Dynamic functional brain network connectivity during pseudoword processing relates to children's reading skill

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Declarations of interest: none

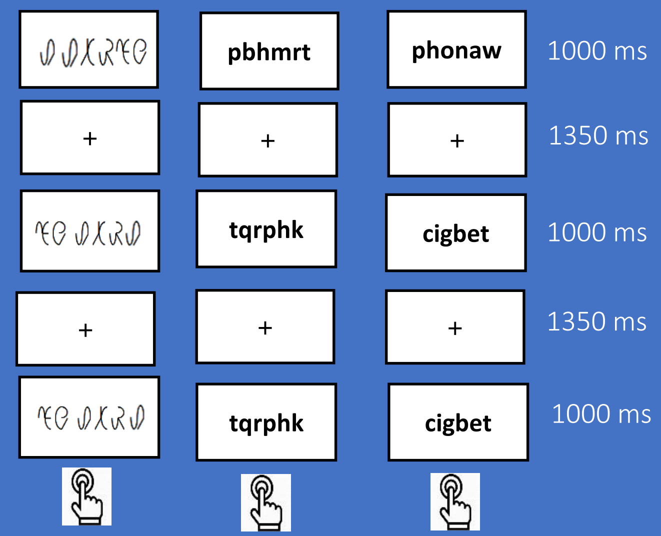
This is a pre-print. The final article is published as Panda, E. J., Kember, J. D., Emami, Z., Nayman, C., Valiante, T. A., & Pang, E. W. (2022). Dynamic functional brain network connectivity during pseudoword processing relates to children's reading skill. *Neuropsychologia*, 108181. https://doi.org/10.1016/j.neuropsychologia.2022.108181

Dynamic Functional Brain Network Connectivity During Pseudoword Processing Relates to Children's Reading Skill

How does the brain recognize print and link visual and phonological processing?

Which process (functional specialization vs. functional integration) relates to children's reading skill?

1-Back Task

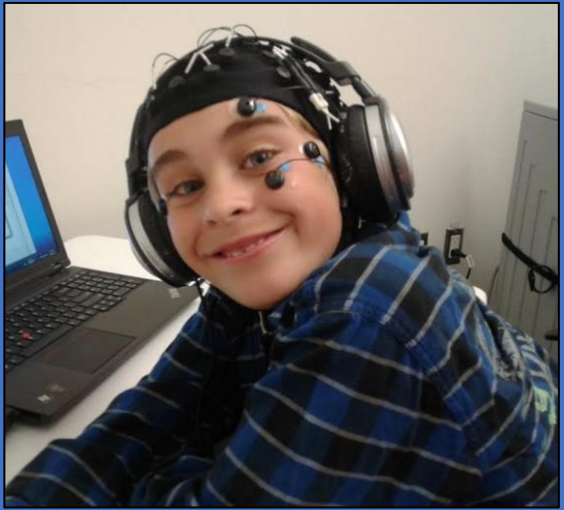


False Fonts	Consonants	Pseudowords	
	pbhmrt	phonaw	1000 ms
+	+	+	1350 ms
	tqrphk	cigbet	1000 ms
+	+	+	1350 ms
	tqrphk	cigbet	1000 ms

Unfamiliar → Unpronounceable → word-like

Coarse vs fine grained orthographic processing

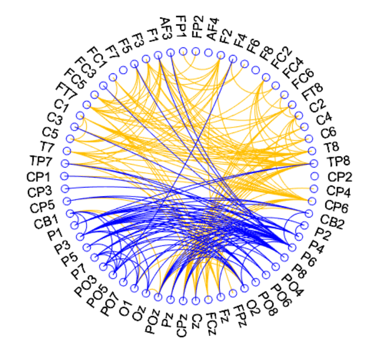
Participants



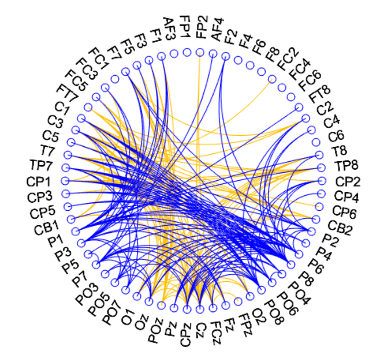
Adults and Children (ages 4-14)

Pseudowords – False Fonts

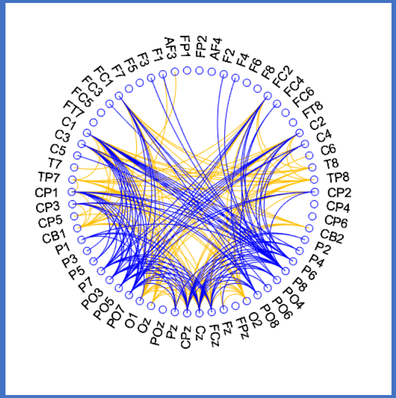
Delta (1-3 Hz) synchronization 314-475 ms



Lower Ability Readers (Children)



Higher Ability Readers (Children)



Highly Experienced Readers (Adults)

Posterior-Occipital areas (visual processing) show more brain network connectivity for (pronounceable) pseudowords in stronger readers

Reading development ≠ enhanced visual processing (N170 ERP specialization for print)

Reading development = more functional brain network connectivity/ more linking of visual print & speech sound processing

EEG phase synchrony → promising tool to study development of brain's function reading networks

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Dynamic functional brain network connectivity during pseudoword processing relates to children's reading skill | submitted to Neuropsychologia

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Abstract

Learning to read requires children to link print (orthography) with its corresponding speech sounds (phonology). Yet, most EEG studies of reading development focus on emerging functional specialization (e.g., developing increasingly refined orthographic representations), rather than directly measuring the functional connectivity that links orthography and phonology in real time. In this proof-of-concept study we relate children's reading skill to both orthographic specialization for print (via the N170, also called the N1, event related potential, ERP) and orthographic-phonological integration (via dynamic/event-related EEG phase synchronization – an index of functional brain network connectivity). Typically developing English speaking children (n=24; 4-14 years) and control adults (n=20; 18-35 years) viewed pseudowords, consonants and unfamiliar false fonts during a 1-back memory task while 64-channel EEG was recorded. Orthographic specialization (larger N170 for pseudowords vs. false fonts) became more left-lateralized with age, but not with reading skill. Conversely, children's reading skill correlated with functional brain network connectivity during pseudoword processing that requires orthography-phonology linking. This was seen during two periods of simultaneous low frequency synchronization / high frequency desynchronization of posterior-occipital brain network activity. Specifically, in stronger readers, left posterior-occipital activity showed more delta (1-3Hz) synchronization around 300-500ms (simultaneous with gamma 30-80 Hz desynchronization) and more gamma desynchronization around 600-1000ms (simultaneous with theta 3-7Hz synchronization) during pseudoword vs. false font processing. These effects were significant even when controlling for age (moderate – large effect sizes). Dynamic functional brain network connectivity measures the brain's real-time sound-print linking. It may offer an under-explored, yet sensitive, index of the neural plasticity associated with reading development.

Keywords: reading development; N170; functional brain network connectivity; EEG phase synchrony (phase lag index PLI); orthography; phonology

Highlights:

- Reading requires us to link visual print with speech sound processing
- Yet, most EEG reading research explores functional specialization not integration
- While children's age relates to ERPs (N170) associated with print specialization
- Children's reading skill relates to real-time functional brain network connectivity
- EEG phase synchrony = sensitive index of functional integration during reading

1. Introduction

An important part of reading is learning to automatically associate the sounds of speech with their visual representation. In fact, this ability to efficiently integrate phonology (speech sounds in language) with orthography (spelling and letter combinations in words) is considered the hallmark of skilled word reading and a core deficit in those with dyslexia or reading disability (Pugh et al., 2001). However, as we review below, most brain-based studies of reading development tend to examine the functional specialization associated with improved orthographic processing; far fewer have explored the functional brain network connectivity associated with integrating orthography and phonology in real time. This is a major gap in the literature (Bailey et al., 2018; Salmelin & Kujala, 2006; Schlaggar & McCandliss, 2007). Characterizing how functional network communication changes with orthographic specialization and reading skill development in typically developing children could allow us to better distinguish atypical from underdeveloped responses and inform our understanding of the potential functional reorganization that may occur for struggling readers with targeted reading remediation.

As (typically developing) children learn to read, their neural networks specialize and show preferential brain responses to the written/orthographic properties of words (Pleisch et al., 2019). Electrophysiological studies measure this functional specialization for print via the N170 (also sometimes called the N1 in children), an event related potential (ERP) component associated with specialized visual processing. A large body of research has shown that as children learn to read, the N170 becomes larger in response to print (e.g., words, pseudowords and consonants) than visually matched, unfamiliar symbol strings/false fonts (Fraga-González et al., 2021; Maurer et al, 2006; Schlaggar & McCandliss, 2007). This specialization is referred to as coarse orthographic tuning and seems to develop as abstract visual representations of letters and their sounds become associated with print (Pleisch et al, 2006). Coarse orthographic tuning follows an inverted U-shaped development, appearing largest shortly after children learn to read then becoming attenuated in older children and adults who have had more print exposure (Dehaene-Lambertz et al., 2018; Fraga-González et al., 2021; Maurer et al., 2006). With further reading experience, the N170 specializes for finer aspects of visual word recognition, like orthographic regularity. This specialization is referred to as fine orthographic tuning, and appears as a larger, left-lateralized response to orthographically regular print (words, pseudowords) compared to orthographically irregular print (consonant strings; Zhao et al., 2014). Together, coarse and fine orthographic tuning, which are typically measured through changes in the relative amplitude and left-lateralization of the N170 response to print, have been associated with increased reading experience throughout childhood, adolescence and into adulthood (Shallager & McClandis, 2007).

