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Patterns of Cortical Activity in a Silent Single-Word Reading Task Depend on Word Frequency and Age-Related Differences: An MEG Study

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ABSTRACT

This study investigates how word frequency and age modulate the amplitude, temporal, and spatial patterns of cortical activation during silent single-word reading, as measured by magnetoencephalography (MEG). We recorded MEG data from 30 neurotypical adults and 30 typically developing children during a silent reading task involving high-frequency words, low-frequency words, and pseudowords, with cortical activation analyzed using event-related fields (ERF) and peak latency (PL). In both adults and children, high-frequency words elicited lower ERF amplitudes and faster processing times compared to low-frequency words and pseudowords. While similar neural regions were activated across stimulus types, children demonstrated significantly higher amplitudes and longer processing times than adults. These results indicate that word frequency significantly modulates the neural dynamics of reading, with high-frequency words processed more efficiently. Furthermore, the data suggest that the reading pathways in children are still maturing, as evidenced by their increased neural activation and delayed processing. This developmental difference, particularly the demonstration of frequency-dependent processing in the superior temporal gyrus of children, offers unique evidence for the maturation of distinct lexical and sublexical reading pathways, consistent with the dual-route cascaded theory.

1 | Introduction

Neural processing during reading involves functionally distinct stages such as analysis of visual features and letters, access to morphological and lexical units, and the activation of word meaning (Coltheart et al. 2001). However, detailed accounts of the sequences of cortical activation and their spatiotemporal characteristics remain relatively understudied (Caffarra et al. 2017). One of the dominant theoretical frameworks for understanding single word recognition is the dual-route cascaded (DRC) model (Coltheart et al. 2001). This model proposes two distinct routes for processing written words. The lexical route directly maps visual input to meaning, operating in parallel across the entire input string, which enables skilled readers to rapidly recognize familiar words and words with irregular pronunciations. In contrast, the sublexical route processes words serially one by one by applying a concise set of grapheme-to-phoneme correspondence rules. These rules are essential not only for producing accurate pronunciations of regular words but also for facilitating the reading of unfamiliar and novel words. Although the DRC model provides a comprehensive explanation of the cognitive processes underlying reading and illustrates how skilled readers adjust their strategies based on word familiarity, it is primarily based on analyses of behavioral reaction times and error types observed in acquired and developmental reading disorders (Salmelin 2007).

A widely acknowledged meta-analysis (Jobard et al. 2003) of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of word and pseudoword reading has differentiated two reading pathways: the dorsal pathway, which functionally corresponds to the sublexical reading route, and the ventral pathway, which corresponds to the lexical reading route in the DRC theory. The dorsal pathway comprises the left superior temporal gyrus, the left dorsal inferior parietal lobe, the insula, the precentral gyrus, and the left opercular and triangular parts of the inferior frontal gyrus (Price 2012; Rapcsak and Beeson 2015). It plays a crucial role in the serial phoneme-to-grapheme conversion necessary for novel word processing. The ventral pathway consists of the left fusiform gyrus, the left basal inferior temporal area, the left posterior part of the middle temporal gyrus, and the left orbital and triangular parts of the inferior frontal gyrus and has been implicated in rapidly processing the phonology of whole-word forms in relation to word meaning (Jobard et al. 2003; Price 2012; Taylor et al. 2015). Additionally, most fMRI studies have identified the left ventral occipitotemporal cortex as a crucial hub connecting the dorsal and ventral pathways; it is involved in the discrimination of letters, letter combinations, and the processing of letter strings with and without lexical meaning (Caffarra et al. 2021; Di Pietro et al. 2023).

Magnetoencephalography (MEG) studies of single-word reading have identified three spatially and temporally distinct functional components that reflect the stages of both word and pseudoword processing (Salmelin 2007). The first component, which is associated with basic visual feature analysis, is detected around the occipital midline approximately 100 ms after stimulus onset (Tarkiainen et al. 1999; Wydell et al. 2003). This is followed by a second, left-lateralized component in the occipitotemporal cortex, observed at around 150 ms, which is associated with letter-string analysis (Gwilliams et al. 2016; Tarkiainen et al. 1999). This component has been reported to reflect pre-lexical processing, as its response does not differentiate between words, pseudowords, or even consonant strings (Salmelin et al. 1996; Wydell et al. 2003). The third component is evident as a subsequent activation of the left superior temporal cortex, occurring between 200 and 600 ms after stimulus onset (Halgren et al. 2002; Helenius 1998) and has been linked to lexical, semantic, phonological, and morphosyntactic processing in word recognition (Halgren et al. 2002; Salmelin 2007).

Numerous studies have demonstrated both amplitude and temporal distinctions between word and pseudoword processing within the time window of the third component (Salmelin et al. 1996; Wilson et al. 2005; Wydell et al. 2003). By way of illustration, Wilson et al. (2003) show that word processing recruited the left perisylvian cortex at ~236 ms, whereas pseudoword processing delayed this region's involvement by ~106 ms. Words also elicited similar sources in the left perisylvian cortex, but the average amplitude of these sources was significantly greater for pseudowords. Recent MEG and electroencephalography (EEG) studies have shown that the amplitude and temporal patterns of cortical activity vary according to the word frequency. Specifically, high-frequency words have been shown to elicit lower amplitudes than low-frequency words (Barber et al. 2004; Hauk and Pulvermüller 2004; Kutas and Federmeier 2011; Larionova and Martynova 2022; Vergara-Martínez et al. 2013; Wang et al. 2021). However, the results provide unequal temporal data, with some studies reporting differences in the 150–250 ms window (Hauk and Pulvermüller 2004; Wang et al. 2021) and others observing differences in the 300–400 ms range (Barber et al. 2004; Kutas and Federmeier 2011; Larionova and Martynova 2022; Vergara-Martínez et al. 2013). Consequently, although the primary functional components of single-word reading in MEG are well-established, the detailed relationship between temporal dynamics and word frequency remains understudied.

Another research question is how the processing of word frequency is modulated by age? Several fMRI (see Houdé et al. (2010), for review) studies on children demonstrated similar patterns of activation during the processing of words with different frequencies in the left dorsal temporo-parietal, ventral occipitotemporal, and inferior frontal circuits as those observed in adults. On the other hand, to the best of our knowledge only two age-related MEG studies have been reported. Simos et al. (2001) found that children exhibited significantly greater activation than adults in the left temporoparietal region in response to both words and pseudowords, but showed significantly lower activation in the left inferior frontal gyrus for both types of stimuli. Notably, while the activation peaks during real-word reading did not differ between groups, children demonstrated an earlier peak in the left temporoparietal region during pseudoword reading (~297 ms for children versus ~579 ms for adults) and a significantly delayed peak in the left inferior frontal gyrus (~886 ms for children versus ~640 ms for adults). By contrast, Parviainen et al. (2006) reported that activity in the left temporal area during word reading was significantly greater in children compared with adult findings reported by Tarkiainen et al. (1999). In addition, temporal activation in children, relative to adults, was progressively delayed across cortical regions, with differences of ~12 ms in the occipital area, ~84 ms in the occipitotemporal area, and ~227 ms in the temporal area. Although these studies revealed significant age-related differences in both amplitude and latency measures, the limited number of investigations and the inconsistency in findings highlight the need for further research.

