# Cortical tracking of spoken and written language structures in (dys)fluent readers

**Citation for published version (APA):**

**Document status and date:**
Published: 01/01/2022

**DOI:**

**Document Version:**
Publisher's PDF, also known as Version of record

**Please check the document version of this publication:**

# Cortical tracking of spoken and written language structures in (dys)fluent readers

Manli Zhang

# Cortical tracking of spoken and written language structures in (dys)fluent readers

DISSERTATION

to obtain the degree of Doctor at the Maastricht University,
on the authority of the Rector Magnificus, Prof.dr. Pamela Habibović
in accordance with the decision of the Board of Deans,
to be defended in public
on Tuesday, 4th of October 2022, at 10:00 hours

by

## Manli Zhang

**Supervisor:**

Prof. dr. Milene Bonte


**Co-supervisor:**

Dr. Lars Riecke


**Assessment Committee:**

Prof. dr. Sonja A. Kotz (chair)

Prof. dr. Jarmo A. Hämäläinen (University of Jyväskylä, Finland)

Dr. Lars Hausfeld

Prof. dr. Lucia Melloni (Max Planck Institute for Empirical Aesthetics, Germany)

# Table of Contents

# Chapter 1

General Introduction

Human language is hierarchical in structure, with lower-level units (e.g., phonemes, syllables) being integrated into higher-level ones (e.g., words, sentences) to express increasingly complex meanings (Greenfield, 1991). As speech unfolds over time, it essentially conveys quasi-rhythmic energy patterns associated with this hierarchical structure (Kotz & Schwartze, 2010). These patterns are carried through to comprehension in a seemingly effortless way via oscillation-based neural decoding (Giraud & Poeppel, 2012; Peelle & Davis, 2012). Speech also forms the basis for the acquisition of written language, or as put forward by Mattingly (1972), 'reading is parasitic on speech'. Thus, not only are oral language skills critical for reading development (Hulme & Snowling, 2014), but during this development, the speech processing system in the brain is recruited and modified to merge with the visual processing system into an integrated audiovisual reading network (Dehaene et al., 2010; Romanovska & Bonte, 2021; Rueckl et al., 2015; van Atteveldt, Formisano, Goebel, & Blomert, 2004). Hence, it is of interest to investigate the cortical tracking of spoken and written language structures, and its association with (a)typical reading development.

This chapter introduces how hierarchically constructed human language, an evolutionarily recent means of communication, is represented in the brain. First, a global overview regarding the neurophysiological and neuroanatomical correlates of speech processing is provided. This lays the foundation for investigations on written language processing, which are introduced in the second section. Building upon a theoretical framework on mechanisms for the temporal sampling of various linguistic units, the key research questions of this thesis are presented, focusing on the contribution of hierarchical language tracking (both spoken and written) to (a)typical reading development. Finally, three electrophysiological approaches to measure or modulate the cortical tracking of (non-)linguistic units are introduced, characterizing both the temporal and spatial aspects of neural oscillations.

## 1 Spoken language processing

When it comes to speech perception, one of the most fundamental questions is how discrete phonological units (e.g., syllable sounds) are extracted from connected speech, and put together to form words, i.e., the basic building blocks

of semantic information, and their higher order assemblies (e.g., phrases, sentences). Such hierarchical organization of language is presumably inherited from the nested nature of motor planning in the articulatory system (Dehaene & Changeux, 1997; Fitch & Martins, 2014; Lashley, 1951), where single operations, i.e., the quasi-periodic movements of jaw, lip, tongue and vocal cords, are serially ordered and combined to produce coherent acoustic signals (Liberman & Mattingly, 1985). During the evolution of human speech, the auditory system has become adapted to such complex signals by spontaneously aligning its intrinsic rhythms, i.e., neural oscillations, to the ongoing energy (amplitude) changes in speech over time (Giraud & Poeppel, 2012; Peelle & Davis, 2012), so as to dynamically decipher the hierarchical structure.

## 1.1 Neurophysiological correlates of speech tracking

Neural oscillations refer to the synchronized rhythmic patterns of electrical activity, reflecting cyclical fluctuations in the excitability of neuronal ensembles (Bishop, 1932). These oscillations are a prevalent feature of neural processing that operates across multiple temporal and spatial scales (Buzsáki & Draguhn, 2004; Cole & Voytek, 2017), and is suggested to support a series of (temporal) coordination mechanisms of neural processes, including the coding, binding, and communication of information (Buzsáki & Draguhn, 2004; Fries, 2005; Gupta, Singh, & Stopfer, 2016; Singer, 1993) that underlie perception, cognition and behavior (Neustadter, Mathiak, & Turetsky, 2016). During speech processing, neural oscillations are found to track linguistically meaningful acoustic properties of varying sizes across distinct frequency bands, namely: (1) gamma oscillations (>30 Hz) follow the fine-grained acoustic features, such as formant transitions and voice onset times, at the phonemic scale; (2) theta oscillations (4-8 Hz) are correlated with the segmentation and identification of syllabic rate information; (3) delta oscillations (0.5-4 Hz) reflect supra-syllabic processing, including the prosodic analysis of syllable stress and the concatenation of syllables into words and higher-order units (Giraud & Poeppel, 2012; Luo & Poeppel, 2007). Moreover, the oscillatory activities for the analysis of low-frequency (< 5 Hz; primarily via phase entrainment) temporal features may be dominant in the right hemisphere auditory areas, while more rapidly occurring features (primarily via amplitude entrainment) may lateralize to the left (Gross et al., 2013; Poeppel, 2003).