According to the phonological mapping hypothesis, the left-lateralization of the N170 for print reflects the linking of the predominantly left-lateralized auditory language system with the (initially bilateral) visual system during reading acquisition (Maurer & McCandliss, 2008). Support for this theory come from the finding that the left N170 has been consistently linked to the left ventral occipital-temporal cortex (vOT; e.g., Brem et al., 2006; Pleisch et al.2019), an area often termed the “visual word form area” due to a preferential activation to printed words compared to non-orthographic stimuli that emerges during the first year of reading instruction in most children (Dehaene-Lambertz et al., 2018). This area shows structural connectivity with the predominantly left-lateralized areas responsible for phonology and semantics even prior to reading instruction, and further develops this connectivity (both structurally and functionally) during the first year of reading acquisition (Saygin et al., 2016; Moulton et al., 2019). Reduced connectivity of the vOT with the rest of the brain's language network may also account for different N170 lateralization patterns sometimes reported in children with dyslexia compared to age-matched typically developing peers (Fraga-González et al., 2014) although group differences are not always observed (Setten et al., 2019). A core prediction stemming from this hypothesis is that children with stronger phonological awareness and decoding/reading skills should show greater left-lateralization of the N170 to print (Maurer & McCandliss, 2008); however, this has been inconsistently supported (Coch & Meade, 2016; Eberhard-Moscicka, et al., 2014; Fraga-González et al., 2021; Maurer & McCandliss, 2008; Sacchi & Laszlo, 2016; Setten et al., 2019; Zhao et al., 2014). Perhaps this is because the N170 for print measures the brain's localized functional specialization for orthography, and thus the outcome of orthographic-phonological linkages that developed during reading development (Share, 2008), rather than measuring the functional integration of orthography and phonology directly. In other words, measuring interactive specialization, or the interactions between brain areas that have become specialized for orthographic and oral language processing, may provide a more useful framework for understanding reading development (Johnson, 2011; Schlaggar & McCandliss, 2007).

The neural plasticity associated with children's reading development might then be better measured with methods that rely on the coordination of activity across the brain, as opposed to localized neural activity (e.g., N170). One such method of measuring functional brain network connectivity, EEG phase synchrony, involves correlating the phase of EEG oscillations from different electrodes. Unlike ERPs and oscillatory power (time-frequency) analysis, which measure the amount of activity at each electrode, EEG phase synchrony measures the coordination of frequency-specific activity *between* electrodes. Two areas are thought to be functionally connected (and so communicating with each other) if they show consistent synchronized dynamics (Fries, 2015). A handful of studies comparing children with dyslexia and typically developing readers suggest that EEG phase synchrony may provide insights into the functional communication that supports reading development (Bedo et al., 2021; Fraga-González et al., 2016; Vourkas et al., 2011; Xue et al., 2020; Zarić et al., 2017). For example, while a similar *amount* of global phase synchrony exists in the resting-state EEG networks of typically developing Grade 3 Dutch children and those with dyslexia, children with dyslexia show *less efficient* functional network configurations than typically developing readers (less integrated and more globally inefficient network communication, particularly at low frequencies, 4-8 Hz; Fraga-González et al., 2016). Similarly, Xue et al., (2020) also report no differences in global resting-state phase synchrony between Chinese children with and without dyslexia but show group differences in various graph-theory metrics of network integration configurations. Group differences in global phase synchrony may be even more pronounced when contrasting different reading-related tasks. For example, Zarić et al., (2017) found that when viewing words, children with moderate and severe dyslexia showed weaker high frequency (gamma: 60-70 Hz) phase synchrony than typical readers between left occipital and left inferior-temporal EEG sites, suggesting reduced left-posterior connectivity during visual word processing in dyslexia. Additionally, children with severe dyslexia showed stronger connectivity among right occipital, inferior-temporal and left central sites at beta and low gamma frequencies (~13-60 Hz) relative to typical readers when viewing words and relative to both typical readers and those with moderate dyslexia when viewing false fonts, perhaps suggesting compensatory right hemisphere involvement during word (and in some cases non-linguistic visual) processing that scaled with the severity of reading difficulties. Together this was interpreted as “altered” patterns of connectivity within the reading network in children with dyslexia. However, as highlighted by Fletcher, Lyon, Fuchs and Barnes (2019), underlying most brain studies of dyslexia is a "chicken-and-egg" dilemma: do differences in brain processing cause reading difficulties or are they a consequence of limited reading experience? Little research to date has focused primarily on typically developing children to examine whether variations in the functional network connectivity during print processing also relates to individual differences in typically developing children's reading skill level. Such work would help to differentiate atypical from typical functional communication within the network of brain areas involved in reading and for understanding the possible changes that may emerge for struggling readers with greater reading experience and targeted intervention.

Another gap in the literature is the reliance on static and time-invariant snapshots of the brain's functional network interactions. In contrast, dynamic, event-related (as opposed to resting state) EEG phase synchrony allows us to examine how functional network interactions dynamically reorganize to support cognition on the scale of milliseconds and during different reading-related tasks (Bola & Borchardt, 2016). This is achieved by calculating EEG phase synchrony over trials at each data time point and time-locked to stimulus onset, rather than collapsing across time. In this way, phase synchrony of the brain's oscillatory signals has been used to explore the time-frequency dynamics of the functional interactions that support reading in adults (Bedo et al., 2014; Molinaro et al., 2013). For example, using source-modeling of high-density EEG data Bedo et al., (2014) showed that during word reading the activity of vOT synchronizes with a network of mostly left-hemisphere brain areas involved in visual, semantic, and phonological processing to support word recognition. This synchronization occurred at low frequency theta (3-7 Hz) and high frequency gamma (30-50Hz) oscillations that largely overlapped in space and time[i]. This is consistent with the hypothesis that fundamental neural computations may be processed at high (gamma) frequencies within localized brain regions distributed throughout the brain, which are integrated together via low (theta) oscillations (Doesburg et al., 2012; Lisman & Jensen, 2013; Solomon et al., 2017). Additionally, bidirectional feedforward and feedback interactions between vOT and both early visual and higher-language areas such as the angular, superior temporal and inferior frontal gyri were seen at different time points from around 100-600 ms after word onset. This is consistent with the view of the vOT as the interface between bottom-up visual and top-down semantic and phonological orthographic processing (Price & Devlin, 2011) and highlights the benefit of examining how phase synchrony unfolds over time as opposed to static approximations.

The purpose of this study is to explore how typically developing children's reading skills relate to patterns of both functional specialization and integration during orthographic processing. To this end, we measured both ERPs and event-related (dynamic) EEG phase synchrony while typically developing children varying in age (4-14 years) and reading level were presented with pseudowords, consonants and unfamiliar false fonts in a 1-back memory task. Grounding our study in previous literature, we explore functional specialization for orthography via the N170 ERP responses. For coarse orthographic tuning to print we compare the N170 amplitude during the processing of pseudowords to unfamiliar non-orthographic false fonts); for fine tuning, we compare processing of orthographically regular/pronounceable pseudowords to irregular/unpronounceable consonant strings. For functional integration we explore how orthographic processing is communicated within the broader language network by comparing the time course of frequency-specific phase synchronization of EEG activity during pseudoword, consonant and false font processing. We compare how EEG phase synchrony changes over time while processing pronounceable pseudowords (involves integrating orthography and phonology) vs. unpronounceable consonants and unfamiliar false font (involves fine and coarse grain orthographic processing, respectively, but no integration with phonology). In doing so we can directly measure the time course of brain network integration that readers engage in as they specifically link speech sounds with their visual representations. We predict greater synchronization of posterior-occipital brain areas during pseudoword processing (for which orthography can be mapped onto phonology) in stronger readers. As we consider this an exploratory proof-of-concept study, a control group of highly experienced readers (University educated adults) are first reported to illustrate processing seen at end states of development.

2. Methods

2.1 Participants

Twenty-four children (age: 4.75-14.42 years, mean = 9.90; 10 females) and twenty adults (18-35 years; mean = 25.8; 10 females; University educated) participated in the study. They were recruited through word of mouth and poster advertisements in the community. We selected children from a large age range to explore the relationship between typical language/reading development and brain specialization for print across the elementary school years using a correlational design that controls for children’s age. The data from one child were excluded from analyses involving pseudowords because they chose not to complete that condition. All participants were native English speakers, righthanded (Edinburgh Handedness Inventory; Veale, 2014), had normal neurological health and normal or corrected-to-normal vision. All children were in the age-appropriate grade in school. All participants and parents of children provided informed consent; children provided assent. This study was approved by the Research Ethics Board at the Hospital for Sick Children and Brock University.

2.2 Stimuli

Figure 1 illustrates the experimental paradigm, which was adapted from Fraga-González et al., (2014). Participants were presented a series of character strings (each six characters long) consisting of either orthographically regular (pronounceable) pseudowords, consonants, or unfamiliar false font presented in a blocked design. Pseudowords (created using the pseudoword generator “Wuggy”, Keuleers & Brysbaert, 2010) were used instead of words, because they elicit similar N170 responses during one-back paradigms without the confounding effects of semantics (Zhao et al., 2014). Consonant strings were randomly generated strings of six consonants. False fonts were created by converting consonants into “3 Element False font 1600”, which matches the consonant strings on lower-level visual features (number of line elements, spatial frequency, contrast characteristics; Fraga-González et al., 2014).

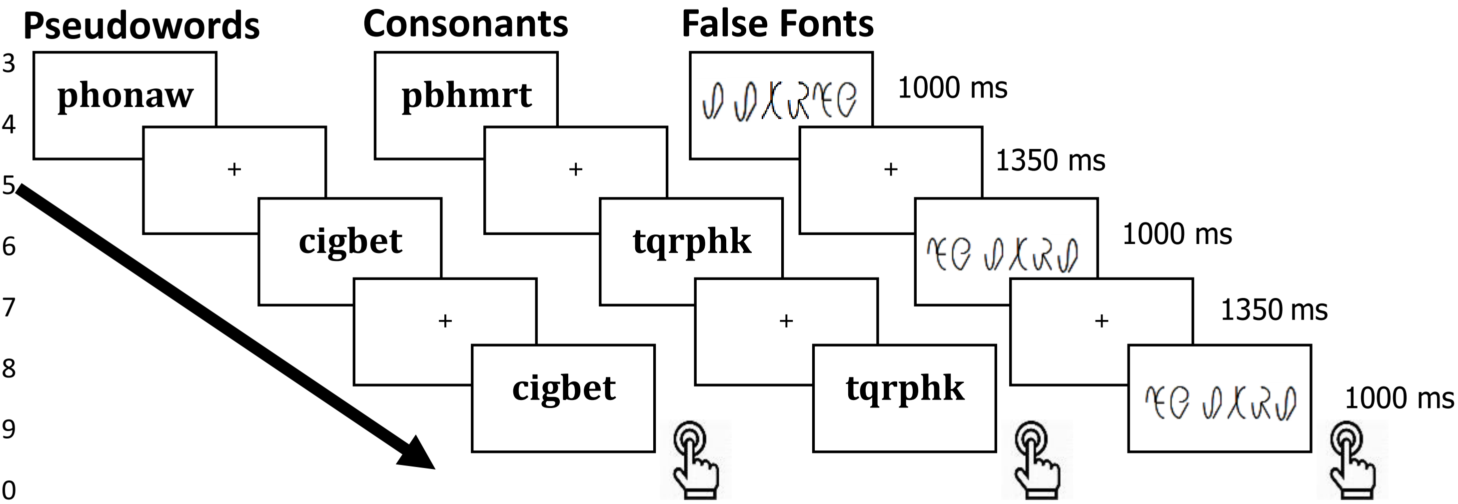

Figure 1. Experimental Paradigm. Pseudowords, Consonants, and False Font were presented in separate blocks. Participants were instructed to press a button when an item was repeated (1-back task). For each condition, there were 70 non-repeating trials.