The aim of the present study was to investigate how word frequency and age influence the patterns of cortical activity measured by MEG, during a single-word silent reading paradigm in adults and elementary school-aged children. Based on previous studies, we hypothesized that: (1) cortical activity patterns vary with stimulus frequency, with pseudowords and low-frequency words eliciting higher amplitude and longer latency responses compared to high-frequency words; (2) cortical activity patterns differ between children and adults for all stimulus types, with children showing higher amplitudes and longer latencies than adults. To address these hypotheses, our results are structured to first present the within-group analyses for adults and children separately, followed by a direct statistical comparison between the groups.

2 | Method

2.1 | Participants

The final sample included 30 neurotypical adults (16 females; $M_{age} = 25.1$, age range 18.9–45.4 years, SD = 6.1) and 30 typically developing children (12 females; $M_{age} = 9.7$, age range 7.2–12 years, SD = 1.3). The initial cohort consisted of 35 adults and 38 children. From the adult group, five participants were excluded due to technical issues during the MEG recording ($n = 3$), anomalous right-hemispheric brain activity ($n = 1$), and inability to undergo MRI scanning ($n = 1$). From the child group, eight participants were excluded due to excessive movement artifacts in the scanner ($n = 2$), poor data quality from external noise unrelated to participant activity ($n = 2$), inability to undergo MRI scanning ($n = 2$), improper positioning in the MEG helmet that obstructed screen visibility ($n = 1$), and poor performance on the engagement monitoring task ($n = 1$). This resulted in the final sample of 30 adults and 30 children reported here. All participants were native Russian speakers. Exclusion criteria for the selection of the participants were the following: diagnosis of any learning disability, presence of a neurological or psychiatric disorder or having non-removable magnetic metal in their body.

The study protocol was approved by the HSE University Committee on Interuniversity Surveys and Ethical Assessment of Empirical Research in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans. Prior to data collection, all adult participants and the parents or legally authorized representatives of the children signed a written consent form.

2.2 | Behavioral Assessment in Children

The non-verbal intelligence of all children was assessed using Raven's Colored Progressive Matrices (Raven 2000). The language assessment was conducted using the Russian Child Language Assessment Battery (RuCLAB; Arutiunian et al. 2022), a standardized assessment tool for the evaluation of phonology, vocabulary, morphosyntax, and discourse in both production and comprehension domains. A mean language score (MLS) was calculated for each child. To assess children's reading abilities, the Standardized Assessment of Reading Skills (SARS, Kornev 1997) was used. SARS is a standardized instrument to assess reading fluency and comprehension, in Russian (Dorofeeva et al. 2019). According to the guidelines of SARS, the number of words read correctly in the first minute served as a reading fluency measure, while the number of correct answers served as a reading comprehension evaluation. The demographic and behavioral characteristics of the child participants are summarized in Table 1.

TABLE 1 | Demographic and behavioral characteristics of the child participants ($n = 30$).

	Range	Mean	SD
Age (years)	7.2–12	9.7	1.3
IQ	29–36	32.6	1.6
MLS	0.88–0.99	0.92	0.03
Fluency	29–162	82.3	36.8
Comprehension	4–10	8.5	1.7

Note: Reading fluency and comprehension scores are based on the Standardized Assessment of Reading Skills (SARS).
Abbreviations: IQ, intelligence quotient, based on Raven's Colored Progressive Matrices; MLS, mean language score, based on the Russian Child Language Assessment Battery (RuCLAB).

2.3 | Stimuli

The experimental stimuli were 65 high-frequency words, 65 low-frequency words, and 65 pseudowords. The initial selection of words was made from the Frequency dictionary of the modern Russian language (Lyashevskaya and Sharov 2009), comprising 100 high-frequency and 100 low-frequency words. Furthermore, for each word, its category was specified (e.g., animal, food, etc.) to ensure the diversity of the stimuli during selection. Additionally, for each word the age of acquisition was indicated (Akinina et al. 2014) to select those words that children acquire in the first stages of language acquisition ($M_{\text{age of acquisition}} = < 1.69$, SD = 0.63). The selected high-frequency words exhibited a familiarity rate of 4.9–5.0, while the low-frequency words exhibited a familiarity rate of 1.2–3.0. Pseudowords were generated with the multilingual word generator (Keuleers and Brysbaert 2010) based on selected words of varying frequency: 2.6–7.8 ipm (instances per million words in corpus), 50–200 ipm, 250–709 ipm, and 500–35,801 ipm (Lyashevskaya and Sharov 2009). The final pseudowords list comprised 65 items, 32 of which were based on low-frequency words (2.6–7.8 ipm) and 33 on high-frequency words (50–35,801 ipm). The stimuli were of equal length, containing five, six, or seven letters, and were distributed equally within each stimuli type. A complete list of all 195 stimuli (65 high-frequency words, 65 low-frequency words, and 65 pseudowords), including their original Russian form (Stimulus), an English translation (Gloss), and phonetic transcription (IPA), is provided in Table S1.

2.4 | Experiment Design

The design of the experiment was a silent single-word reading task programmed with PsychoPy (Peirce et al. 2019). The stimuli were presented as white text on a black background at the center of the screen. Each stimulus was displayed for a duration of 3000 ms, followed by a 1000 ms inter-stimulus interval (ISI) during which a central fixation cross was displayed to maintain participants' gaze. The stimuli were divided into three balanced blocks of 65 stimuli. The order of stimuli presentation within each block was randomized for each participant. To prevent adaptation, no stimuli of the same type appeared more than three times in succession. It is important to clarify that this constraint applied to the stimulus *category* (high-frequency, low-frequency, pseudoword), as each specific stimulus item was presented only once. This pseudorandomization resulted in the majority of trials being non-repeated (i.e., preceded by a trial from a different category; ~71%), with a smaller proportion of trials repeating twice (~22%) and rarely three times (~7%). To confirm that this trial sequence did not introduce systematic adaptation effects, a post hoc control analysis was conducted. We found no significant differences in mean whole-brain signal amplitude between non-repeated and repeated trials for either the adult group or the child group, confirming that category repetition did not systematically confound our main findings.

To monitor participant engagement, they were instructed to vocalize the last word they had read whenever a question mark appeared on the screen. An experimenter, observing the participant from outside the MEG chamber via a video feed with an integrated microphone, manually recorded the accuracy of each vocalization, marking it as correct (+) or incorrect (–). This engagement check occurred 16 times per block, for a total of 48 instances throughout the experiment. These trials were pseudorandomly distributed and balanced across the three stimulus conditions (16 high-frequency words, 16 low-frequency words, and 16 pseudowords). Consequently, the duration of each of the three experimental blocks was approximately 5 min (306 s). The order of the blocks was alternated for each participant.

2.5 | MRI Data Acquisition and Preprocessing

The T1 weighted MRI images were acquired with a 1.5 T Siemens Avanto scanner with the following parameters: repetition time = 1900 ms, echo time = 3.37 ms, flip angle = 15°, matrix size = 256 × 256 × 176, voxel size = 1.0 × 1.0 × 1.0 mm^3. MRI segmentation and reconstruction of the cortical surface was performed in FreeSurfer. The co-registration of structural (MRI) and functional (MEG) data was performed in the Brainstorm toolbox (Tadel et al. 2011) using six reference points: left and right pre-auricular points, nasion, anterior and posterior commissure, and interhemispheric point and about 150 digitized head points.