Nevertheless, such a lateralization effect is still under debate, as it is likely driven by higher order linguistic processing demands (Overath, McDermott, Zarate, & Poeppel, 2015), and may manifest as more complex spatial patterns of preference, e.g., antero-ventral regions for low-frequency and posterior-lateral regions for high-frequency temporal information, respectively, in both hemispheres (Peña & Melloni, 2012; Santoro et al., 2014). There has been evidence from magneto-encephalography (MEG), electroencephalography (EEG), and electrocorticography (ECoG) experiments showing that low-frequency neural oscillations can concurrently synchronize to the syllabic, word, and phrasal/sentential rhythms in speech based on existing lexical/syntactic knowledge (Ding et al., 2017a, 2017b; Ding, Melloni, Zhang, Tian, & Poeppel, 2016; Jin, Zou, Zhou, & Ding, 2018). Although all participants show synchronized responses to physically presented syllable-rate information, only the listeners who could understand the language demonstrated cortical tracking of phrasal and sentential structures embedded in isochronous speech (Ding et al., 2016).

On the other hand, the real-time tracking of units along the linguistic hierarchy becomes difficult when encountering an unknown language (Batterink & Paller, 2017). A powerful computational mechanism underpinning speech segmentation and chunking is "statistical learning", the development of sensitivity to statistical regularities in the sensory environment (Saffran, Aslin, & Newport, 1996). Saffran and colleagues found that adult (Saffran, Newport, & Aslin, 1996; Saffran, Newport, Aslin, Tunick, & Barrueco, 1997), child (Saffran et al., 1997) and even infant (Saffran, Aslin, et al., 1996) learners are able to discover the boundaries of artificial words over recurring exposure solely based on the transitional probabilities between adjacent syllables, which were higher within the words than across their boundaries (Saffran, Aslin, et al., 1996). Subsequent electrophysiological research has captured the oscillatory dynamics of neural speech tracking, with a particular focus on the online learning process. Specifically, the cortical responses to novel higher-order structures (e.g., words and phrases) gradually increases with accumulating exposure (Batterink & Paller, 2017; Getz, Ding, Newport, & Poeppel, 2018; Henin et al., 2021; Kabdebon, Pena, Buiatti, & Dehaene-Lambertz, 2015; Zhang, Riecke, & Bonte, 2021). This increased tracking of higher-order structures tends to be accompanied by a suppression of neural tracking at the syllable level, indicating a perceptual shift from isolated syllables to higher-level integrated units as learning takes place (Batterink & Paller, 2017; Buiatti, Pena, & Dehaene-

Lambertz, 2009; Choi, Batterink, Black, Paller, & Werker, 2020). Such rapid changes in neural representations of lower-level sensory input and their higher-order chunks were also reported during the statistical learning of visual non-linguistic stimuli (Henin et al., 2021; Jin et al., 2018). Furthermore, it is suggested that our brain represents hierarchical structures at multiple levels, from simple and local properties (e.g., transitional probability) to more complex forms (e.g., ordinal position, recurrent fragment and chunk identity) (Henin et al., 2021; Ordin, Polyanskaya, Soto, & Molinaro, 2020). The operations on simple, local properties may engage generally modality-specific circuits in the corresponding sensory cortices, whereas the processing of more complex features may be performed in higher heteromodal and memory-related systems (e.g., the inferior frontal gyrus, anterior temporal lobe and hippocampus) for both visual and auditory sequences (Henin et al., 2021).

## 1.2 Neuroanatomy of the spoken language network

Alike other higher cognitive functions, speech perception is thought to build on dynamic interactions in a large-scale brain network, rather than on operations in single brain regions (Salmelin & Kujala, 2006). The cortical spoken language network (Figure 1; for review, see Fedorenko & Thompson-Schill, 2014; Friederici, 2012, 2020) involves both relatively specialized functional subsystems (Tyler & Marslen-Wilson, 2008; Vigneau et al., 2006) and brain regions considered as part of a domain-general cognitive control network (also known as the "multiple-demand system") occupying frontal and parietal cortices (Duncan, 2010; Thompson-Schill, Bedny, & Goldberg, 2005). The language-selective component involves a ventral pathway for mapping sound to meaning and a dorsal pathway for mapping sound to articulation (Hickok & Poeppel, 2000; Saur et al., 2008). More specifically, the ventral pathway connects the temporal cortex and the anterior inferior frontal gyrus (IFG), and is responsible for the processing of semantic information and simple rule-based sequences (Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Saur et al., 2008). Meanwhile, the dorsal temporo-parieto-frontal pathways link (1) the auditory and motor cortices for speech sound perception and auditory-to-motor mapping (Hage & Nieder, 2016; Hickok & Poeppel, 2007; Vigneau et al., 2006), and (2) the posterior superior temporal gyrus (STG) and posterior IFG for higher-order structural analysis and

