (Coch 2015). During this period, the typical reading network undergoes significant functional maturation, developing fine-grained sensitivity to orthographic and lexical properties (Coch et al. 2012; Larionova et al. 2024).

As highlighted by Araújo et al. (2015), fluent reading ultimately relies on this highly automatized, fast-acting, and specialized left-lateralized neural network. Therefore, the age-related decrease in PL observed in our TD group likely reflects the progressive automatization of left-lateralized linguistic circuits driven by successful reading experience, while the amplitude increase in the right hemisphere may reflect the consolidation of holistic visual recognition strategies during this developmental window.

Conversely, the lack of an age-related decrease in PL in the DD group suggests that the neural mechanisms associated with reading do not follow typical age-related patterns. In the context of reading automatization (Araújo et al. 2015), the left hemisphere in children with DD fails to reach the shorter PL values characteristic of typical readers across the investigated age range. This absence of a typical left-lateralized age-related decrease aligns with longitudinal findings indicating impaired “print tuning” in the dyslexic reading network (Maurer et al. 2011).

The neural patterns of TD group

In the TD group, we observed a hierarchical activation sequence moving from occipital to temporal regions. Regarding lateralization, TD children demonstrated significant left-hemispheric amplitude dominance during the third component (380 to 680 ms), aligning with previous MEG findings for the language network in children (Simos et al. 2000a). While the ERF amplitude was left-dominant, the dominant PL occurred significantly earlier in the right hemisphere. As noted in the Results, these latency values capture the most prominent peaks within the ROI waveforms rather than the same late component. This right-hemisphere precedence suggests that the right temporal cortex may support an early stage of visual-attentional processing, which precedes and facilitates the more detailed linguistic analysis in the left hemisphere (Parviainen et al. 2006; Salmelin 2007). Furthermore, our analysis revealed a stimulus-specific age-related pattern in the TD group: PL significantly decreased with age in the superior temporal cortex for HFW and PW, and in the occipito-temporal cortex for LFW. This fine-grained age-related decrease in PL underscores the automatization of distinct stages within the reading network in typical readers. This functional dissociation highlights the complementary roles of bilateral temporal regions in fluent reading.

The neural patterns of DD group

Within the DD group, we observed no significant amplitude differences between the left and right hemispheres during the third component (380 to 680 ms). As confirmed by the significant Group $\times$ Region $\times$ Hemisphere interaction for ERF amplitude in the global LMM, this absence of lateralization statistically differs from the left-lateralized pattern observed in the TD group. However, despite this atypical amplitude pattern, the inter-hemispheric relationship of PLs remained consistent with the TD group: the dominant PLs in the superior temporal cortex occurred significantly earlier in the right hemisphere than in the left. This preservation of the inter-hemispheric PL pattern was statistically supported by the absence of a Group $\times$ Region $\times$ Hemisphere interaction for PL. This suggests that while the inter-hemispheric relationship of PLs is generally preserved in DD, the core atypicality lies in the reduced amplitude of left-hemispheric neural responses (Trauzettel-Klosinski et al. 2006). Thus, while the regions reach their maximum amplitude at comparable PLs, the

overall neural activation remains reduced, which may limit efficient linguistic processing.

Conclusion

In conclusion, the present study provides a detailed characterization of the neural mechanisms underlying single-word reading in Russian-speaking children, offering new insights into the nature of DD. Our findings highlight 3 key conclusions.

First, contrary to models emphasizing early lexical sensitivity, neither TD nor DD children showed significant sensitivity to word frequency or lexicality across the 3 analyzed components. Rather than reflecting a uniform processing mechanism, this absence of modulation highlights the constraints of implicit reading paradigms in children, suggesting that neural differentiation may heavily depend on explicit task demands and top-down engagement. Furthermore, lexicality effects may be absent in early time windows and only emerge later, such as during the LPC. Finally, the current study did not categorize the DD group by reading deficit subtypes (eg cRSD, iRD, iSD), and high inter-individual variability may have masked subtle effects, as opposing neural patterns within the DD sample could have canceled each other out at the group average level.

Second, the neural differences in the DD group were characterized by a clear dissociation; while ERF amplitudes were significantly reduced, PL remained consistent with typical patterns. Although the DD group exhibited significantly reduced activation in the bilateral occipito-temporal stream and the left superior temporal cortex, the inter-hemispheric relationship of PLs remained preserved. This indicates that the core atypicality is related not to a fundamental shift in PL, but to the reduced overall strength of neural activation. We propose that the reading difficulties observed in children with DD may be a consequence of these atypical neural signals, which likely require a prolonged integration period to reach the threshold for word recognition.