2.6 | MEG Data Analysis

MEG was collected using 306-channel cryogenic MEG (Vectorview, Elekta Neuromag) with a sampling rate of 1000 Hz. The position of participants' heads within the MEG helmet was monitored every 4 ms during the experiment via four head position indicator (HPI) coils digitized together with fiducial points using a 3D digitizer 'Fastrak' (Polhemus). We applied the temporal signal space separation (Taulu and Simola 2006) and movement compensation procedures implemented in MaxFilter software (Elekta Neuromag) to remove external interference signals generated outside the brain and to compensate for head movements. An electrooculogram (EOG) was recorded using four electrodes placed above and below the left eye (to detect the blinks) as well as at the left and right outer canthi (to detect horizontal eye movements). An electrocardiograph (ECG) was monitored with ECG electrodes to compensate for cardiac artifacts. MEG was recorded at a 1000 Hz sampling rate and filtered off-line with a band-pass (0.1–40 Hz) filter applied to continuous MEG files. Preprocessing included a two-step artifact rejection procedure. First, ICA was performed to remove physiological artifacts: components showing high temporal correlation with ECG/EOG channels, characteristic cardiac/ocular topographies, and power spectra consistent with these artifacts were identified and removed. Second, each epoch was inspected manually in Brainstorm. Epochs were rejected if they showed a peak-to-peak amplitude exceeding ±3000 fT/cm on gradiometers or otherwise contained clear artifacts (e.g., sudden SQUID jumps, muscle bursts, or flatline segments). Channels identified as bad during inspection were removed and interpolated. After this procedure, adult participants retained an average of 63.1 (SD = 4.01) trials (97%) for high-frequency words, 63.1 (SD = 4.03) trials (97%) for low-frequency words, and 63.2 (SD = 3.81) trials (97%) for pseudowords. Children retained an average of 63.3 (SD = 2.55) trials (97%) for high-frequency words, 63.4 (SD = 2.58) trials (98%) for low-frequency words, and 62.8 (SD = 3.42) trials (97%) for pseudowords. The filtered MEG recording was segmented into epochs with a duration of 4500 ms ranging from –1000 to 3500 ms, and DC offset correction from –100 to –2 ms was applied.

2.7 | MEG Source Analysis

For source reconstruction, we analyzed gradiometer data exclusively. Our choice was confirmed during initial data quality inspection, where magnetometer channels were observed to contain higher levels of noise, particularly in our pediatric participants—a common challenge in pediatric MEG due to factors such as head motion (Gross et al. 2013). This data-driven decision was further supported by our focus on cortically generated activity related to reading. Gradiometers are physically more robust against distant environmental noise (Hämäläinen et al. 1993) and often provide a superior signal-to-noise ratio (SNR) for the superficial neocortical sources central to our hypotheses (Baillet 2017). While this approach may reduce sensitivity to deep sources, it was chosen to maximize the reliability and spatial precision of our primary cortical findings. Individual head models were constructed using the Overlapping Spheres approach (Huang et al. 1999), fitting a separate sphere to each sensor. The ill-posed inverse problem was solved using depth-weighted linear L2-minimum norm estimation (MNE; Lin et al. 2006), with dipole orientations constrained to be normal to the cortical surface. To ensure numerical stability and mitigate the effects of measurement noise (Hämäläinen and Ilmoniemi 1994), we applied regularization when computing the inverse operator. The regularization parameter (λ) was set to 0.33, corresponding to an assumed signal-to-noise ratio of 3, estimated from the pre-stimulus baseline period (–100 to –2 ms) of the averaged event-related field (ERF) data. A single, common imaging kernel was computed per participant and subsequently applied to all epochs to reconstruct source activity for individual trials. Source estimation incorporated a noise covariance matrix derived from a 2-min empty-room recording acquired immediately after each participant's session. To facilitate group-level analysis and comparisons, individual cortical source estimates were spatially normalized to the standard "fsaverage" surface aligned with the ICBM152 nonlinear symmetric template. This normalization procedure involved: (1) coregistering individual T1-weighted MRI scans to the ICBM152 template using nonlinear volumetric registration; (2) generating individual cortical surface reconstructions; (3) performing spherical surface-based alignment of individual cortical surfaces to the fsaverage template; (4) interpolating individual source activity estimates (per vertex) onto the vertices of the fsaverage surface. ERF analysis was subsequently performed at the source level. Epochs were averaged, and the mean time course was calculated for each of ~15,000 vertices on the fsaverage surface. Cortical activation maps were normalized using a *z*-score transformation relative to the pre-stimulus baseline period (−100 to −2 ms).

2.7.1 | ROI Analysis

In accordance with the findings of previous studies and our own data, we have selected three sets of regions of interest (ROIs), anatomically defined using the Desikan-Killiany atlas implemented in Brainstorm, corresponding to functional components in the left hemisphere, which are known to be highly involved in the processing of single words during reading, and, similarly, we have identified the time windows of highest peak activity for each set of ROIs (Parviainen et al. 2006; Salmelin 2007; Tarkiainen et al. 1999; Vartiainen et al. 2011). The first set of ROIs corresponds to the first functional component and includes solely the lateral occipital cortex, with the signal reaching its maximum at 70 to 130 ms in both the adults and children. The second set corresponds to the second functional component and comprises two ROIs: the fusiform gyrus and the inferior temporal gyrus. The signal peaks at 120 to 200 ms in the adults and at 160 to 240 ms in the children. The third set corresponds to the third functional component and comprises eight ROIs: the middle temporal gyrus, the superior temporal gyrus, the inferior parietal lobule, the insula, the precentral gyrus, and three parts of the inferior frontal gyrus (pars opercularis, pars triangularis, and pars orbitalis). The signal reached its maximum value at 250 to 550 ms in the adults and at 380 to 680 ms in the children. For each ROI with an advised time window, averaged *z*-score normalized absolute values were extracted. First, data were extracted individually for every participant, and then averaged for each group. To perform within-group and between-group peak latency (PL) analyses, activation peaks for each region and each stimulus type were extracted individually. Subsequently, the number (*N*) of clearly identified peaks for each stimulus within a time window was quantified for each ROI (Figure 1). Detailed descriptive statistics for ERF and PL values are provided in Tables S1 and S2, with a corresponding visualization of the grand-average waveforms for each ROI presented in Figure S3.

2.7.2 | Whole-Brain Analysis

To complement the ROI analysis and provide a comprehensive examination of the spatial distribution of effects, we conducted a whole-brain analysis. This analysis was performed on the same *z*-scored source data from each individual participant. We conducted a series of vertex-wise permutation *t*-tests to identify significant cortical effects. Two sets of analyses were performed for each of the three functional components (time windows). *Within-group analyses*: To identify stimulus-dependent modulations within each group, paired-samples *t*-tests were used to compare the three stimulus types separately for adults and children. *Between-group analyses*: To identify age-related differences, independent-samples *t*-tests were used to compare the two groups (Adults vs. Children) for each of the three stimulus types separately. To correct for multiple comparisons across the ~15,000 vertices, we employed a non-parametric permutation test (1500 permutations) with a maximum statistic approach ("Max-T"). This robust method controls for the family-wise error rate across the entire source space. The statistical significance for all tests was set at a corrected *p*-value of < 0.05. Finally, to ensure the spatial robustness of the findings, only clusters comprising 15 or more significant vertices were retained for reporting and interpretation.