syntactic processing (Friederici, 2002; Hagoort & Indefrey, 2014; Vigneau et al., 2006). In particular, the inferior frontal cortex (including Broca's area and its right hemisphere homolog) is suggested to be closely associated with hierarchical structure building (Fedorenko, Duncan, & Kanwisher, 2012; Friederici, 2020; Friederici et al., 2006), a process that plays a critical role in not only higher-order semantic/syntactic computations (Baldassano et al., 2017; Friederici, 2011, 2012; Hagoort & Indefrey, 2014; Tyler & Marslen-Wilson, 2008; Vigneau et al., 2006), but also in the cognitive parsing of non-linguistic information (Fitch & Martins, 2014; Koechlin & Jubault, 2006). Throughout language development, the cortical language network undergoes an early stage of rapidly growing capacity for acoustic-phonological processing, which is primarily implemented in bilateral temporal cortices, followed by a protracted process into adolescence where top-down semantic/syntactic computation gradually improves with increasing functional selectivity of the left inferior frontal cortex (Skeide & Friederici, 2016), and thus achieves a left-lateralized network organization (Hickok & Poeppel, 2007; Parker et al., 2005).
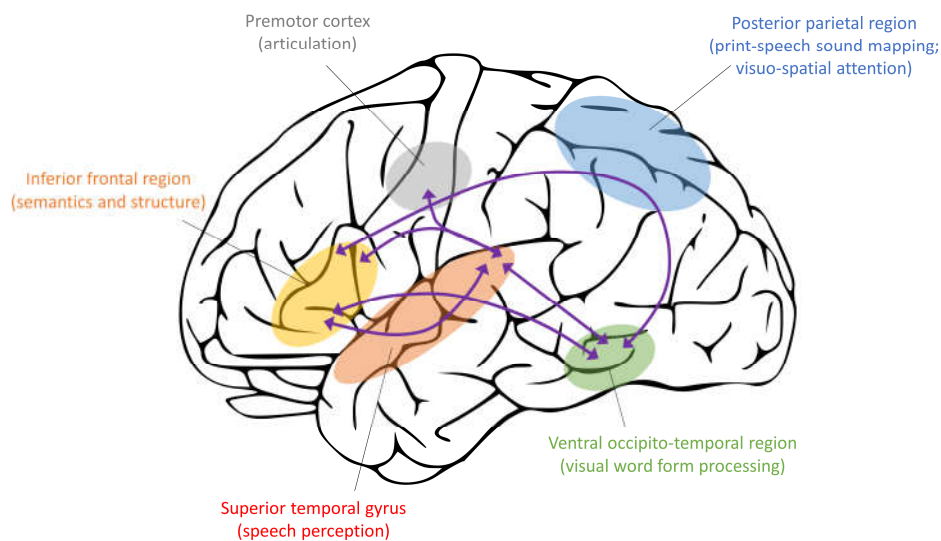


**Figure 1**. The cortical language network (schematic view of the left hemisphere). The major regions involved are color-coded based on their functions.

## 2 Language tracking and (a)typical reading development

Reading is a complex multimodal process that relies on the integration and retrieval of phonological, orthographic, and semantic information (Saha, Del Tufo,

& Cutting, 2019). The association between written symbols and their spoken forms is the first hurdle of learning to read (Blomert, 2011; Froyen, Bonte, van Atteveldt, & Blomert, 2009). Research has shown that during reading development, existing brain circuits for speech and visual perception, such as the left frontal, temporo-parietal and occipito-temporal areas, become increasingly integrated and specialized for reading (Figure 1) (Bonte, Correia, Keetels, Vroomen, & Formisano, 2017; Booth et al., 2004; Chyl et al., 2018; Cohen et al., 2002; Cone, Burman, Bitan, Bolger, & Booth, 2008; Dehaene-Lambertz, Monzalvo, & Dehaene, 2018; Martin, Schurz, Kronbichler, & Richlan, 2015; Monzalvo & Dehaene-Lambertz, 2013; Romanovska & Bonte, 2021; van Atteveldt et al., 2004). Besides the left-hemispheric spoken and written language networks, literacy acquisition involves interactions among multiple anatomically distributed brain systems subserving more general cognitive functions including visuo-spatial processing, attention, memory and executive control (Bailey, Aboud, Nguyen, & Cutting, 2018; Black, Xia, & Hoeft, 2017; Dehaene, Cohen, Morais, & Kolinsky, 2015; Edwards, Burke, Booth, & McNorgan, 2018; Krishnamurthy et al., 2019; Smith, Booth, & McNorgan, 2018). It has been suggested that disrupted brain activity (Richlan, 2012, 2020) and altered connectivity between critical brain regions/networks (Boets et al., 2013; Finn et al., 2014; Morken, Helland, Hugdahl, & Specht, 2017; Schurz et al., 2015; van der Mark et al., 2011; Žarić et al., 2017) may lead to reading impairment.