Each condition (pseudowords, consonants, and false fonts) was presented as a pair of blocks, and each block consisted of 35 unique items and 7 randomly spaced repetitions which served as targets (brain responses to repetitions were not included in analyses). Participants completed a one-back task by pressing a button when an item was repeated. This 1-back memory task and block-design was chosen because it was used in previous studies that examined the N170 specialization for print (e.g., Eberhard-Moscicka et al., 2015; Fraga-González et al., 2014; Maurer et al., 2005; 2006) and in the functional connectivity study by Zarić et al., (2017). Stimuli were on screen for 1000ms, followed by a 1350ms interstimulus interval, during which participants viewed a fixation cross. There were 70 trials per condition.

2.3 Psychometric Tests

Children's reading ability was measured using three tests. Word reading accuracy and pseudoword decoding were captured with the Woodcock Johnson III's Letter-Word Identification and Word Attack subtests, respectively (Woodcock et al., 2001). Word reading fluency was measured using the Test of Word Reading Efficiency (TOWRE; Torgesen et al., 2012). We also measured children's vocabulary and visuospatial skills to explore whether any correlations with reading were truly reading-specific or generalized to other developmental domains. Receptive vocabulary was measured using the Peabody Picture Vocabulary Test-4 (PPVT; Dunn & Dunn, 2007). Expressive vocabulary and visuospatial reasoning were measured using the vocabulary and matrix reasoning subtests of the Weschler Abbreviated Scale of Intelligence (WASI-II; Wechsler, 2002). Age was used as a covariate in all correlations to control for maturation and explore language/reading specific effects (Coch and Meade, 2016). The reliability of these psychometric tests range from around .80 to .95 (TOWRE: .95, Tarar et al., 2015; PPVT: .94, Pae, Greenberg & Morris, 2012; WASI-VC: .94 and WASI-MR: .87, Maccow, 2011; WJ Letter-Word ID and Word Attack: .83 - .92, Mather & Gregg, 2001). Control adults were not measured on these abilities.

2.4 Procedure

Most children (n = 20) arrived for testing with a sibling or friend, while adults arrived alone. For participant pairs, one child was tested with EEG while the other completed the psychometric tests, and vice versa after a lunch break. Children's caregivers were not in the room during testing. During EEG recording, participants sat approximately 40 cm away from a laptop. They were given instructions before each task, then completed four practice trials (more if needed). EEG testing took approximately one hour, including other tasks reported elsewhere (Panda et al., 2020; White et al., 2018).

2.5 Data Recording and Preprocessing

Continuous EEG data were recorded from 64 electrodes (1000 Hz sampling, 0.01-200 Hz filter, impedance < 10kΩ), referenced to an electrode between Cz and CPz using a NeuroScan v4.5 Synamps2 (Compumedics, El Paso, TX). Data were processed in Matlab R2020a and Brain Vision Analyzer 2 using in-house scripts and the Fieldtrip toolbox (Oostenveld et al., 2011). Data were low-pass filtered at 100 Hz, re-referenced to the common average, epoched into individual trials from -3.0 to 3.0 seconds relative to stimulus onsets, de-trended, and downsampled to 500 Hz. Consistently noisy channels were replaced with interpolated proximal channels. Artifact rejection involved excluding trials with amplitude >±200 µV and independent component analysis to remove eyeblink and heartbeat artifacts (Jung et al., 2000). The outcome was an average of 63.01 trials (SD= 8.01) per condition entering analyses in children and 68.20 trials (SD= 2.38) per condition in adults; with a significant difference between groups ($p < .01$) but not conditions ($p > .10$).

2.6 Event-Related Potentials

ERPs provide a measure of functional specialization for print. To calculate this, ERPs were averaged relative to a 100ms pre-stimulus baseline for each participant. Grand-averaged waveforms for two groups (adults, children) were created for three conditions (pseudowords, consonants, false fonts). For each group, significant condition differences were identified using FieldTrip's cluster-based permutation tests (Oostenveld et al., 2011). At each electrode, conditions were compared with a two-tailed paired t-test. When at least two neighbouring electrodes exceeded a significance level corresponding to $p < .05$, they were grouped into clusters and their t-statistics were summed. This value was compared to a null distribution (created from 1000 random data partitions) and was considered significant if it was smaller than the 2.5th or larger than the 97.5th percentile. Permutation testing was applied to data averaged within 150-300ms for children, and 125-210ms for adults; time windows were selected based on visual inspection and previous N170 research in children (Zhao et al, 2014) and adults (Maurer et al., 2006). Effect sizes were calculated with Cohen's d by averaging across these time-windows, and across electrodes found in the cluster.

Developmental differences in the N170 effect among children was explored in two ways. First, using traditional time window analyses we identified regions of interest (electrode clusters that showed consistent condition differences). These included left (electrodes: P3-P5-P7-PO3-PO5-PO7-O1) and right (P4-P6-P8-PO4-PO6-PO8-O2) occipital-parietal, and bilateral frontal (AF3-AFz-AF4-F3-F1-Fz-F2-F4) regions, consistent with previous research to create averaged ERP waveforms for each region (Fraga-González et al., 2014). Differences between the magnitude of each component for each condition contrast (pseudowords-consonants; pseudowords-false fonts) were then averaged across time (150-300ms) and region, and correlated with children's age, receptive (PPVT) and expressive (WASIvc) vocabulary, visuospatial reasoning (WASImr), word reading (WJ letter/word ID), word decoding (WJ word attack), and reading fluency (TOWRE). Partial correlations that removed variance due to age allowed us to control for maturation and explore effects specific to reading/language (Coch & Meade, 2016). Given our sample size (24 children), we achieve a statistical power level of 0.8 for correlations with $r \geq .55$, power of 0.70 for correlations with $r \geq .50$, power of 0.60 for correlations with $r \geq .45$ and power of 0.50 for correlations with $r \geq .40$ (Algina & Olejnik, 2003).

Second, given the N170 latency changes thought to occur with development, we then used the 50% area latency measure to identify the peak latency for each participant and used the mean amplitude within a 100ms time-window surrounding this latency as a measure of component magnitude (Luck, 2014). This approach, which accounts for individual differences in N170 latency, involves defining the latency of each participant's component as the point at which the area under the 'curve' of the component is divided into equal portions. The curve, in this case, is defined as the ERP waveform within a certain time range underneath a certain amplitude boundary (Kiesel et al., 2008). A conservative time window of 125-300ms, and an amplitude boundary of 6.0 μV (which captured the ERP components of all participants across all conditions) were chosen. Across all children, the average latencies for pseudowords were 218ms (SD = 21) on the left and 219ms (SD = 20) on the right; for consonants, 215ms (SD = 19) on the left, 215ms (SD = 20) on the right; for false fonts 207ms (SD = 22) on the left and 208ms (SD = 25) on the right. The difference between conditions was then correlated with psychometric test scores in the same way as described above.

2.7 Phase Synchrony

Phase synchrony measures how coordinated the activity is between two electrodes (or, as is the case here, a group of posterior-occipital electrodes with all other electrodes) and indexes functional integration. In the present study, it was calculated as is described in Panda et al., (2020). Specifically, trial-by-trial data from each participant were z-scored and filtered into canonical frequency bands: delta (1-3Hz), theta (4-7Hz), alpha (8-13Hz), beta (14-30Hz) and gamma (30-80Hz; 60 Hz notch filter to remove electrical interference). Phase estimates of the band-limited data were obtained using the Hilbert transform. Cross-trial phase synchrony was measured using the Phase Lag Index (PLI; Stam et al., 2007). PLI calculates phase synchrony between electrodes with a slight time delay. This mitigates spurious effects of volume conduction and is preferred for EEG analyses that compare conditions over time (Cohen, 2014). PLI can therefore measure coordinated activity between brain regions, but does not imply a causal or directed relationship.

For each participant, phase synchrony of left and right posterior-occipital regions (average PLI values of electrodes P3-P5-P7-PO3-PO5-PO7-O1 and P4-P6-P8-PO4-PO6-PO8-O2, respectively) was computed for each condition and frequency band. The raw PLI values (which range from 0 to 1: no to perfect time-delayed phase-locking) were then normalized by subtracting the mean connectivity for each frequency band from each participant. Condition differences were evaluated for each group (adults, children), region (left, right) and frequency (delta, theta, alpha, beta, gamma) separately using two-tailed paired t-tests at each time point. A strict criterion was set to control for multiple comparisons: condition differences were considered meaningful only if they lasted longer than chance (i.e., outside the 95th percentile of a null distribution created from 10,000 random data partitions; Cohen, 2014). This resulted in time windows of frequency-specific synchronization (effects with positive PLI values) and desynchronization (negative PLI values). Effect sizes were calculated with Cohen’s d by averaging over the time windows of any significant effects. We then explored developmental differences in these synchronization/desynchronization effects by averaging PLI values across the time window, subtracting conditions, and correlating the outcome with children's psychometric test scores in the same way as reported for ERP effects.

2.8 Analysis of Behavioural Data

Behavioural results (i.e., performance during the 1-back task) were calculated as the hit rate (percent repetitions correctly identified) and false alarm rate (percent non-repetitions incorrectly identified as a repetition) These results were analyzed using separate repeated measures ANOVAs to test for possible performance differences between condition (pseudowords, consonants vs. false fonts) or between adults and children.