2.8 | Statistical Analysis

Statistical analysis and data visualization were performed in RStudio (R Core Team 2021), using linear models with the lme4 package (Bates et al. 2015) and the ggplot2 package (Wickham 2016) respectively. To assess ERF and PL between stimulus differences in both adults and children, we fitted a linear mixed-effects model with main effects of stimuli (high-frequency words vs. low-frequency words vs. pseudowords), a region (according to the set of ROIs), a stimuli × region interaction, and participants as a random effect. Then we applied the ANOVA function with Satterthwaite approximation for degrees of freedom and when main effects or interactions were significant, post hoc comparisons using Tukey's corrections were implemented. Moreover, for between-groups analysis, an effect of group (adults vs. children) was added.

Since the aim of our study was to investigate word frequency and developmental effects on patterns of neural activity, in this section we present only relevant post hoc results of the main effect of stimuli, stimuli × region interaction and group × stimuli interaction.

To assess the relationships between neural responses and behavioral measures in children, we fitted two linear mixed-effects models with ERF amplitude and PL time as the dependent variables, behavioral measures such as MLS, nonverbal IQ, reading fluency, reading comprehension and age as fixed effects, and participants as a random intercept.

3 | Results

3.1 | Task Performance

Analysis of the behavioral data from the engagement monitoring task confirmed that all participants were attentive and performing the task with high accuracy. The adult group demonstrated near-perfect performance across all conditions: high-frequency words ($M = 15.97$, $SD = 0.18$; 99.8% accuracy), low-frequency words ($M = 15.93$, $SD = 0.26$; 99.6% accuracy), and pseudowords ($M = 15.83$, $SD = 0.53$; 98.9% accuracy). The children's group also performed with high accuracy, showing slightly more variability on less frequent items: high-frequency words ($M = 15.79$, $SD = 0.62$; 98.7% accuracy), low-frequency words ($M = 14.93$, $SD = 0.96$; 93.3% accuracy), and pseudowords ($M = 14.79$, $SD = 0.94$; 92.5% accuracy). No participants were excluded based

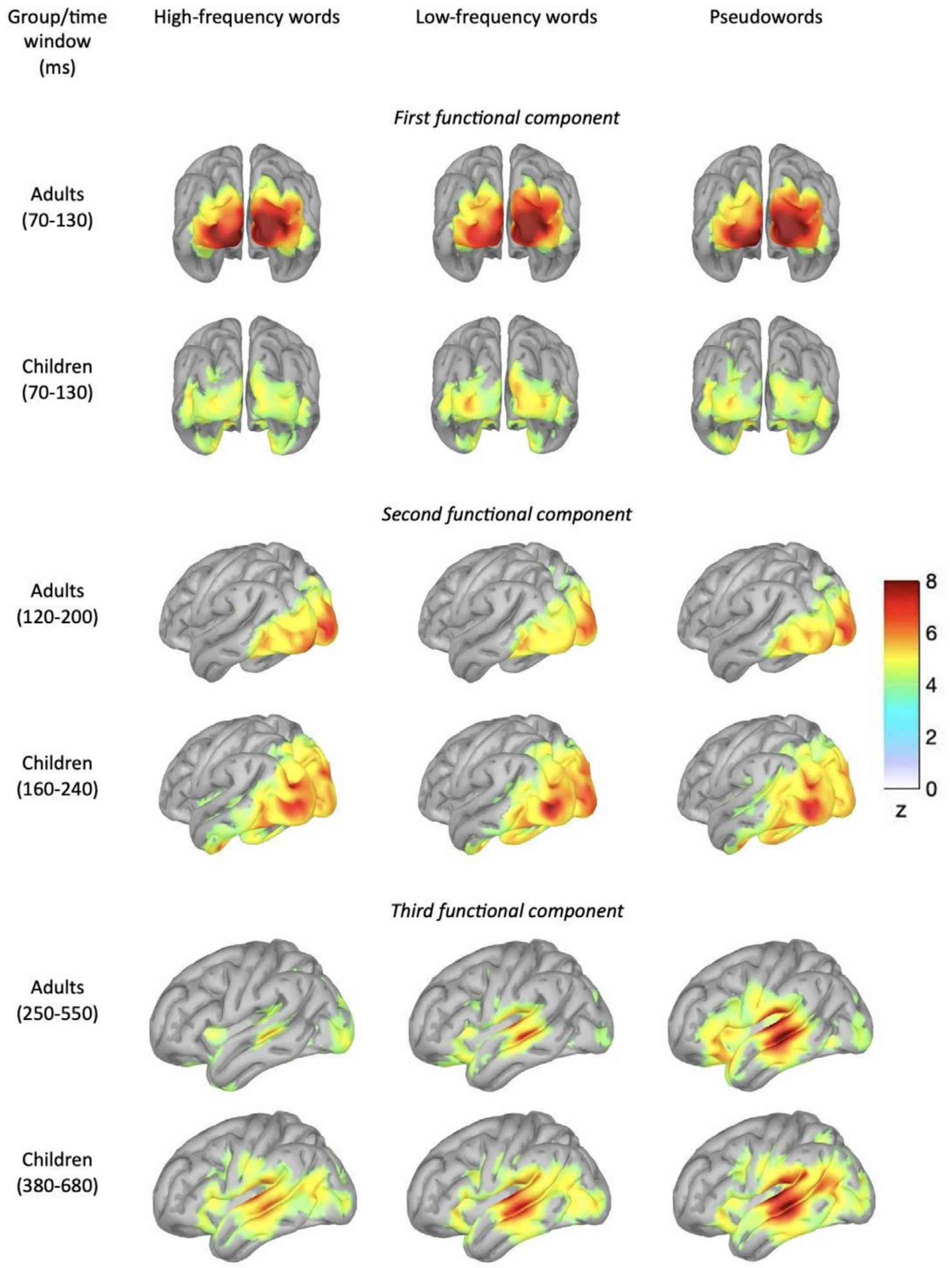

FIGURE 1 | Grand average *z*-score waveforms by ROI functional component during single word reading in adults and children.

on performance, as the high accuracy rates indicate sustained engagement with the task in both groups.

3.2 | ROI Analysis in Adults

3.2.1 | ERF Analysis

The results showed a significant main effect of stimuli ($F = 29.93$, $p < 0.001$), region ($F = 30.76$, $p < 0.001$), and the stimuli × region interaction ($F = 2.05$, $p < 0.005$), indicating that the amplitude of activation in adults differed between stimuli and between regions, and reflected inter-stimulus differences within regions. Post hoc analyses revealed that high-frequency words and pseudowords differed significantly ($t = -7.67$, $p < 0.001$), as did high- versus low-frequency words ($t = -3.00$, $p = 0.007$) and pseudowords versus low-frequency words ($t = 4.67$, $p < 0.001$). These comparisons indicated that pseudowords produced a larger ERF amplitude than both low- and high-frequency words, and that low-frequency words elicited a smaller amplitude than pseudowords but a larger amplitude than high-frequency words. Consequently, high-frequency words produced the smallest ERF amplitude among the three stimulus types (Figure 2a).