**2.1 A temporal sampling framework for developmental dyslexia**

Developmental dyslexia (hereafter "dyslexia") is a specific learning disorder affecting 5-17% of the population worldwide, primarily manifested in substantial and persistent difficulties in reading and spelling, despite adequate education and adequate intellectual abilities (Lyon, Shaywitz, & Shaywitz, 2003; Pennington & Peterson, 2015). In spite of certain variabilities across different writing systems (Li & Bi, 2022; Paulesu et al., 2001), dyslexia is universally characterized by deficient phonological processing (Ramus, 2003; Snowling, 1980), lack of visual specialization for print analysis (McCandliss, Cohen, & Dehaene, 2003; Richlan, Kronbichler, & Wimmer, 2009), and sluggish establishment/retrieval of speech-print associations (Blomert, 2011; Wolf & Bowers, 1999). These difficulties can be accounted for by multiple origins at the genetic, neural, and cognitive levels (Benitez-Burraco, 2010; Hancock, Pugh, & Hoeft, 2017; Shaywitz et al., 2001), such

as neural encoding difficulties with incoming information spanning across different timescales during both spoken and written language processing (Archer, Pammer, & Vidyasagar, 2020; Goswami, 2011; Lallier, Molinaro, Lizarazu, Bourguignon, & Carreiras, 2017).

The processing of rapidly changing attributes of a specific event and/or serially ordered events in brief succession has been found to be particularly challenging for individuals with dyslexia. This was first reported in the auditory modality where dyslexic readers were found to be unable to reliably represent rapidly changing phonological information such as formant transitions, voice onset time. Thus, deficient auditory temporal perception was adopted as an explanation for the phonological deficit of dyslexia (Habib, 2000; Tallal, 1980). Such impairment was subsequently demonstrated for non-verbal stimuli (Heiervang, Stevenson, & Hugdahl, 2002; Kinsbourne, Rufo, Gamzu, Palmer, & Berliner, 1991; Zhang, Xie, Xu, & Meng, 2018) and in other sensory modalities (Casini, Pech-Georgel, & Ziegler, 2018; Chung et al., 2008; Laasonen, Service, & Virsu, 2001; Van Ingelghem et al., 2001), pointing to a general temporal processing deficit in dyslexia. Goswami (2011) proposed a temporal sampling framework (TSF) for dyslexia, which initially focused on the temporal aspects during auditory (speech) processing, postulating the phonological (and perceptual) difficulties in dyslexia as inefficient oscillation-based temporal coding at one or more temporal rates.

As introduced in Section 1.1, the brain is capable of processing various units of human speech by aligning its inherent neural oscillations to the temporal structure of speech input at specific frequencies (e.g., gamma, theta and delta bands for sub-syllabic, syllabic and supra-syllabic processing, respectively) (Giraud & Poeppel, 2012; Meyer, 2018). Across languages, dyslexic readers were found to show difficulties in tracking the intensity fluctuations of acoustic (speech) signals, e.g., the onsets (rise times) of (speech) amplitude envelopes (Goswami et al., 2002; Goswami et al., 2011; Hämäläinen, Leppänen, Torppa, Müller, & Lyytinen, 2005; Poelmans et al., 2011) and the amplitude modulation of (non-)speech input (Hämäläinen, Rupp, Soltész, Szücs, & Goswami, 2012; Lizarazu et al., 2015; Power, Colling, Mead, Barnes, & Goswami, 2016). Such impaired temporal sampling may reside in inefficient phase locking to speech input by neural oscillations (Goswami, 2011). This may include atypical neural entrainment to slow rate prosodic (delta) and syllabic (theta) information (Abrams, Nicol, Zecker, & Kraus, 2009; Hämäläinen et al., 2012), and higher frequency neural oscillations related to phonemic

sampling (~gamma) (Giraud & Ramus, 2013; Lehongre, Ramus, Villiermet, Schwartz, & Giraud, 2011). The functional interpretation of such deficits in neural oscillations could be threefold. First, according to Goswami (2011) (and also see Peelle & Davis, 2012), altered neural sampling of the acoustic signal, particularly at a slow temporal rate, may affect the efficiency of syllable segmentation, which in turn may hamper the perception and integration of various acoustic features that contribute to the representation of constituting phonemes. Second, impaired slow temporal sampling may bias the developing phonological system toward high-frequency modulations (e.g., >40 Hz) coded by gamma oscillations, which then leads to an oversampling and therefore less accurate extraction of phonemic information (Giraud & Poeppel, 2012; Lehongre et al., 2011). Third, it has been demonstrated more recently that slow cortical entrainment might directly contribute to the categorical representation of phonetic features in continuous speech streams (Di Liberto, O'Sullivan, & Lalor, 2015), which was found to be altered in dyslexia (Di Liberto et al., 2018).

## 2.2 The functional role of hierarchical language tracking to (a)typical reading development

### 2.2.1 Sub-syllabic level auditory processing

The proposed TSF has highlighted a central role of slow neural oscillations to phonemic processing and reading development. Thus, prior work in dyslexia showed impaired low-frequency cortical tracking to phonetic features during natural speech perception (Di Liberto et al., 2018), and a reduced phase resetting effect on low-frequency oscillations in left auditory cortical regions (Lizarazu, Lallier, Bourguignon, Carreiras, & Molinaro, 2021) induced by transient sound amplitude changes (Doelling, Arnal, Ghitza, & Poeppel, 2014; Gross et al., 2013; Peelle & Davis, 2012). Moreover, the slow cortical tracking of speech envelope and phonetic features in the right central-frontal cortex, not only distinguished dyslexic children from their age (or reading-level)-matched controls, but also showed significant correlations with their phonological skills (Abrams et al., 2009; Di Liberto et al., 2018). However, there is still much debate as to whether there is a causal link between slow cortical oscillations and the auditory temporal perception in a sub-syllabic time window (e.g., phonemic rate). It has been argued that if