3. Results

3.1 Psychometric Tests

Raw scores on all reading, vocabulary and visuospatial tests were widely distributed, as expected from the wide age range of children (4.75-14.42 years). Word reading accuracy scores ranged from 5 – 71 (M = 50.61, SD = 16.28), word decoding from 3 – 32 (M = 21.04, SD = 9.03), reading fluency from 0 – 99 (M = 63.39, SD = 26.38), receptive vocabulary from 90 - 214 (M = 160.04, SD = 30.60), expressive vocabulary from 13 – 41 (M = 28.48, SD = 7.74) and visuospatial reasoning scores ranged from 7 – 27 (M = 16.35, SD = 5.68).

3.2 Behavioural Performance on the 1-Back Task

The average hit and false alarm rate to repeating (target) pseudowords, consonants and false fonts in adults and children are presented in Table 1. Generally high hit rates and low false alarm rates suggest that participants were completing the task as intended and that unfamiliar false fonts tended to be more difficult to identify, as expected. Results of the repeated measures ANOVA calculated on hit rate showed a main effect of condition [$F(2,39) = 8.36$, $p < .001$]. Follow-up paired samples t-tests showed that participants were less accurate at responding to repetitions in the false font condition compared to both consonants [*t*(42) = 2.87, *p* < .01] and pseudowords [*t*(41) = 3.90, *p* < .001], which did not differ from each other (*p*>.10). A similar main effect of condition was also found for the analysis of the false alarm rate [*F*(2,39) = 17.48, *p* < .001]. Participants made more false alarms during the false font condition compared to both consonants [*t*(42) = 5.08, *p* < .001] and pseudowords [*t*(41) = 2.90, *p* < .001], which did not differ from each other (*p*>.10). Additionally, overall children made more false alarms than adults [*F*(1,40) = 8.55, *p* < .01], with no significant condition x group interaction (*p*>.10).

Table 1

Behavioural performance on the 1-back task

Group	Hit Rate (%)			False Alarm Rate (%)		
	P	C	FF	P	C	FF
Adults	95.1 (15.2)	90.2 (13.2)	84.2 (10.9)	0.08 (0.33)	9.8 (1.3)	7.6 (3.78)
Children	89.3 (13.6)	88.7 (15.9)	82.0 (17.5)	9.7 (21.7)	10.8 (14.7)	18.8 (18.4)

P=pseudowords, C=consonants, FF=False Fonts

3.3 ERPs

Figure 2a shows ERPs at posterior-occipital electrodes averaged across all adults, and results of the cluster-based permutation tests. In adults, a negativity occurring around 150 ms, consistent with the N170, can be seen for all three conditions. At left hemisphere electrodes, this negativity appears to be largest for pseudowords, then consonants, then false fonts; on the right, largest for false fonts, with little difference between pseudowords and consonants. Permutation tests that compared pseudowords and false fonts between 125-210ms found two significant clusters, showing a negativity for false fonts (max sum = -20.23, *p* = .046, SD = .0059, CI = .0115, d = .587) most prominent at right posterior-occipital electrodes and a positivity for false fonts (max sum = 21.70, *p* = .028, SD = .0060, CI = .0117, d = .622) at bilateral frontal electrodes. Permutation tests that compared pseudowords and consonants showed no significant effects ($p > .1$)[ii].

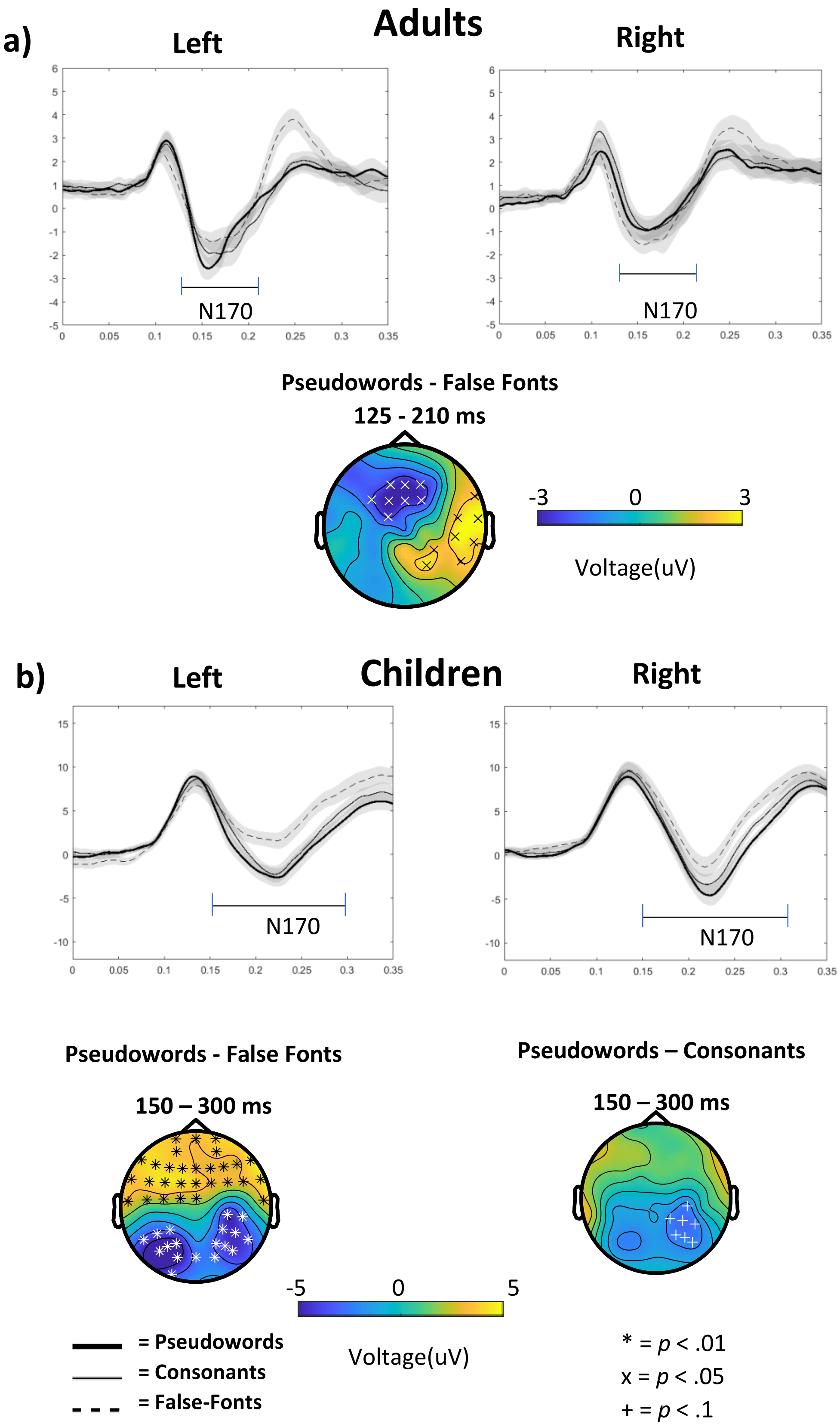

Figure 2. N170 ERP effects in Adults and Children. This figure show ERPs at left (average of electrodes: P3, P5, P7, PO3, PO5, PO7, O1) and right (P4, P6, P8, PO4, PO6, PO8, and O2) posterior-occipital sites for pseudowords, consonants and false fonts in adults (a) and all children (b) from 0 to 0.35s after stimulus onset. Standard error is plotted as a shadow bar. Below, the results of the cluster-based permutation tests are shown on topographical head maps to highlight the distribution of significant condition differences. In adults, permutation tests were run between 125-210ms. These show a right lateralized N170 effect that is larger for false fonts vs. pseudowords. In children, permutation tests were run between 150-300ms. These show a bilateral N170 effect that is larger for print (pseudowords and consonants) versus false fonts (coarse-grain) and a trend towards a right-lateralized N170 for pseudowords versus consonants (fine-grain). In children, N170 effects became larger on the left with children's age, vocabulary and visuospatial skills, but not with their reading (see Table 2 for correlations).

Figure 2b shows ERPs at posterior-occipital electrodes averaged across all children, and results of the cluster-based permutation tests. In children, a negativity occurring later than in adults, around 225ms, can be seen for all three conditions. On the left, this negativity appears larger for pseudowords and consonants compared to false fonts; on the right, largest to pseudowords, then consonants, then false fonts. Indeed, permutation tests that compared pseudowords and false fonts between 150-300ms found a significant cluster showing a negativity for pseudowords (max sum = -76.17, $p < .001$, SD = .0014, CI = .0028, d = .882), most prominent at bilateral posterior-occipital electrodes. Permutation tests that compared pseudowords and consonants found a marginally significant cluster showing a negativity for pseudowords (max sum = -17.60, $p = .053$, SD = .0071, CI = .0014, d = .524), largest at right posterior-occipital electrodes. These permutation tests also revealed significant clusters showing positive responses for pseudowords vs. false fonts (max sum = 101.15, $p < .001$, SD = .0009, CI = .0020, d = .727) and consonants vs. false fonts (max sum = 74.10, $p < .001$, SD = .0009, CI = .0020), most prominent at bilateral frontal electrodes.

Correlations between the amplitude of these effects and individual differences in children's age, language, reading and visuospatial reasoning skills are reported in Table 2.

Although these revealed developmental differences in the N170, none of these effects related specifically to children's reading skills. Both the pseudowords vs. false fonts (coarse-grain) and the pseudowords vs. consonants (fine-grain) effects became larger at left posterior-occipital electrodes as children aged, and as their receptive/expressive vocabularies and visuospatial reasoning developed (*r* values ranged from .42 to .48, *p*s < .05). Partial correlations that controlled for age were not significant. Importantly, no significant relationships were found for scores on any of the reading tests. No significant correlations were found for the frontal positive ERPs. The same pattern of results was found for the 50% latency analyses: when controlling for age, no significant partial correlations were found[iii].

Table 2

Correlations between children's age, psychometric test scores and ERP (N170) effects between 150-300 ms.