Further post hoc analyses of the stimuli × region interaction uncovered significant differences between high-frequency words and pseudowords in the middle temporal gyrus ($t = -3.73$, $p < 0.001$), superior temporal gyrus ($t = -4.78$, $p < 0.001$), inferior parietal lobule ($t = -3.00$, $p < 0.008$), pars opercularis ($t = -3.67$, $p < 0.001$), and pars triangularis ($t = -4.99$, $p < 0.001$), all showing higher amplitude for pseudowords. A significant difference between high- and low-frequency words was found in the

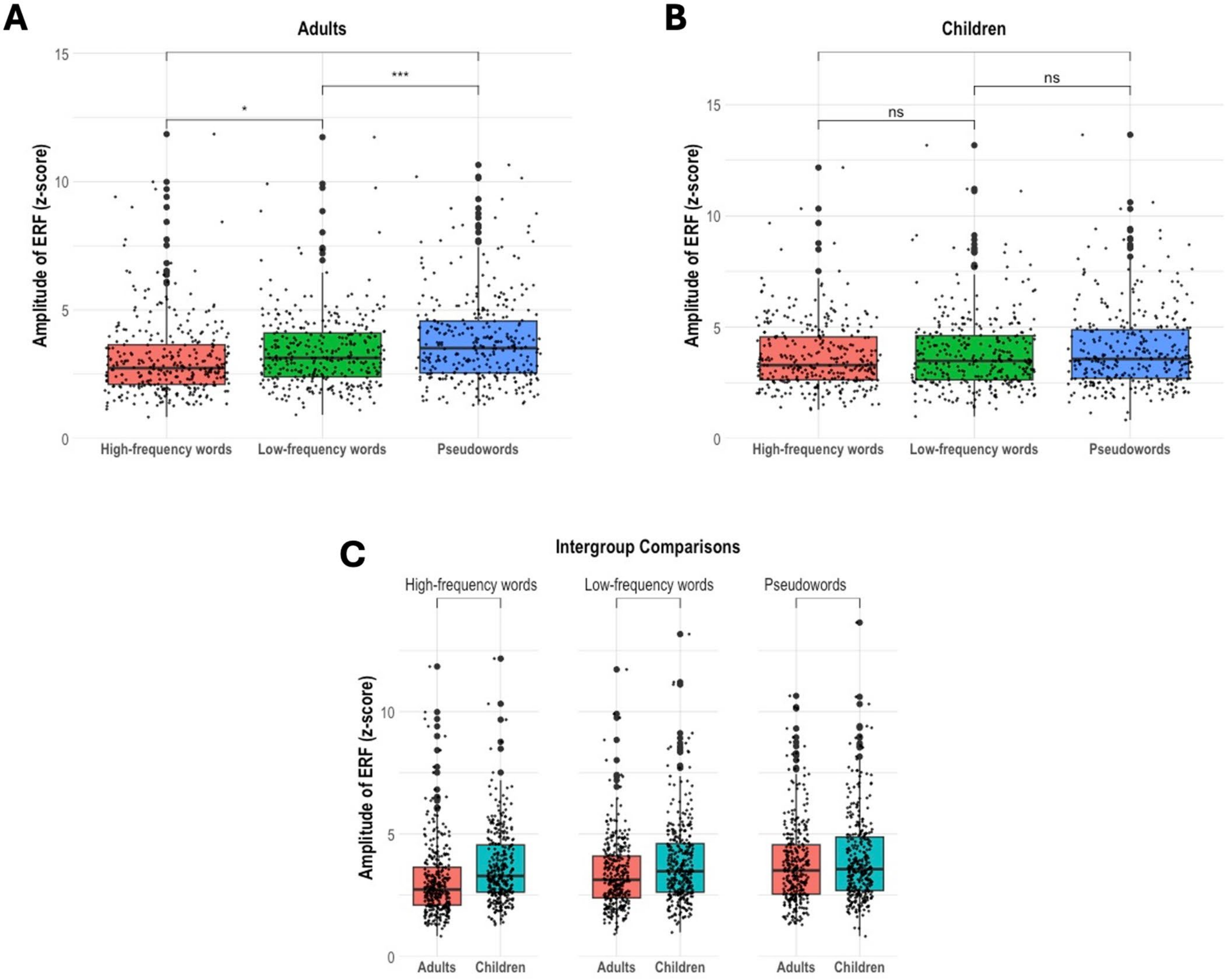

FIGURE 2 | Global averaged amplitude of event related fields (ERF) stimuli differences (A) in adults (B) in children (C) between groups.

superior temporal gyrus ($t = -2.44$, $p < 0.05$), with greater amplitude for low-frequency words. Finally, comparisons between pseudowords and low-frequency words revealed significant differences in the superior temporal gyrus ($t = -2.33$, $p < 0.05$) and pars triangularis ($t = -2.78$, $p < 0.02$), also demonstrating higher amplitude for pseudowords.

3.2.2 | PL Analysis

The findings revealed a significant main effect of stimuli ($F = 137.93$, $p < 0.001$), region ($F = 338.89$, $p < 0.001$), and the stimuli × region interaction ($F = 15.66$, $p < 0.001$), showing that PL differed between stimuli and regions, and reflected inter-stimulus differences within regions.

Post hoc analyses indicated that pseudowords elicited a significantly delayed PL compared to high-frequency words ($t = -16.01$, $p < 0.001$) and low-frequency words ($t = 4.16$, $p < 0.001$), and that low-frequency words produced an intermediate PL, larger than that for high-frequency words but smaller than that for pseudowords. High-frequency words exhibited the shortest PL among the three categories (Figure 3a).

Post hoc analyses of the stimuli × region interaction revealed that pseudowords produced a higher PL than high-frequency words in the middle temporal gyrus ($t = -10.57$, $p < 0.001$), superior temporal gyrus ($t = -10.37$, $p < 0.001$), inferior parietal lobule ($t = -10.65$, $p < 0.001$), precentral gyrus ($t = -12.90$, $p < 0.001$), pars opercularis ($t = -2.91$, $p < 0.02$), pars triangularis ($t = -3.11$, $p < 0.005$), and pars orbitalis ($t = -2.56$, $p < 0.03$). Comparisons between high- and low-frequency words showed a higher PL for low-frequency words in the middle temporal gyrus ($t = -5.84$, $p < 0.001$), superior temporal gyrus ($t = -8.49$, $p < 0.001$), inferior parietal lobule ($t = -8.90$, $p < 0.001$), and precentral gyrus ($t = -11.65$, $p < 0.001$). Finally, pseudowords elicited a significantly higher PL than low-frequency words in the middle temporal gyrus ($t = -4.75$, $p < 0.001$).