oscillations in a specific frequency range were essential for a given cognitive function, then this function should be altered when these oscillations are selectively modulated (Sejnowski & Paulsen, 2006). Recent developments of non-invasive brain stimulation techniques (see Section 3.2 for detailed introduction) enable such investigations by driving brain oscillations in a frequency-specific manner (Herrmann, Rach, Neuling, & Strüber, 2013). Therefore, these techniques can be utilized to evoke temporary deficits/symptoms in e.g., typically reading participants, better controlling the potential influence of prior experience and compensatory strategies. In **Chapter 2**, we apply electrical stimulation over the bilateral auditory cortices in typical adult readers to investigate whether the phase of 4 Hz cortical oscillations contributes causally to sound-onset perception.

*2.2.2 Supra-syllabic speech tracking and learning*

It is noteworthy that research to date tends to focus on the processing of isolated units targeted in specific tasks, such as those engaging the conscious manipulation of phonemes (Boets et al., 2013), often overlooking the hierarchical nature of language and the influence of higher-order semantic/syntactic computation on phonological speech representation. Lallier et al. (2017) argued that slow neural oscillations might not only subserve the temporal processing of syllable and prosody, but also reflect a general oscillatory mechanism for the between-unit parsing of sequences. In line with this view, a recent study with neurotypical participants confirmed the involvement of delta/theta-band oscillations in spoken word and sentence tracking, with a developmental change from a relatively bilateral topographic distribution in children to left-lateralized responses in adults (Kolozsvári et al., 2021). Meanwhile, a deficient speech-brain synchronization in delta/theta frequency bands was also reported in adults and children with dyslexia when they listened to continuous speech forming sentences/stories (Di Liberto et al., 2018; Mandke et al., 2022; Molinaro, Lizarazu, Lallier, Bourguignon, & Carreiras, 2016). However, the specific impact of these slow oscillations on supra-syllabic processing, e.g., syllable-to-word chunking and phrasal/sentential level processing, remains unclear.

Furthermore, it has been recognized that the rhythm in connected speech carries acoustic statistical cues to phonotactic constraints, word boundaries and syntactic

structures (Goswami, 2019), and that the brain can encode these statistical patterns via (low-frequency) neural oscillations (Bosseler et al., 2013; Buiatti et al., 2009; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Toth et al., 2017). Individuals with (familial risk of) dyslexia tend to be less sensitive to implicit statistical regularities in speech and orthography (Bonte, Poelmans, & Blomert, 2007; Noordenbos, Segers, Mitterer, Serniclaes, & Verhoeven, 2013; Tong, Zhang, & He, 2020; Vandermosten, Wouters, Ghesquiere, & Golestani, 2019) and the correspondence rules linking these two forms of linguistic information (Aravena, Snellings, Tijms, & Van der Molen, 2013; Karipidis et al., 2017). They show poor behavioral performance during various learning tasks, including statistical learning (for review, see Schmalz, Altoè, & Mulatti, 2017) and associative learning (Litt & Nation, 2014). Since incremental learning processes are difficult to investigate merely with behavioral measures (Buiatti et al., 2009), implementing neurophysiological approaches to assess the fluctuations in brain activity over the learning course provides a promising means to better understand dyslexia as a learning disorder. Given that efficient speech segmentation (both knowledge-guided and statistically-informed) is considered a crucial step for fine tuning the phonological representations of words, syllables and phonemes (Hämäläinen et al., 2012; Leong & Goswami, 2014; Rodriguez-Fornells, Cunillera, Mestres-Misse, & de Diego-Balaguer, 2009), the work presented in this thesis investigates whether and how dyslexic readers differ from their typically reading peers in terms of the cortical tracking and learning of higher-order language structures in connected speech (**Chapter 3 and 4**).

### 2.2.3 Hierarchical tracking of written language structures

Despite a body of research capturing a close association between deficient oscillation-based temporal sampling of speech and atypical reading development, investigation into oscillatory activities during reading is still limited. Compared to speech comprehension, natural reading is a more complex process, additionally involving visuo-spatial aspects, such as eye movements and attentional shifting (Pammer, 2013). Vidyasagar (2013) suggested that aberrant neural oscillations in the visual domain might account for many magno-dorsal visual processing deficits in dyslexia (e.g., reduced sensitivity to low-spatial- and high-temporal-frequency patterns, deficient visuo-spatial attention) (Livingstone, Rosen, Drislane, &

Galaburda, 1991; Stein, 1997; Vidyasagar & Pammer, 2010), relying on the fact that the spatiotemporal sampling of written characters during reading engages similar resources as those required for visual search (Vidyasagar, 2013). His team proposed a nested model analogous to the auditory TSF: (1) low gamma oscillations may control the serial sampling of text that falls into the attentional spotlight, whereas (2) theta oscillations may guide eye saccades and fixations to shift the focus of attention (Archer et al., 2020). As such, the visual TSF tends to heed the (bottom-up) visuo-spatial aspects of temporal sampling, whereas the incremental integration of sampled information is also at play to build up coherent comprehension during reading (Lallier et al., 2017; Perfetti & Helder, 2021), and adjust the subsequent landing point of attention accordingly (Itti & Koch, 2001). Disruptions in the latter (top-down) processes may lead to persistent fluency deficits in dyslexia (Blomert, 2011; Wimmer & Schurz, 2010; Ziegler, Perry, Ma-Wyatt, Ladner, & Schulte-Körne, 2003).