	Coarse grain Pseudowords – False Font		Fine grain Pseudowords - Consonants	
	Left	Right	Left	Right
Age	*.44*	-	*.47*	-
PPVT	*.42*	*.43*	-	-
Partial corr.	-	-	-	-
WASI V	*.44*	-	*.42*	-
Partial corr.	-	-	-	-
WASI MR	*.46*	-	*.48*	-
Partial corr.	-	-	-	-

For all correlations reported: p < .05

3.4 Phase Synchrony

Figure 3 demonstrates phase synchrony (mean PLI values) of left and right posterior-occipital electrodes over time in adults (3a) and children (3b) in the delta (1-3Hz) and gamma (30-80Hz) frequency bands. Phase synchrony in other frequency bands is shown in the supplemental figure. Solid boxes indicate time windows in which a significant difference between conditions was observed.

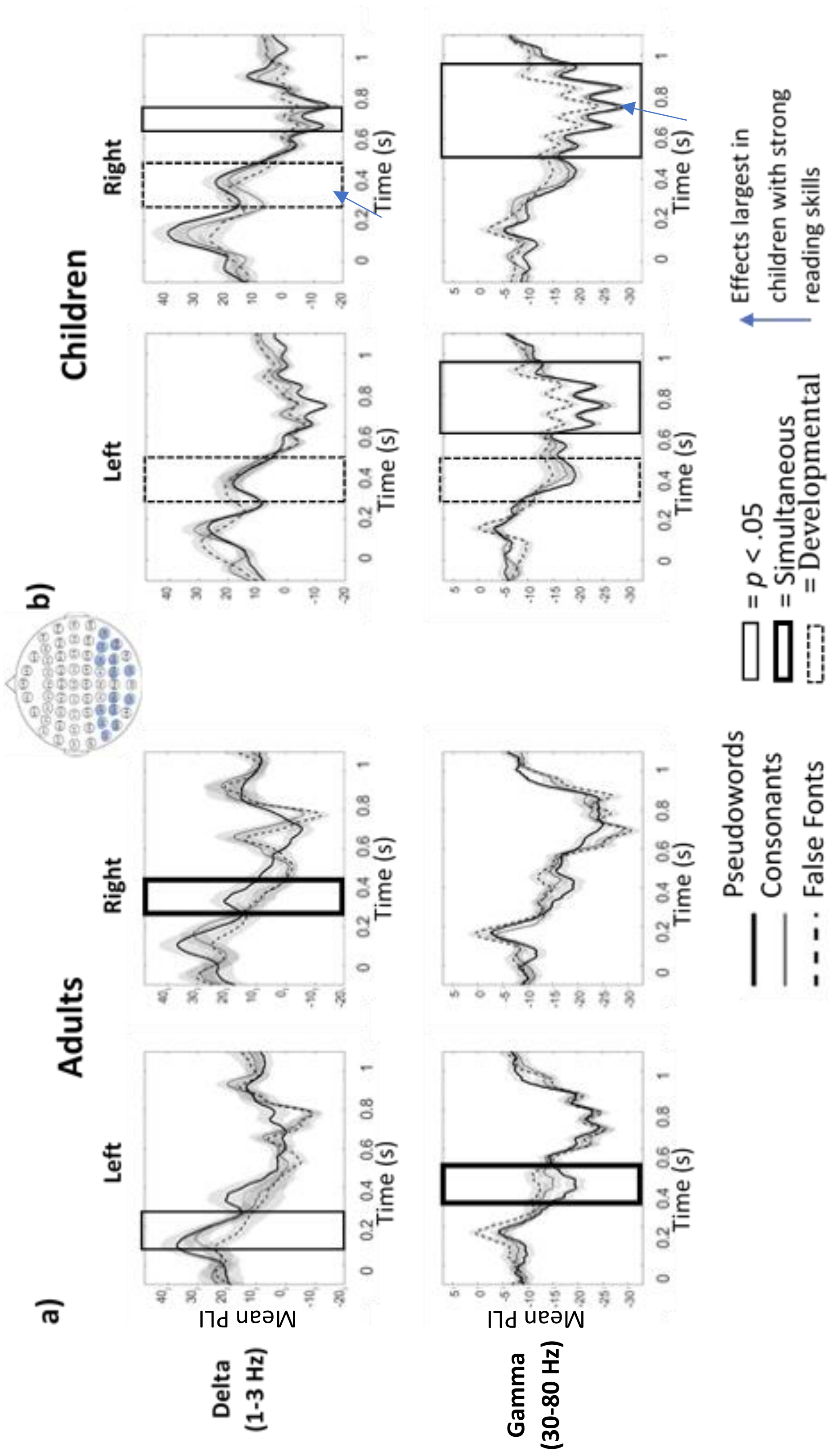
a)
Adults
Left
Right
b)
Children
Left
Right
Delta (1-3 Hz)
Gamma (30-80 Hz)
Mean PLI
Time (s)
Pseudowords
Consonants
False Fonts
= p < .05
= Simultaneous
= Developmental
Effects largest in children with strong reading skills

Figure 3. Regional Phase Synchrony Effects in Adults and Children. This figure shows phase synchrony (mean phase lag index, PLI) over time of left (electrodes: P3, P5, P7, PO3, PO5, PO7, O1) and right (P4, P6, P8, PO4, PO6, PO8, and O2) posterior-occipital sites for pseudowords, consonants and false fonts within Delta (1-3Hz) and Gamma (30-80Hz) in adults (a) and children (b). Notably, in adults, significantly greater delta *synchronization* for pseudowords vs. false fonts can be seen at the same time as greater gamma *desynchronization* for pseudowords vs. false fonts, both occurring ~315-480ms (dark black boxes). Although these were not significant across all children, correlations with the delta synchronization effect and children's reading skill, suggest it emerges with reading development. Additionally, children showed later effects (~600-1000ms) for pseudowords vs. false fonts including bilateral beta/gamma desynchronization (which was largest in children with strong reading/ poor visuospatial skills) and theta synchronization. Correlations with children's age and psychometric scores are presented in table 3 and 4; the beta and theta effects are shown in the supplemental figure.

Adults showed three effects that passed the multiple comparison control for significance. Two of these occurred around the same time and can be seen in the dark black boxes in figure 3a (larger delta synchronization and gamma desynchronization for pseudowords than for both consonants and false fonts around 315-475ms). The multiple comparison control revealed delta *synchronization* of right posterior-occipital electrodes at 314-475ms that was significantly greater for pseudowords vs. consonants ($p$corr < .05, d = .538; trending towards significance on the left). It also showed greater gamma *desynchronization* of left posterior-occipital electrodes at 315-486ms for pseudowords vs. false fonts ($p$corr < .05, d = .886). The simultaneous delta *synchronization* and gamma *desynchronization* effects were strongly correlated with one another (left: r = .-67, p < .001; right r = .-68, p < .001). Additionally, adults showed an earlier delta synchronization effect, between 56-216ms seen in the box within the top left plot in Figure 3a. This effect shows greater delta synchronization of left posterior-occipital electrodes for pseudowords vs. false fonts around the same time as the N170 ($p$corr < .05, d = .662).

Analysis of phase synchrony over time in the children is presented in Figure 3b, which shows the emerging of some adult effects, as well as a later gamma effect, not seen in adults. We first explored the three synchronization/desynchronization effects seen in adults. Although these were non-significant across all children, significant correlations were found between the ~315ms delta synchronization and gamma desynchronization and various developmental measures, suggesting both may become available with development (See Figure 3b dotted boxes and Table 3 for correlation results). Specifically, the delta synchronization of activity from left posterior-occipital electrodes between 314-475ms for pseudowords vs. false fonts increased with children's reading skill, even after controlling for age. Specifically, significant partial correlations that controlled for age were seen with this effect and children's pseudoword decoding (WJ word attack: partial $r = .41$, $p < .05$) and word reading fluency (TOWRE partial $r =.42$, $p < .05$) scores, highlighting that this effect is specific to children's developing reading skills. Similarly, delta synchronization of right posterior-occipital electrodes for pseudowords vs. consonants increased with children's receptive vocabulary, even when controlling for age (partial $r =.60$, $p < .05$). These correlations have moderate to high statistical power (Cohen's d 0.7-0.95; Algina & Olejnik, 2003). All other correlations became non-significant after controlling for age, suggesting these effects may emerge with maturation. Figure 4 (a and b) show a scatter plots of these relationships. No significant correlations or trend towards the adult's earlier delta effect at 56-216 ms was found for children.

Table 3
Correlations between children's development and early (~300-500ms) phase synchrony effects

	Coarse grain Pseudowords vs. False Font				Fine Grain Pseudowords vs. Consonants			
	Delta Synchronization		Gamma Desynchronization		Delta Synchronization		Gamma Synchronization	
	Left	Right	Left	Right	Left	Right	Left	Right
Age	-	-	-	*.42*	*.43*	-	*.52*	-
PPVT	*.51*	*.50*	-	-	*.45*	*.63*	-	-
Partial corr.	-	-	-	-	-	*.60*	-	-
WASI VC	-	-	-	-	-	-	-	-
Partial corr.	-	-	-	-	-	-	-	-
WASI MR	-	-	-	-	*.49*	*.43*	*.49*	-
Partial corr.	-	-	-	-	-	-	-	-
WJ Letter/Word ID	*.46*	*.49*	-	*.46*	-	-	-	-
Partial corr.	-	-	-	-	-	-	-	-
WJ Word Attack	*.54*	*.54*	-	*.45*	-	-	-	-
Partial corr.	*.42*	-	-	-	-	-	-	-
TOWRE	*.53*	*.50*	-	*.49*	*.41*	-	-	-
Partial corr.	*.41*	-	-	-	-	-	-	-