3.3 | ROI Analysis in Children

3.3.1 | ERF Analysis

The results showed a significant main effect of stimuli ($F = 4.07$, $p < 0.02$) and region ($F = 8.01$, $p < 0.001$), but not a stimuli × region interaction ($F = 0.59$, $p = 0.92$), indicating that ERF

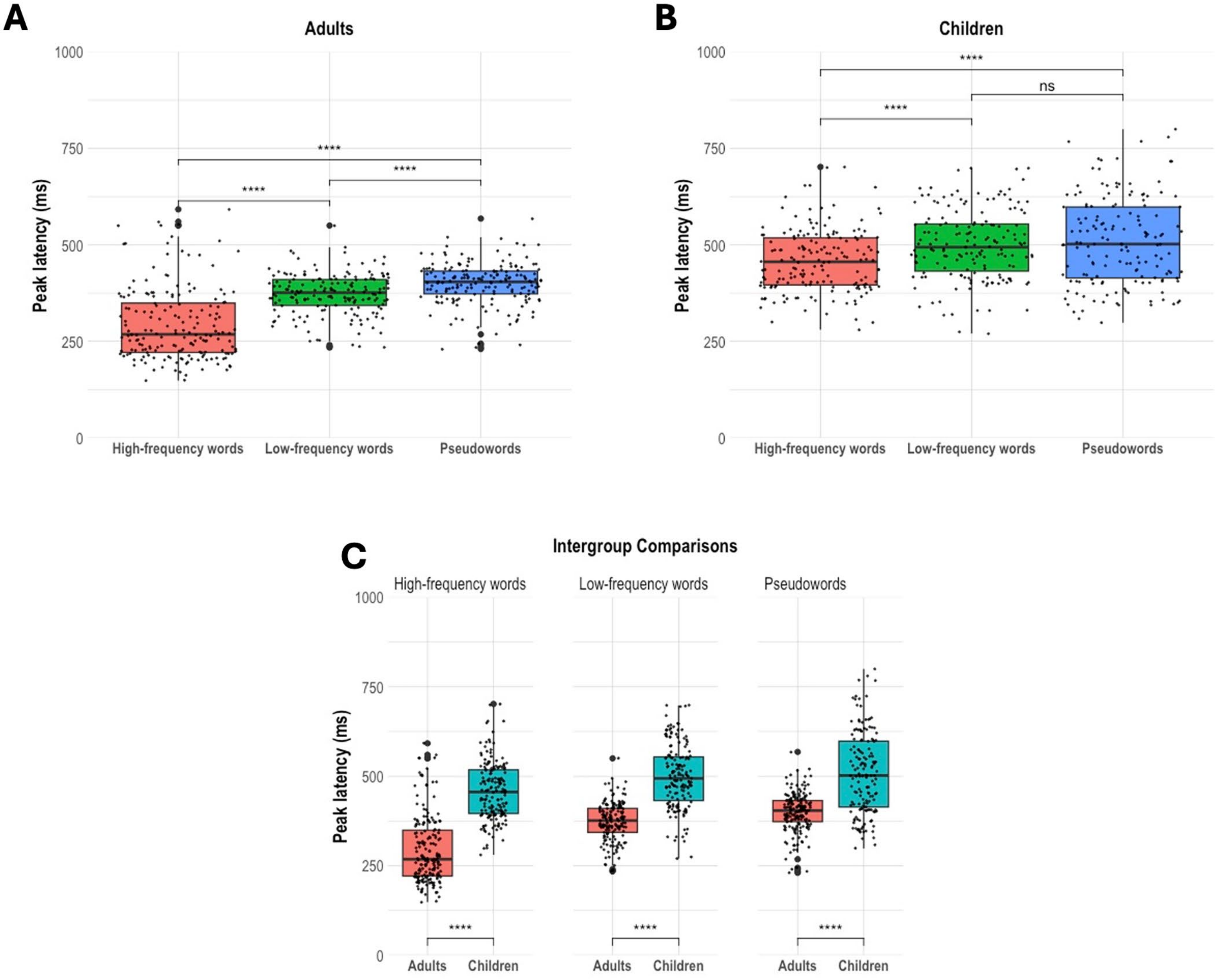

FIGURE 3 | Global averaged peak latency stimuli differences (A) in adults (B) in children (C) between groups.

amplitude in children differed between stimuli and between regions, but not within regions. Post hoc analyses revealed that pseudowords elicited a greater ERF amplitude than high-frequency words ($t = -2.85$, $p = 0.01$). Comparisons between high- and low-frequency words ($t = -1.32$, $p = 0.38$) and between pseudowords and low-frequency words ($t = 1.53$, $p = 0.27$) were not significant (Figure 2b).

3.3.2 | PL Analysis

The results showed a significant main effect of stimuli ($F = 18.87$, $p < 0.001$), region ($F = 331.25$, $p < 0.001$), and a stimuli × region interaction ($F = 2.23$, $p = 0.001$), indicating that PL differed between stimuli and regions, and reflected inter-stimulus differences within regions. Post hoc analyses revealed that pseudowords ($t = -5.55$, $p < 0.001$) and low-frequency words ($t = -5.10$, $p = 0.001$) elicited significantly later PLs than high-frequency words, whereas there was no significant difference between pseudowords and low-frequency words ($t = 0.43$, $p = 0.90$; Figure 3b).

Post hoc analyses of the stimuli × region interaction showed that pseudowords produced a higher PL than high-frequency words in the middle temporal gyrus ($t = -3.62$, $p < 0.001$), superior temporal gyrus ($t = -4.28$, $p < 0.001$), precentral gyrus ($t = -2.78$, $p < 0.02$), and insula ($t = -3.52$, $p < 0.002$). Comparisons between high- and low-frequency words revealed a higher PL for low-frequency words in the superior temporal gyrus ($t = -2.55$, $p < 0.03$), precentral gyrus ($t = -3.94$, $p < 0.001$), and pars orbitalis ($t = -2.63$, $p < 0.03$).

3.3.3 | Comparison of ERF and PL Data With Behavioral Scores and Age

To explore potential relationships between neural responses and individual differences in the children's group, we fitted linear mixed-effects models with ERF amplitude and PL as dependent variables, and age, nonverbal IQ, language scores (MLS), reading fluency, and reading comprehension as fixed effects. These analyses revealed no significant relationships between neural measures and any of the behavioral or demographic variables (all $p > 0.05$).

3.4 | Comparison of ROI Data Between Adults and Children

3.4.1 | Comparison of ERF

The findings demonstrated a significant group × stimuli interaction ($F = 3.78$, $p < 0.03$). Post hoc comparisons revealed that children exhibited greater ERF amplitudes than adults when processing high-frequency words ($t = -2.44$, $p = 0.01$), whereas no significant group differences were found for low-frequency words ($t = -1.89$, $p = 0.06$) or pseudowords ($t = -0.80$, $p = 0.42$; Figure 2c).

3.4.2 | Comparison of PL

The results showed a significant group × stimuli interaction ($F = 10.37$, $p < 0.001$). Post hoc comparisons indicated that children exhibited later PLs than adults for high-frequency words ($t = -15.86$, $p < 0.001$), low-frequency words ($t = -11.15$, $p < 0.001$), and pseudowords ($t = -13.20$, $p < 0.001$; Figure 3c).

3.5 | Whole-Brain Analysis

The whole-brain permutation analyses revealed several significant clusters of activity. For the within-group analyses in adults, the most prominent effects were found in the third component time window (250–550 ms), where pseudowords elicited significantly greater activation than high-frequency words. These effects were localized in a broad network in the right hemisphere, including the superior frontal gyrus (peak $t = 7.15$, $p < 0.001$), superior parietal lobule (peak $t = 7.98$, $p < 0.001$), and precentral gyrus (peak $t = 6.94$, $p < 0.001$).