Prior research has provided evidence that low-frequency oscillations likely reflect an intrinsic temporal parsing mechanism, which could be shared with spoken language processing (Henin et al., 2021; Roux & Uhlhaas, 2014). For instance, widespread fronto-posterior theta oscillations have been associated with the lexical-semantic retrieval (Bastiaansen, Linden, Keurs, Dijkstra, & Hagoort, 2005; Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008), syntactic analysis (Bastiaansen, Van Berkum, & Hagoort, 2002), as well as the temporal organization and retention of working memory (Meyer, Grigutsch, Schmuck, Gaston, & Friederici, 2015; Roux & Uhlhaas, 2014) during written word/sentence processing. Thus far, however, there is no direct empirical research investigating how linguistic units are represented and integrated to higher-order structures on a real-time basis during reading. Accordingly, in **Chapter 5**, we set out to investigate the commonalities and differences between spoken and written language tracking using fully matched and serially presented language streams.

## 2.3 Key research question: the spatial organization of slow cortical oscillations underlying spoken and written language tracking

The multi-time resolution model for cortical speech processing suggested that slow temporal information is preferentially processed in the right hemisphere

(Boemio, Fromm, Braun, & Poeppel, 2005; Poeppel, 2003), of which the oscillatory underpinnings are altered in dyslexia (e.g., Cutini, Szucs, Mead, Huss, & Goswami, 2016; Di Liberto et al., 2018; Hämäläinen et al., 2012). Yet, much less attention has been paid to *where* in the brain such synchronized activity originates and *how* isolated brain regions could work together to accomplish coordinated functions such as speech tracking and comprehension. It has been found that auditory regions in both hemispheres may be engaged in slow speech processing, with the spatial organization of such activities varying across task demands (Overath et al., 2015; Peña & Melloni, 2012; Santoro et al., 2014). Other than bilateral auditory cortices (Abrams et al., 2009; Boemio et al., 2005; Peelle & Davis, 2012; Poeppel, 2003), a broad frontal-temporal system (Giraud & Poeppel, 2012; Kotz & Schwartze, 2010; Tyler & Marslen-Wilson, 2008) and specific subcortical structures (e.g., the thalamus and the cerebellum; beyond the scope of this dissertation) (Ackermann, Mathiak, & Ivry, 2004; Kotz & Schwartze, 2010) are also sensitive to the decoding of slow temporal structures (in speech). Besides representing information, the inter-regional synchronization of oscillatory activities is suggested to regulate the information flow and assist the storage/retrieval of information in neural circuits (Sejnowski & Paulsen, 2006), with its functional configuration dynamically adapting to the demand of different tasks (for review, see Shine & Poldrack, 2018).

Previous research highlighted dyslexia-related aberrant spatial organization of brain networks (both structural and functional), characterized by altered interplay within the left hemisphere language network (e.g., Boets et al., 2013; Cao et al., 2017; Klingberg et al., 2000; Schurz et al., 2015; van der Mark et al., 2011) and between the language and other brain networks (e.g., Cao et al., 2017; Cui, Xia, Su, Shu, & Gong, 2016; Richards & Berninger, 2008; Schurz et al., 2015; Wolf et al., 2010). From a large-scale brain network-based perspective (introduced in Section 3.3), dyslexic readers may show reduced local clustering of both structural (Qi et al., 2016) and intrinsic functional connectivity (i.e., during the resting state) (Dimitriadis et al., 2013; Finn et al., 2014) in the left hemisphere as compared to typical readers. Meanwhile, the hub nodes, i.e., brain regions that are centrally located in the network and have a significant impact on global network function (van Den Heuvel & Sporns, 2013), have been found to be more bilaterally and anteriorly distributed in dyslexic readers (Cao, Huang, Peng, Dong, & He, 2016; Finn et al., 2014; Mao, Liu, Perkins, & Cao, 2021; Qi et al., 2016). However, the

large-scale properties of network topology during reading-related tasks tends to vary across studies and writing systems. For instance, Greek-speaking dyslexic children showed reduced network integration and segregation during phonological tasks such as pseudoword reading and letter naming (Vourkas et al., 2011), while a relative intact topology (Yang & Tan, 2020) or increased network segregation (Mao et al., 2021; J. Zhang et al., 2021) during homophone/rhyming judgment were reported in Chinese-speaking dyslexic children. In contrast, when performing an orthographic judgment task, Chinese-speaking dyslexic children were found to display reduced global network integration along with increased network segregation in the bilateral visual cortices (Yang & Tan, 2020). Therefore, more work is needed to reveal how the organization of brain networks is dynamically modulated by the interaction between intrinsic brain functions and different sensory stimuli and/or task demands (Bullmore & Sporns, 2012; Hutchison et al., 2013; van den Heuvel & Sporns, 2013). Moreover, it is of interest to investigate how atypical brain network organization, e.g., during hierarchical language tracking, may relate to the altered processing of spoken and written languages in individuals with reading difficulties.