For all correlations reported: $p < .05$

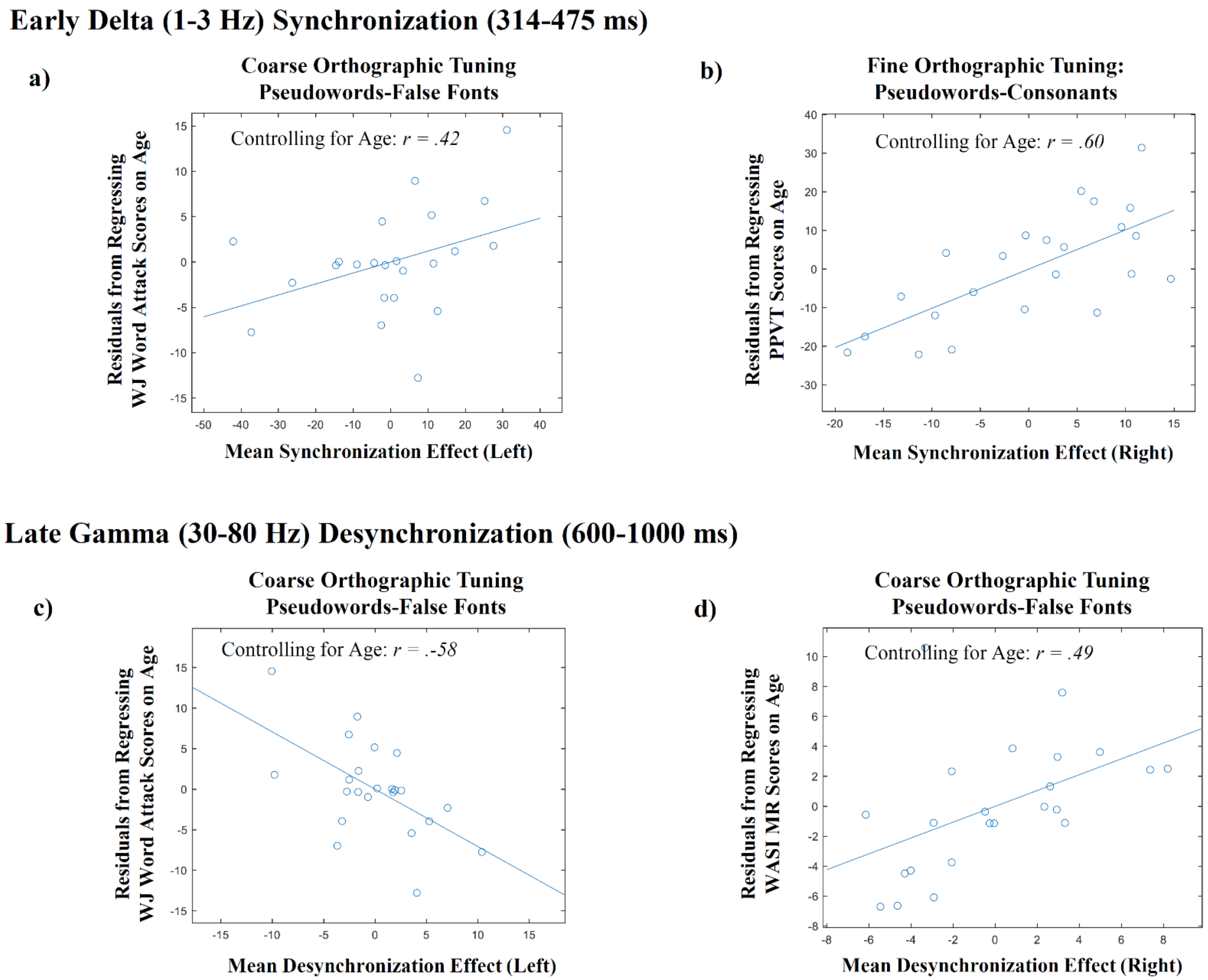

Figure 4. Relation between psychometric test scores and phase synchronization effects. This figure shows the relationship between the early delta (1-3 Hz) phase synchronization effect (314-475ms) from (a) left posterior-occipital electrodes and children's nonword decoding (WJ Word Attack); and (b) from right posterior-occipital electrodes and children's receptive vocabulary (PPVT); and the late gamma (30-80 Hz) phase desynchronization effect (600-1000ms) from (c) left posterior-occipital electrodes and children's nonword decoding (WJ Word Attack); and (d) from right posterior-occipital electrodes and children's visuospatial (matrix) reasoning (WASI MR). For all plots, the residuals from the linear regression that first controlled for age are plotted against the synchronization and desynchronization effects.

Figure 5 shows the distribution of the top connections that drove the low frequency synchronization effect for pseudowords in lower ability readers, higher ability readers and adults. This figure shows a shift in the distribution of connections with reading development: whereas in lower ability readers communication of bilateral posterior-occipital electrodes occurs mostly with itself, in higher ability readers and adults communication of posterior-occipital electrodes extends further to involve central electrodes as well. To quantify this observation, and to tease apart the effects of age and reading level in the shift from connections that are more localized within posterior-occipital sites to more distributed throughout across the brain, we correlated age and psychometric test performance with the phase synchrony (mean PLI) of posterior-occipital electrodes with other (non posterior-occipital) electrodes. As shown in Table 4, even when controlling for age, significant partial correlations between children's reading skills and delta phase synchrony at 314-475 ms between posterior-occipital sites and left hemisphere and midline electrodes can be seen. These partial correlations were most notable for TOWRE and word attack, which measure reading fluency and pseudoword decoding skills, respectively.

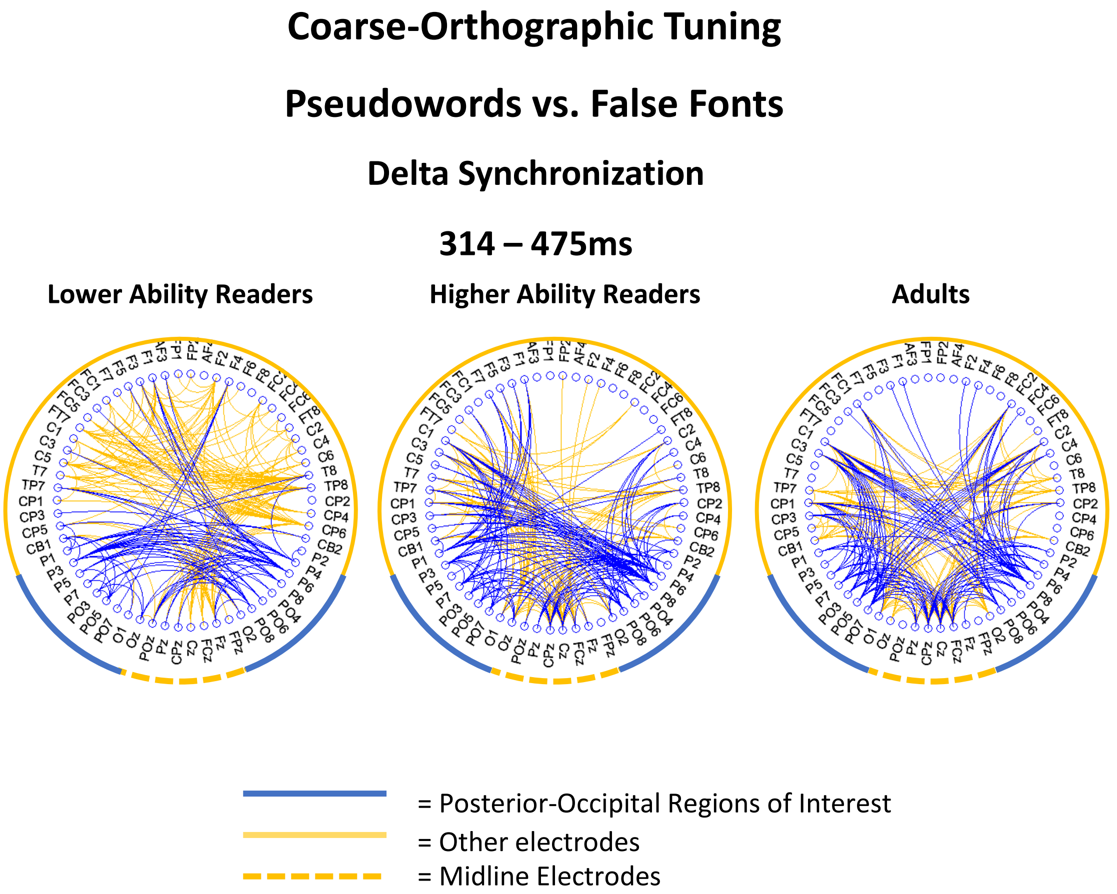

Figure 5. Developmental Differences in Network Connectivity. This figure shows developmental differences in the distribution of the top 10% strongest connections (phase synchrony) of left and right posterior-occipital with other electrodes (blue) for the delta (1-3Hz; 314–475ms) synchronization effect. The networks show delta (1-3Hz) synchronization between 314-475ms is mostly localized to posterior-occipital sites in lower ability readers (n = 11, WJ word attack: M = 13.45, SD = 7.16) but comes to involve more long-ranging connections to left hemisphere and midline sites in higher ability readers (n = 12, WJ word attack: M = 28, SD = 2.48) and adults (n=20).

Table 4
Correlations between children's development and the early delta phase synchrony effect (mean PLI) of left and right posterior-occipital electrodes with other electrodes

	Left	Midline	Right
Age	-	.49	.50
PPVT	*.47*	*.56**	.57*
Partial corr.	*.45*	-	-
WASI VC	-	-	.43
Partial corr.	-	-	-
WASI MR	-	-	.46
Partial corr.	-	-	-
WJ Letter/Word ID	*.43*	*.61**	.53*
Partial corr.	-	.45	-
WJ Word Attack	*.54**	*.67***	.52
Partial corr.	*.40*	.53	-
TOWRE	*.50*	*.68***	.55*
Partial corr.	*.45*	.56*	-

* = $p < .01$; **= $p < .001$ for all other correlations: $p < .05$

Additionally, across all children, notable bilateral *synchronization* and *desynchronization* effects for print (significantly greater for pseudowords vs. false fonts) were found around 600-1000ms that span a wide range of frequencies[iv]. The gamma frequency effect can be seen in the wide black boxes in Figure 3b; the effects in other frequencies can be seen in the supplementary figure. After controlling for age, more beta/ gamma desynchronization was seen for pseudowords vs. false fonts in children with stronger reading skills (partial r values range from -.44 to -.58) and weaker visuo-spatial skills (gamma left: partial r =.44, gamma right: partial r =.49, *ps* <.05). Notably the strongest correlations were seen with between the pseudoword-false font effect and scores on the Word Attack subtest, which measures children's pseudoword reading accuracy. These correlations have moderate to high statistical power (Cohen's d 0.7-0.9; Algina & Olejnik, 2003). Table 5 presents correlation analyses and figure 4(b) shows scatter plots[v].