The between-group analyses demonstrated significant age-related differences, predominantly in the first component (70–130 ms) and the second component (120–200 ms for adults vs. 160–240 ms for children) time windows. In the first component time window, adults showed significantly greater activation than children for high-frequency words, with one left-hemispheric cluster located in the superior frontal gyrus (peak $t = 5.38$, $p < 0.001$) and one right-hemispheric cluster in the postcentral gyrus (peak $t = 5.66$, $p < 0.001$). For the pseudoword comparison, adults showed a cluster of greater activation in the superior frontal gyrus in the left hemisphere (peak $t = 5.73$, $p < 0.001$), while children showed a cluster of greater activation in the same atlas region but in the right hemisphere (peak $t = -5.32$, $p < 0.001$). In the second component time window, the largest group difference was observed for low-frequency words, with children showing two clusters with greater activation in the bilateral superior frontal gyrus (left hemisphere: peak $t = -6.80$, $p < 0.001$; right hemisphere: peak $t = -6.33$, $p < 0.001$).

A complete list (with MNI coordinates) of all significant clusters for all 27 comparisons is provided in Table S5.

4 | Discussion

We investigated the amplitude, temporal and spatial patterns of cortical activation during the reading of single words with varying frequency in adults and children. We found a negative association between word frequency and both the amplitude of ERF and PL in both groups, with children exhibiting greater ERF and PL values compared to adults. The source localization was comparable across all stimulus types in both groups. Additionally, we investigated the associations between neural and behavioral data in the children group; however, no significant results were observed.

4.1 | The Neural Patterns of Adults

Our results indicate that the amplitude of cortical activation varies depending on word frequency. Specifically, the lowest ERF amplitude was observed in response to high-frequency words, intermediate amplitude for low-frequency words, and the highest amplitude for pseudowords. These findings are consistent with previous MEG studies that reported lower signal amplitude during word reading compared to pseudoword reading (Salmelin et al. 1996; Wilson et al. 2005; Wydell et al. 2003) and with EEG studies that demonstrated lower amplitude during high-frequency word reading relative to low-frequency word reading (Barber et al. 2004; Hauk and Pulvermüller 2004; Kutas and Federmeier 2011; Larionova and Martynova 2022; Vergara-Martínez et al. 2013; Wang et al. 2021).

A similar pattern was observed in the PL of cortical activation for the third functional component. Specifically, PL during the reading of high-frequency words occurred earlier than for low-frequency words, while the PL for low-frequency words was earlier than that for pseudowords. Shorter processing time for real words compared to pseudowords has been reported (Juphard et al. 2011; Whiting et al. 2015; Wilson et al. 2005), but other findings on time-course differences between high- and low-frequency words reading remain inconsistent (Larionova and Martynova 2022). Our results replicate the studies that found shorter processing times for real words and expand our understanding of the relationship between word frequency and temporal processing patterns. The analysis of the cortical sources revealed distinct temporal patterns in the superior temporal gyrus, the precentral gyrus, and the inferior parietal cortices. The processing time for high-frequency words in these regions was significantly shorter than for both low-frequency words and pseudowords. The linguistic sensitivity of the superior temporal area and adjacent regions has been demonstrated in previous MEG studies of single-word reading and is considered a key region for semantic processing (Salmelin 2007; Wydell et al. 2003).

Beyond the core reading network, our whole-brain analysis revealed how the adult brain flexibly engages an effortful, right-lateralized network when the automated lexical pathway is insufficient. Specifically, processing pseudowords compared to high-frequency words recruited a tripartite system in the right hemisphere. This system integrates: (1) articulatory planning for phonological assembly in the precentral gyrus (Fiez et al. 1999; Simos et al. 2000); (2) heightened visuospatial attention for sequential, letter-by-letter analysis in the superior parietal lobule, a key node of the dorsal attention network (Corbetta et al. 1993; Gitelman et al. 1999; Hopfinger et al. 2000); and (3) top-down executive functions, such as working memory and performance monitoring, in the superior frontal gyrus (du Boisgueheneuc et al. 2006). Collectively, the engagement of this problem-solving network demonstrates a strategic shift from effortless lexical access to a deliberate, resource-intensive decoding process, essential for navigating unfamiliar orthography.

Our findings in adults indicate that both the amplitude and time of cortical activation increase as word frequency decreases. This may reflect an increased neural involvement for orthographic coding and phonological processing (Jobard et al. 2003). We observed significantly shorter processing time for high-frequency words in regions associated with semantic processing, while the processing time for low-frequency words and pseudowords did not differ significantly. This pattern likely reflects different processing routes (i.e., lexical and sublexical pathways) and provides MEG evidence supporting the DRC theory. According to this theory, high-frequency words bypass phonological decomposition and are rapidly processed for meaning, thereby reducing processing time compared to low-frequency words and pseudowords.

4.2 | The Neural Patterns of Children

In the children's group, we found significantly lower ERF amplitude during the reading of high-frequency words compared to pseudowords, whereas no significant differences were observed between high- and low-frequency words. The finding that children exhibit greater activation when reading pseudowords compared to real words partially agrees with some previous studies (Coch et al. 2012; Kemény et al. 2018; Simos et al. 2001; Sun et al. 2023). By contrast, other studies (Coch et al. 2002; Khalifian et al. 2016) have reported similar signals during pseudoword reading compared to real-word reading. These discrepancies may be attributed to differences in experimental conditions, such as task demands for stimulus interpretation, judgment, and the presence of additional contextual information (Sun et al. 2023). In our study, we refined previous findings by demonstrating that children's ERF amplitude can differ under identical conditions, depending on the frequency of real words. In particular, the signal amplitude may not differ between real words and pseudowords when the real words are of low frequency, whereas significant amplitude differences emerge when real words are of high frequency.

Another word frequency effect was revealed in the PL analysis. We found that high-frequency words were processed faster than pseudowords and faster than low-frequency words, while no significant latency difference was found between low-frequency words and pseudowords. To the best of our knowledge, there was only one EEG study on the PL differences among real words and pseudowords, and no differences were reported (Hasko et al. 2013). Nevertheless, our results are consistent with extensive children's behavioral data indicating shorter processing time for high-frequency words relative to low-frequency words and pseudowords (Burani et al. 2002; Davies et al. 2013). Further analysis of the sources of cortical activation revealed significantly shorter processing time for high-frequency words compared to pseudowords in the middle temporal gyrus, the superior temporal gyrus, the insula, and the precentral gyrus. The key role of the superior temporal gyrus and its neighboring regions in semantic processing in children has also been demonstrated in previous MEG studies (Parviainen et al. 2006; Simos et al. 2001). However, our study is the first to show a difference in processing time depending on word frequency in this region.

In summary, the neural signals in the children's group exhibit distinct amplitude and temporal activation patterns when processing high-frequency words compared to pseudowords, while the activation patterns for low-frequency words and pseudowords do not differ. This may indicate the presence of distinct functional reading pathways in beginning readers, as well as the ongoing maturation of these pathways. Overall, these results underscore the critical role of word frequency in modulating neural activation in children and contribute to our understanding of the developmental trajectory of reading-related neural circuits.