Therefore, the current dissertation gives a particular emphasis on the spatial organization of oscillatory activities during hierarchical language tracking in different contexts (e.g., **Chapter 3**: implicit learning versus knowledge-based tracking; **Chapter 4**: random syllable versus real word tracking) and sensory modalities (**Chapter 5**). Building upon recent developments in network science (see Section 3.3) and emerging evidence of atypical brain network organization in dyslexia, **Chapter 4** specifically investigates the dyslexia-related alteration in large-scale network topology during the tracking of local and higher-order structures in speech.

# 3 Electrophysiological approaches to investigate cortical language tracking

## 3.1 Frequency-tagging

Cortical tracking of hierarchical structures in continuous speech can be assessed with MEG, EEG and ECoG responses using e.g., isochronous syllable sequences and a frequency-tagging approach. This approach exploits the steady-state evoked

potential (SSEP) elicited by periodic stimulation that is induced by either sensory input or internally constructed percepts (Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015; Regan, 1989). Because frequency-tagging leads to a narrowband response directly related to the frequency of interest, it provides a robust measure against the experimental noise spread over the entire frequency spectrum (Norcia et al., 2015). Another advantage of this approach is that it allows implicit assessment of multiple cognitive processes even in the absence of overt behavior (Lochy et al., 2018; Wang et al., 2021). Hence, the frequency-tagging paradigm is widely adopted to study the analysis, memory, comprehension and generation of temporal structures and/or regularities embedded in (non)linguistic sequences (e.g., Buiatti et al., 2009; Lu, Sheng, Liu, & Gao, 2021; Nozaradan, Peretz, Missal, & Mouraux, 2011; Volfart, Rice, Lambon Ralph, & Rossion, 2021).

M/EEG evidence suggests that neural responses spontaneously track syllabic, word, and phrasal/sentential rhythms at the corresponding frequency, based on segmental cues informed by acoustic features (e.g., Elmer, Valizadeh, Cunillera, & Rodriguez-Fornells, 2021), statistical regularities (e.g., Batterink & Paller, 2017; Henin et al., 2021), and existing lexical/syntactic knowledge (e.g., Ding et al., 2017; Ding et al., 2016; Peña & Melloni, 2012). The frequency-tagging approach has also been used to study visual perception, segmentation, discrimination, and integration of multiple inputs (for review, see Norcia et al., 2015). During visual word form processing, in particular, periodically inserted real words were rapidly discriminated from pseudofonts, nonwords and pseudowords with robust SSEPs elicited over the occipito-temporal and dorsal parietal regions at the frequency of deviant stimuli (Lochy, Van Reybroeck, & Rossion, 2016; Wang et al., 2021). Moreover, when words were split into two parts and flickered at different frequencies, SSEPs were stronger when the segments matched the syllabification compared to when they did not retain the constituent syllabic structure (Montani, Chanoine, Grainger, & Ziegler, 2019). These findings suggest that visual SSEPs are not only sensitive to sensory features, but may also reflect higher-level processing such as (pre-)lexical analyses (Lochy et al., 2018; Lochy, Van Belle, & Rossion, 2015).

Since attending to a certain event can produce higher amplitudes and/or phase synchronizations of SSEP as compared to when that event is ignored (Joon Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007; Müller, Teder-Sälejärvi, & Hillyard, 1998), frequency-tagged responses are also widely adopted to index the (dynamic) allocation of attention, which is otherwise difficult to assess behaviorally. This

includes a battery of studies orienting the participants' attention to distinct stimulus attributes (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005; Niesen et al., 2020; Symons, Dick, & Tierney, 2021), spatial locations (Ahveninen et al., 2011; Gray, Frey, Wilson, & Foxe, 2015; Keitel, Thut, & Gross, 2017), temporal sequences of varying size or onset (Ding et al., 2018; Farthouat, Atas, Wens, De Tiège, & Peigneux, 2018; Farthouat et al., 2017; Jin et al., 2018), and sensory input in different modalities (De Jong, Toffanin, & Harbers, 2010; Keitel, Maess, Schröger, & Müller, 2013). Therefore, SSEP may serve as a sensitive neural marker of fluctuations in covert attention during the incremental process of language tracking and learning. In this dissertation, the frequency-tagging approach is used to investigate the (establishment of) cortical tracking of spoken (**Chapter 3 and 5**) and written (**Chapter 5**) language structures.

## 3.2 Non-invasive brain stimulation

Numerous studies have demonstrated a close association between (slow) brain oscillations and speech/reading-related cognitive functions (e.g., De Vos, Vanvooren, Vanderauwera, Ghesquiere, & Wouters, 2017; Doelling et al., 2014; Hämäläinen et al., 2012; Henry & Obleser, 2012; Lizarazu et al., 2015; Power, Mead, Barnes, & Goswami, 2013). However, it remains unclear whether such oscillatory activities contribute functionally to specific cognitive processes (Heerebout & Phaf, 2010; Herrmann et al., 2013; Thut, Schyns, & Gross, 2011).