Table 5
Correlations between children's development and late (600-1000ms) phase desynchrony effects

	Coarse Grain Pseudowords vs. False Fonts			
	Beta Desynchronization		Gamma Desynchronization	
	Left	Right	Left	Right
Age	-	-	-	-
PPVT	-	-	-	-
Partial corr.	-	-	-	-
WASI VC	-	-	-	-
Partial corr.	-	-	-	-
WASI MR	-	-	-	-
Partial corr.	-	-	*.44*	*.49*
WJ Letter/Word ID	-	-	-	-
Partial corr.	-*.46*	-	-*.55*	-
WJ Word Attack	-	-	-	-
Partial corr.	-*.53*	-	-*.58*	-*.48*
TOWRE	-	-	-	-
Partial corr.	-*.49*	-	-*.49*	-*.44*

For all correlations reported: $p < .05$. Note negative correlation means larger desynchronization effect

Around the same time (~600-1000ms), across all children there was significantly greater theta *synchronization* for pseudowords vs. false fonts (*p*corr < .05), although no significant correlations were seen with development. This low frequency synchronization showed a strong relationship with the high frequency desynchronization, particularly over the left hemisphere (Left: theta-beta: $r = -.71$, $p = <001$; theta-gamma: $r = -.62$, $p = .002$; Right: theta-beta: $r = -.44$, $p = .034$; theta-gamma: $r = -.43$, $p = .034$) [vi].

4. Discussion

This is the first study to characterize typical developmental patterns in the dynamic functional networks underlying the mapping of orthography and phonology in real time during print processing. We asked how children's reading level relate to: (1) the N170 specialization for print (a localized brain response to orthographic regularity); and (2) integration of orthographic and phonological information during pseudoword processing (a dynamic modulation of functional brain network communication). We found that children's reading ability was linked to more efficient coordination of activity from posterior-occipital areas with the rest of the functional brain networks (functional integration), rather than to the left-lateralization of N170 for print (functional specialization). Specifically, stronger reading skill was associated with more network communication of posterior-occipital activity (simultaneous low frequency synchronization/high-frequency desynchronization ~ 315 ms) during pseudoword processing, which involves integrating orthographic and phonological information. Additionally, around 600-1000ms, children, but not adults, showed more broadband high-frequency desynchronization of posterior-occipital activity for print (pseudowords and consonants) vs. false fonts simultaneously with low frequency synchronization. This effect was largest in the strongest readers and smallest in children with strong visuospatial skills. In contrast, local activation of posterior-occipital areas in response to print, as measured by the N170, related to children's age rather than reading level specifically. These results suggest that our understanding of the neural plasticity associated with reading development might be enhanced by examining the functional integration that occurs when brain areas involved in orthographic analysis dynamically coordinate activity with other brain areas involved in visual and phonological processing.

4.1 N170: specialization for print depends on age and domain-general development

In children, the N170 was larger for both pseudowords and consonants versus unfamiliar false fonts, reflecting enhanced coarse-grained processing of print. It was also larger for word-like pseudowords than consonant strings, reflecting enhanced fine-grained processing of orthographic regularities. Although, across all children, these effects were significant bilaterally (print vs. false fonts) or over the right (pseudowords vs. consonants), both became more left-lateralized with age, improved vocabulary and visuospatial abilities. Our results suggest three things about the specialization of the ventral occipitotemporal cortex (vOT; whose localized activity has been linked to the N170; Pleisch et al., 2019).

First, while the right vOT may be involved to some degree in orthographic processing, the left vOT becomes increasingly important across the school-aged years as its component neural populations become increasingly specialized for processing word-like stimuli. This is consistent with findings from previous research (Sacchi & Laszlo., 2016; Maurer & McCandliss, 2008). According to the phonological mapping hypothesis, left-lateralized N170 orthographic specialization develops through linking of phonological information from left hemisphere auditory language regions with visual input (Sacchi & Laszlo, 2016). This would explain why, in the present study, only the contrasts involving pseudowords (and not the consonants vs. false fonts contrast) showed significant correlations with age and skill development. Unpronounceable consonant strings may lack sufficient phonological associations to show specialized activation within the left vOT.

Second, and importantly, our results also suggest that while N170 specialization may be associated with maturation (age) and improved domain-general skills (IQ: visuospatial reasoning, vocabulary), it is not specifically linked to children's reading skill level. Indeed, none of the reading measures showed significant correlations with N170 effects. Although this contrasts with previous research in German by Zhao et al. (2014), languages with different orthographic depths (more consistent letter-phoneme correspondence) may show different developmental patterns. In line with our results, Coch and Meade (2016) found that in English, children's reading ability correlates with N170 amplitude to words, pseudowords, letter strings *and* false fonts, but not when controlling for age, suggesting domain-general development. According to the interactive account of the vOT (Price & Devlin, 2011), specialization for orthography occurs over many years of reading experience as the vOT integrates increasingly higher-quality top-down language input (phonological and semantic representations) with bottom-up sensory input to facilitate processing of print. In the present study, the correlation between children's age and their N170 specialization for print may also reflect more refined top-down representations that developed through increased reading exposure. Importantly, our results suggest that while individual differences in children's reading skills may *not* relate to N170 specialization (i.e., vOT activity at the moment of this facilitated visual recognition), they impact how that information is later communicated back up through the language network as it integrates with phonology (and likely word meaning). We discuss this with respect to our phase synchrony results.

Finally, in adults, the N170 was largest for false font compared to print (pseudowords and consonants) over right posterior-occipital areas. This effect, when considered alongside developmental effects seen in children, could be consistent with the inverted-U model of development and the lateralization typically reported (Fraga-González et al., 2021; Maurer et al., 2005; Zhao et al., 2014). Highly educated English-speaking adults, who process word and word-like stimuli with high automaticity, may show an N170 attenuated to the degree that the visual processing demands required by false fonts is greater than that of print. Consistent with this, during an early and narrow (140-170ms) time window, adults showed a trend towards a larger N170 for pseudowords vs. false fonts at left posterior-occipital electrodes. This suggests that orthographic specialization for print occurred early and quickly in our sample of adult readers.

4.2 Phase Synchrony

While our N170 findings, which reflect localized vOT processing, showed a domain-general developmental relationship, the subsequent coordination of posterior-occipital activity with the rest of children's functional networks related specifically to individual differences in their reading skills.

4.2.1 Early Stage: Integrated Processing within the Functional Reading Network Relates to Reading Development

The first effect, occurring around 300-500ms, appeared in adults as simultaneous greater delta synchronization and gamma desynchronization for pseudowords. In children, both became stronger with development and the increase in delta synchronization in particular related specifically to children reading and receptive vocabulary skills. Interregional communication is often seen through a simultaneous low-frequency synchronization (the driver of long-distance communication) and high-frequency desynchronization (as local regional processing decouples from activity elsewhere; Solomon et al., 2017). In the present study these effects showed strong linear relationships with each other, suggesting they work in conjunction to support coarse-grained, and perhaps to a lesser extent in our sample of participants, fine-grained processing.

In line with our hypothesis, only contrasts involving pseudowords showed enhanced synchronization (see footnote v), suggesting only pronounceable stimuli necessitated extended network communication. Similarly, low frequency synchronization between vOT and other nodes in the brain's reading network has been seen in adults during word reading around this time (~250-550ms), interpreted as bidirectional communication between the vOT and areas involved in phonological and semantic processing (inferior frontal, angular and superior temporal gyri; Bedo et al., 2014). It may be no coincidence that this timing coincides with the N400 ERP response, thought to index lexical access (Lau et al., 2008) and whose onset latency is relatively stable across development (Panda et al., 2020). Here we show, for the first time, that this low frequency synchronization relates specifically to children's reading and vocabulary skills, even when controlling for age. Additionally, while synchronization involved primarily posterior-occipital sites in lower ability readers, in stronger readers and adults it extended to include left-hemisphere and midline frontal and central regions as well (Figure 5). This transition (a decrease in short-range, localized functional connections within posterior-occipital areas towards an increase in long-range functional connections throughout the brain) is consistent with the interactive specialization framework of functional brain development (Johnson, 2011). It appears that with reading development comes dynamic brain reorganization, as the vOT becomes increasingly efficient at integrating visual and phonological information and communicating this throughout a distributed, yet well integrated, reading network. These findings are also inline with our previous study of listening comprehension in the same sample of children, in which we found enhanced delta phase synchronization for semantically congruent/meaningful sentences compared to those containing a semantic violation; an effect that correlated with their receptive vocabulary skill (Panda et al., 2020; See also White et al., 2018 for results in adults). Future studies would benefit from exploring how event-related phase synchronization and its dynamic functional network reorganization relates to other aspects of development and cognition as well.

In the present study, additional developmental differences were seen. In adults, delta synchronization was larger for pseudowords than consonants (fine-grained processing), while in children it became larger for both pseudowords versus consonants and false fonts (fine-and coarse-grained processing) as reading skills improved. Thus, similar patterns of network coordination might underpin coarse-, then fine-grained specialization at progressive stages of development, as readers become increasingly familiar with letters, followed by frequently occurring and pronounceable letter patterns. Regarding topography, delta synchronization in adults was significant over the right hemisphere (trending towards significance over the left) and in children its relationship with development was similar bilaterally. Conversely, gamma desynchronization in adults was larger for pseudowords versus false fonts over the left, whereas in children this coarse-grained effect became larger over the right as reading skills improved. It may be that low-frequency synchronization (indexing integration) and high-frequency desynchronization (indexing decoupling of localized activity) show different developmental trajectories. Delta synchronization of the left vOT for pseudowords may emerge earlier in development than its gamma desynchronization, which may emerge throughout the high school years and so was not observed in our sample of child participants. Synchronization of the left vOT may even become further refined and specialized for integrating orthographic processing of meaningful words compared to pseudowords that lack semantic content. This may explain why the left delta synchronization did not last long enough to reach significance in our sample of University educated adults with extensive reading experience. Future research, with children from an even wider age/skill range and using meaningful words, could delineate this further.

4.2.2 Late Stage: Compensatory network communication may support visual working memory encoding and maintenance

Around 600-1000ms, children, but not adults, showed simultaneous theta synchronization and broadband beta/gamma desynchronization bilaterally for print (pseudowords/consonants vs. false fonts). These effects showed a strong relationship with one another, particularly over the left hemisphere suggesting they work in conjunction to support coarse-grained processing. This may reflect a compensatory processing strategy used by children (particularly those with strong reading) to hold word-like stimuli in working memory during the one-back task. While future research will need to associate this activity with measures of working memory, simultaneous theta-synchronization/ high-frequency desynchronization has been reported around a similar time (400-1200ms) following the presentation of a word to be encoded into memory (Solomon et al., 2017). Similarly, Molarino et al., (2013) suggest that during sentence reading frontal to posterior-occipital theta phase synchronization indexes the working memory operations that help prepare for the perception of upcoming words in a sentence, while simultaneous low gamma phase synchronization reflect the lower-level perceptual processes involved in evaluating orthographic stimuli itself.