Finally, we identified distinct age-related patterns between the groups. Unlike children with DD, who showed stable PL values across the investigated age range, older TD children demonstrated a decreased PL in the left superior temporal cortex and increased ERF amplitude in the right hemisphere. This points to age-related automatization of the reading network in TD, whereas the lack of such an age-related pattern in the DD group highlights a functional atypicality that remains evident across the entire studied age range.

Limitations

Several limitations of the present study should be acknowledged.

First, a methodological constraint is the exclusion of a nonlinguistic baseline, such as false fonts or scrambled letters. While our primary aim was to map the sensitivity of the reading network to lexical status within the orthographic domain, the absence of a low-level visual control prevents the absolute isolation of language-specific activity from general visual-attentional processes. The reduced activation profiles observed in the DD group could partially reflect broader deficits in general visual or attentional processing of letter strings, rather than a strictly language-specific impairment. Future investigations employing MEG source localization would benefit from incorporating such conditions.

Second, the employment of a silent reading paradigm presents a trade-off. On the 1 hand, this naturalistic approach ensures high ecological validity and minimizes motion artifacts, which is particularly critical for children's groups. On the other hand, the lack of explicit behavioral responses precludes trial-by-trial performance monitoring. Furthermore, the implicit nature of silent reading may not engage the lexical access system sufficiently to trigger strong top-down semantic modulation. This likely contributed to the absence of significant frequency and lexicality effects in our sample, suggesting that such effects in children might be task-dependent rather than automatic.

Third, the group differences in behavioral accuracy during the catch trials must be considered as a potential confound. The DD group performed the task less accurately, particularly for the more demanding PW, which could reflect increased cognitive strain and fluctuations in sustained attention. Because attention is known to modulate neural responses, the overall reduction in ERF amplitudes in the DD group might be partially driven by these attentional differences rather than exclusively by reading-specific deficits. However, it is important to note the extremely strict scoring criteria of our task: a response was marked as incorrect if even a single letter was misidentified. Children in the DD group consistently provided responses to all catch trials without omissions, indicating high task engagement and sustained participation. Their errors predominantly involved morphological variations, such as misreading suffixes or word endings, rather than a total failure to process the stimulus. Therefore, while cognitive strain was undoubtedly higher for the DD group, their continuous behavioral responding confirms that they remained actively engaged in the reading process.

Fourth, the internal homogeneity of our dyslexia group represents another limitation. We did not systematically evaluate spelling abilities alongside reading proficiency, which prevents us from differentiating between children with iRD, iSD, or combined difficulties. Because these distinct profiles may arise from different underlying cognitive mechanisms (Kemény et al. 2018), this unassessed heterogeneity could have contributed to the variability of the observed neurophysiological responses and potentially masked specific sub-group effects.

Finally, the generalizability of our findings should be considered in the context of orthographic transparency. Russian is a transparent language with consistent grapheme-phoneme correspondences, which encourages a strong reliance on sublexical phonological decoding. Consequently, the neural patterns observed here may differ from those in deep orthographies (eg English), where whole-word recognition strategies are more prominent. Therefore, cross-linguistic studies are needed to determine whether the activation profile we observed is a universal marker of dyslexia or specific to reading deficits in regular orthographies.

Declaration of generative Artificial Intelligence (AI) and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used Gemini (Google) to evaluate and provide suggestions for improving scientific writing style, correct spelling and grammar issues, correct inconsistencies in transitions, and improve the overall readability and logical flow of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take full responsibility for the content of the publication.

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Author contributions

Ilya Samoylov (Data curation [equal], Formal analysis [lead], Investigation [equal], Methodology [equal], Project administration [equal], Visualization, Writing—original draft, Writing—review & editing [equal]), Tatyana Bolgina (Conceptualization [equal], Data curation [equal], Formal analysis [supporting], Investigation [equal], Project administration [equal], Writing—review & editing [equal]), Georgii Lonshakov (Data curation [equal], Investigation [equal]), Ekaterina Shcheglova (Investigation [equal]), Militina Gomoiova (Investigation [equal]), Tatyana Yashina (Investigation [equal]), Vardan Arutiunian (Data curation [equal], Investigation [equal], Methodology [equal], Writing—review & editing [equal]), and Olga Dragoy (Conceptualization [equal], Methodology [equal], Resources, Writing—review & editing [equal])

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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Conflicts of interest

The authors declare no conflicts of interest.

Data availability

Data will be made available on request.

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