4.3 | Group Comparison

Significant differences in activation amplitude between groups were observed only for high-frequency words, with children showing larger amplitudes. This likely indicates less automatized processing via the lexical pathway in children. Similar results were reported by Parviainen et al. (2006) in children compared with Tarkiainen et al. (1999) in adults, where children's activation amplitude was 1.4–2 times greater when only real words (consisting of four letters and not controlled for frequency) were used. Interestingly, Simos et al. (2001) reported that children exhibited higher activation amplitude than adults during both words and pseudowords reading in temporo-parietal regions, whereas in the inferior frontal gyrus adults showed greater amplitudes. These findings contrast with our results: while we did not find significant group differences in ERF activation for pseudowords, the overall amplitude in parietal, temporal, and frontal regions was significantly higher in children. It is possible that the higher amplitudes observed in adults in Simos et al. (2001) are due to the use of similar time windows for both groups, which did not account for age-related differences in processing time.

We also observed a progressive temporal delay in signal processing for all stimulus types in the children's group compared to the adults. In the regions involved in the second functional component, the delay was approximately 50 ms (inferior temporal gyrus), while in regions associated with the third component, the delay varied from approximately 150 ms (inferior frontal gyrus) to 220 ms (superior temporal gyrus). Similar temporal patterns were reported by Parviainen et al. (2006), who found delays of 84 ms in the left occipitotemporal region and 227 ms in temporal areas. In contrast, Simos et al. (2001) reported the opposite pattern in the temporo-parietal region: adults exhibited delayed processing during pseudoword reading (579 ms) compared to children (297 ms). Notably, when the signal transitioned to the inferior frontal regions, a "temporal lag" was observed in children (886 ms) compared to adults (640 ms). Although the authors of that study attributed the temporal lag in children to dominant processing in the temporo-parietal region and reduced involvement of the inferior frontal gyrus, the reasons for the observed delay in adults remain unclear. In both groups we found shorter activation latencies for high-frequency words compared to pseudowords in the superior temporal gyrus. This finding reinforces the crucial role of this region in single-word reading as demonstrated in experienced readers (Vartiainen et al. 2011; Wilson et al. 2005; Wydell et al. 2003) and extends our understanding of single-word reading in beginning readers.

Directly contrasting the two groups revealed significant age-related differences in processing efficiency. Children exhibited larger ERF amplitudes for high-frequency words and progressively delayed processing times across all stimulus types. While this pattern is often attributed to less automatized processing, a more complete explanation requires considering complementary neurodevelopmental mechanisms. One such mechanism is *compensatory over-recruitment*, where the developing brain engages broader, less specialized networks to support demanding cognitive tasks (Casey et al. 2005; Fair et al. 2009). Our whole-brain analysis provides direct evidence for this strategy: when faced with more demanding low-frequency and pseudowords, children displayed massive bilateral hyperactivation in the superior frontal gyrus relative to adults. This reliance on domain-general executive resources is a hallmark of an immature system compensating for still-developing reading circuits (Schlaggar and McCandliss 2007). This network-level compensation is likely necessitated by more fundamental physiological immaturities, specifically *immature inhibitory control*. The brain's inhibitory circuits, particularly GABAergic mechanisms crucial for refining neural signals, are not fully mature in children (Perica et al. 2022). This can lead to prolonged and exaggerated excitatory responses, providing a direct cellular-level account for the globally higher ERF amplitudes observed in our children group.

These functional and physiological factors are further compounded by the inherent properties of the developing brain's signals. Specifically, children's neural responses are characterized by *increased signal variability* from one trial to the next (McIntosh et al. 2008). When these individually variable responses are averaged to compute an ERF, slight inconsistencies in timing (jitter) can smear the resulting waveform, paradoxically inflating the measured peak amplitude (Ouyang et al. 2016). It is crucial, however, to distinguish this trial-to-trial inconsistency, which reflects less stable processing, from the concept of signal complexity or entropy, which actually increases with maturation and correlates with more stable behavior (McIntosh et al. 2008). Therefore, the elevated ERF amplitudes in children likely represent a composite effect: a genuine increase in neural effort reflecting compensatory cognitive strategies (over-recruitment and poor inhibition), combined with a measurement-related artifact stemming from the inherent variability of an immature system. This multi-faceted view aligns our findings with broader models of brain maturation, which characterize development as a trajectory from diffuse, variable, and effortful processing toward focal, stable, and efficient neural computation (Gogtay et al. 2004; Schlaggar et al. 2002; Turkeltaub et al. 2003).

In summary, children exhibited higher amplitude activation during high-frequency word reading compared to adults, while no group differences were observed for the other stimulus types. Despite longer processing times for all stimulus types in children, the overall spatiotemporal activation patterns were similar between groups. This suggests that although both groups employ similar reading pathways, children require greater neural engagement and longer processing time.

5 | Conclusion

Our study found that word frequency significantly modulates the amplitude and time of cortical activation during reading in both adults and children. High-frequency words elicited lower ERF amplitude and faster processing time compared to low-frequency words and pseudowords, supporting the DRC theory. Children exhibited higher amplitude and prolonged processing time, indicating that their reading pathways are still maturing. Both groups activated similar brain regions, although temporal delays were more pronounced in children. Overall, these results highlight the impact of word frequency and age on the neural dynamics of reading.

Notably, our research offers novel insights by directly comparing neural responses in adults and children under identical experimental conditions, which have rarely been addressed in previous studies. In addition, we are the first to demonstrate that the superior temporal gyrus exhibits frequency-dependent processing time differences in children, thereby refining our understanding of early semantic processing. These findings advance the current models of reading by providing unique evidence for distinct lexical and sublexical pathways during reading development and pave the way for future research on neural markers of reading acquisition.

6 | Limitations

It is important to acknowledge a potential limitation of the present study, namely the absence of a non-lexical, task-matched control condition, such as strings of false fonts or scrambled letters. The inclusion of such a condition would have allowed for a more direct isolation of lexical-semantic processes from more general visual, orthographic, and attentional responses that are inherent to processing any complex visual stimulus. While our design, which contrasts high-frequency words, low-frequency words, and pseudowords, was well-suited to our primary objective of investigating the modulation of neural activity *within* the linguistic domain, we recognize that a non-linguistic baseline would strengthen the specificity of our conclusions regarding language-specific processing. Future research employing MEG source localization would benefit significantly from incorporating such control conditions. This would enable a clearer dissociation of language-specific computations from domain-general perceptual and attentional processes, thereby providing a more complete picture of the neural architecture of reading.

A second limitation concerns the characterization of our adult sample. While all adult participants were highly educated (minimum 11+ years of education), reported no history of neurological or learning disorders, and demonstrated near-perfect accuracy on the in-scanner engagement task, formal cognitive and language screening was not conducted. The absence of standardized measures, such as IQ or language proficiency scores for the adult group, prevents a direct comparison of cognitive profiles between the two groups beyond age and self-reported history. Future studies would benefit from including such assessments to ensure the groups are comprehensively matched and to explore potential relationships between cognitive abilities and neural patterns in the adult cohort as well.

Author Contributions

Ilya Samoylov: methodology, investigation, writing – original draft, writing – review and editing, visualization, project administration, formal analysis, data curation. **Tatyana Bolgina:** investigation, data curation, project administration, formal analysis, conceptualization. **Georgii Lonshakov:** investigation, data curation. **Militina Gomozova:** investigation. **Vardan Arutiunian:** investigation, data curation, writing – review and editing, methodology. **Olga Dragoy:** conceptualization, methodology, writing – review and editing, resources.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.