If our effects also relate to working memory encoding and maintenance of visual word form perception, it suggests two things. First, low-frequency synchronization/high-frequency desynchronization may play different roles, with high-frequency desynchronization associated with the extended processing and encoding of coarse-grained orthographic/visual information, and theta synchronization perhaps reflecting the interregional integration and maintenance of this information in visual working memory. Indeed, we found that while high frequency desynchronization related to children’s reading and visuospatial reasoning abilities when controlling for children's age, theta synchronization showed no relationships with our measures of development (but may have related to children's working memory). Secondly, the relative amount of desynchronization that children show during pseudoword vs. false font processing depended on children's reading and visuospatial skills. Children with strong reading skills showed relatively more decoupling of left posterior-occipital activity during pseudoword vs. false font processing, whereas for children with stronger visuospatial skills a similar amount of right posterior-occipital activity decoupling was seen for pseudowords, consonants and false fonts. Taking a step back, this suggests that children with different profiles of relative strengths/weakness in language/reading, visuospatial and working memory skills may recruit different brain network configurations during orthographic processing. It raises the question for future research to explore the extent to which different children may benefit from different methods of reading instruction to target their unique strengths/weaknesses.

One limitation of our study is that it is difficult to tease apart which of our phase synchrony effects are specific to orthographic-phonological integration versus task demands imposed by the 1-back memory task. Future studies may wish to explore the extent to which patterns of network integration may differ as a function of task demands (e.g., 1-back memory task used here to encourage implicit stimulus processing versus reading for meaning or a more explicit orthographic-phonological learning task; see Vergara-Martínez, Gomez, & Perea, 2020). Given the timing of our early effect (i.e., after the N170 and before the N400 ERP responses which are linked to orthographic and lexical processing, respectively) and its similarity to the phase synchrony effects reported during word recognition by Bedo et al., (2014), we predict that this response may be ubiquitous to any print processing task that involves orthographic-phonological integration. Our later low frequency synchronization/high frequency desynchronization effect, however, may very well differ as a function of task demands.

5. Conclusion

Our results suggest children's reading skill may be more directly linked to their real-time patterns of functional connectivity and brain network organization as they integrate visual and oral language processing, than through their functional specialization for print alone. Our understanding of the neural plasticity associated with reading development would be enhanced by future studies that link individual differences in children's reading, language and cognitive skills to both ERP and EEG phase synchrony responses to explore both functional specialization and integration at the same time. Our findings also point towards the importance of taking a developmental approach to understanding the neurocognitive changes that occur with reading development in typical and atypical populations. For example, we found that typically developing children with weaker reading/stronger visuospatial skills show reduced bilateral posterior-occipital connectivity effects for pseudowords vs. false fonts. A similar pattern was reported by Zarić et al. (2017) in their work that compared word and false font processing in children with dyslexia and age-matched typical readers (note children with dyslexia often show strong visuospatial skills alongside weak reading; Diehl et al., 2014). While Zarić et al. (2017) interpreted these findings as a qualitatively "altered" response seen only with disability, they may also reflect a delayed, yet still typical, response seen in less experienced readers. Future studies may wish to compare children with dyslexia to younger typical readers that are matched in reading skill, rather than age, to explore this further. In the future, this may help us differentiate between children with reading disabilities who show atypical versus underdeveloped responses, and to better support struggling readers through targeted remediation.

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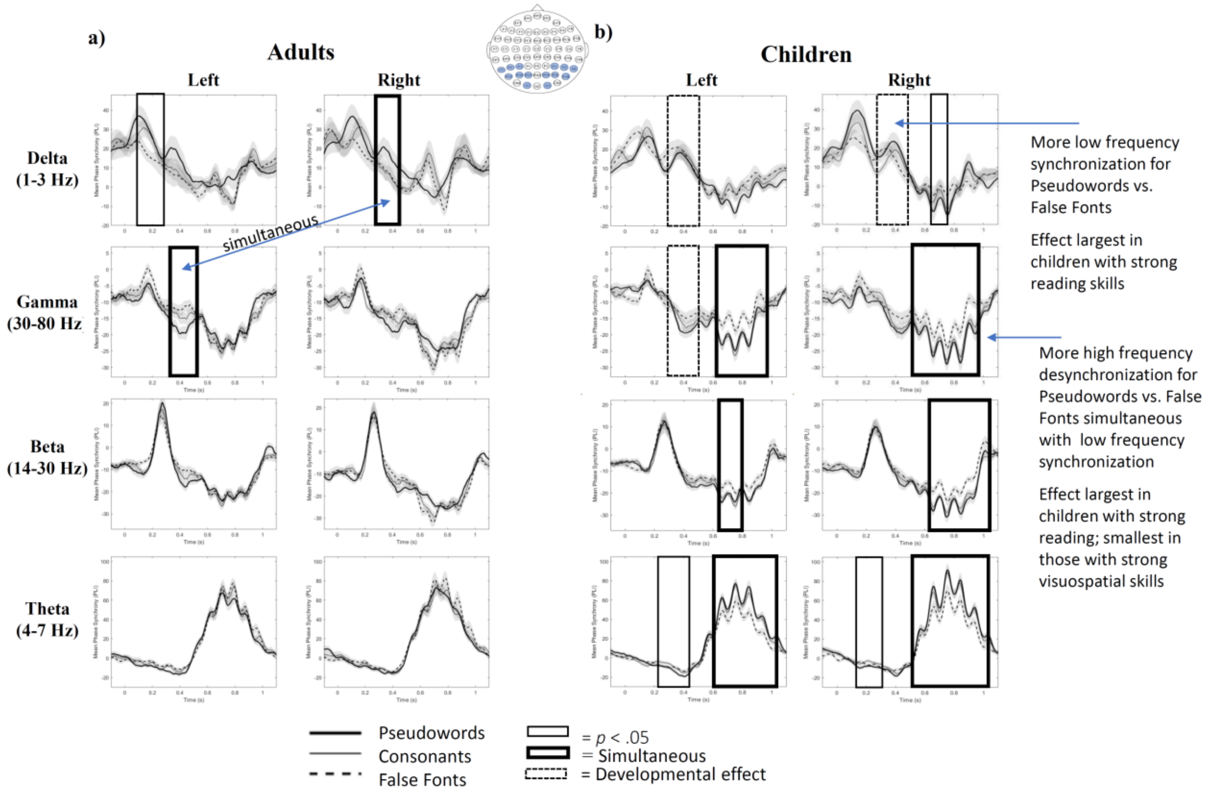
Author Notes

Acknowledgements: This research was supported by EpLink, in partnership with the Ontario Brain Institute. We thank Alexandra Mogadam for helping with data acquisition, Grace Sim and Anne Keller for helping with programming, as well as our participants and families.

Conflict of Interest Statement: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



Supplemental Figure: Regional Phase Synchrony Effects in Adults and Children. This figure shows phase synchrony (average phase lag index) over time of left (electrodes: P3, P5, P7, PO3, PO5, PO7, O1) and right (P4, P6, P8, PO4, PO6, PO8, and O2) posterior-occipital sites for pseudowords, consonants and false fonts within Delta (1-3Hz), Gamma (30-80Hz), Beta (14-30Hz) and Theta (4-7Hz) in adults (a) and children (b).

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[i] Only theta (3-7 Hz) and gamma (30-50 Hz) frequencies were examined by Bedo et al., (2014). The phase synchrony dynamics during word reading at other frequencies (including delta: 1-3 Hz, alpha: 8-13 Hz and beta: 13-30 Hz) are unknown.

[ii] Based on visual analysis of adults' N170 peak latency, analyses were also conducted within a narrower time window (140-170 ms). Permutation tests that compared pseudowords vs. false fonts revealed a marginally significant negative cluster (max sum= -11.54, *p* = .09, SD = .0088, CI = .0183) that was largest at left posterior-occipital electrodes. Permutation tests that compared pseudowords vs. consonants revealed no significant effects (*p* > .1). Thus, a trend towards a larger N170 for pseudowords vs. false fonts at left posterior-occipital electrodes was seen for adults between 140-170ms.

[iii] Although ERPs for consonants and pseudowords appeared similar for children, its relationship with development was different. As reported for the permutations that compared pseudowords and false fonts, permutation tests that compared consonants and false fonts found a significant cluster, indicating a negativity for consonants (max sum = -58.05, $p < .001$, SD = .0014, CI = .0028, d = .794) that was largest at bilateral posterior-occipital electrodes. The amplitude of this effect, however, did not correlate with children's age or any of psychometric test scores (p>.10).
[iv] The exact time windows that reached significance are beta (14-30Hz) right: 619-1034 ms, d = 1.15, beta left: 627-750ms, d = .884; gamma (30-80H) right: 623-997ms, d = 1.07; gamma left: 621-765 ms, d = .922, theta (4-7Hz) right: 618-1060ms, d = .909, theta left: 625-770ms, d = .744, and 782-1067ms, d = 1.05; *p*corr < .05.
[v] We also ran permutation tests that compared consonants vs. false fonts to explore whether effects were specific to pseudowords or generalized to unpronounceable print. Although none of the synchronization effects were significant, a similar late bilateral beta and gamma desynchronization effect was found for consonants vs. false fonts as we found for pseudowords vs. false fonts (*ps*corr < .05). At right posterior-occipital electrodes, this desynchronization effect was also largest in children with weaker visuospatial skills, even when controlling for age (beta: partial $r = .50$, $p < .05$; gamma: partial $r = .54$, $p < .05$).
[vi] Additionally, children showed significant phase synchrony effects (*p*corr < .05) that overlapped with the time window of the N170 (150-300 ms); however, none related to age or psychometric test scores. For pseudowords vs. consonants (fine-grained), delta synchronization was seen from right posterior-occipital electrodes between 211-377ms, theta desynchronization from right posterior-occipital electrodes between 165-331ms and from left posterior-occipital electrodes between 228-421ms. For pseudowords vs. false fonts (coarse-grained), alpha synchronization from left occipital-parietal electrodes was seen between 253-472ms.