In this sense, non-invasive brain stimulation (NIBS) techniques, which include transcranial electric stimulation (tES), bypass the correlative neuroimaging approach, as they provide means to directly modulate ongoing neuronal activities and thereby enable the investigation on how experimentally manipulated brain oscillations causally affect cognition and behavior (Miniussi, Harris, & Ruzzoli, 2013; Polanía, Nitsche, & Ruff, 2018; Vosskuhl, Strüber, & Herrmann, 2018). In tES techniques, the weak electrical currents applied through two electrodes placed on the scalp can either be constant over time (i.e., transcranial direct current stimulation, tDCS), or alternate at a certain frequency (i.e., transcranial alternating current stimulation, tACS) or fluctuate randomly (i.e., transcranial random noise stimulation, tRNS) (Herrmann et al., 2013; Paulus, 2011; Polanía et al., 2018). All these approaches induce changes in the resting membrane potential (i.e.,

subthreshold polarization without triggering action potentials) of cortical neurons, entail the modulation of the likelihood of spontaneous or task-evoked firing, and in turn lead to improvements or deteriorations in task performance (Bindman, Lippold, & Redfearn, 1962; Miniussi et al., 2013; Priori, Hallett, & Rothwell, 2009; Turker & Hartwigsen, 2021). Since alternating currents, typically in a sinusoidal waveform, can entrain the brain oscillations by temporally aligning the intrinsic brain activity with the externally applied currents in a frequency-dependent manner, tACS is particularly useful for investigating the causal relevance of frequency and timing (i.e., the stimulus-brain phase difference) of brain oscillations to certain cognitive functions (Herrmann et al., 2013; Reato, Rahman, Bikson, & Parra, 2013). This approach is supported in previous studies where improved and disrupted perception, cognition and behavior were reported when tACS and the stimulus were in and out of phase with each other, respectively (e.g., Neuling, Rach, Wagner, Wolters, & Herrmann, 2012; Polanía, Michael, Korman, Batsikadze, & Paulus, 2012; Riecke, Formisano, Sorger, Baskent, & Gaudrain, 2018; Riecke, Sack, & Schroeder, 2015; see Klink, Paßmann, Kasten, and Peter (2020) for a recent review).

In addition to enriching our knowledge of the causal brain-behavior relationship, the NIBS approach is also characterized by its translational application in alleviating cognitive deficits/weaknesses (Begemann, Brand, Ćurčić-Blake, Aleman, & Sommer, 2020; Finisguerra, Borgatti, & Urgesi, 2019; Polanía et al., 2018), including generally positive effects of tDCS treatment for children and adolescents with neurodevelopmental disorders, especially when combined with cognitive training programs (Finisguerra et al., 2019; Santos et al., 2021; for a recent review in dyslexia, see Turker & Hartwigsen, 2021). So far, two studies applied tACS over the auditory cortices in dyslexic readers, aiming to modulate the temporal aspects of speech processing and facilitate phoneme perception. Compared to the sham condition, bilateral 40 Hz-tACS amplified the auditory P50-N1 response in adolescents with dyslexia, which led to increased acuity to voice onset time (i.e., the short delay between the release of the closures and the start of voicing). In turn, dyslexic readers showed improved discrimination between voiced (e.g., /d/) and unvoiced consonants (e.g., /t/) while receiving 40 Hz-tACS (Rufener, Krauel, Meyer, Heinze, & Zaehle, 2019). Another study by Marchesotti et al. (2020) found that offline 30 Hz-tACS over the left auditory cortex induced temporary improvement in the participants' phonemic awareness and reading accuracy (text

and pseudowords), compared with sham stimulation or 60 Hz-tACS. These findings suggest that fine-grained temporal sampling and analysis of acoustic signals at the phoneme scale may be facilitated by improving the temporal resolution of the auditory system in the low gamma range (Baltus & Herrmann, 2015; Giraud & Poeppel, 2012). Such modulation approaches may also have the potential to offset the putative phonemic oversampling deficit in dyslexia (Lehongre, Morillon, Giraud, & Ramus, 2013; Lehongre et al., 2011; Marchesotti et al., 2020; Rufener & Zaehle, 2021). However, the NIBS research in dyslexia has not yet addressed the contribution of slow cortical oscillations and the online effects of relative timing on temporal sampling and auditory perception, which are addressed in **Chapter 2**.

## 3.3 Graph theoretical analysis

The human brain is a complex network subserving dynamic interactions of cells and systems that underly various (higher) cognitive functions, including language processing (Sporns, 2011). Its structural and functional organizations exhibit a "small-world" topology characterized by the combination of dense local clusters and relatively few long-range connections that globally link the local neuronal populations (Bullmore & Sporns, 2009; Sporns, 2011; Stam & van Straaten, 2012). Given the high metabolic costs of the human brain relative to its size, the optimal brain network organization is suggested to be shaped by an economic balance between efficient information transmission and the intrinsic need to minimize wiring costs (Bullmore & Sporns, 2009, 2012; Sporns, 2011; van den Heuvel & Sporns, 2019) (Figure 2). In this view, segregated (or specialized) processes (e.g., basic visual perception) would mainly benefit from highly clustered local connections, whereas integrated (or distributed) processes (e.g., higher cognitive functions such as reading) tend to be favored by efficient information transfer across the entire network (Bullmore & Sporns, 2012; Deco, Tononi, Boly, & Kringelbach, 2015). A network-based view on brain architecture thus nourishes the understanding of cognition and behavior (e.g., spoken and written language processing) as a set of spatially (and temporally) coordinated processes (e.g., phonological, orthographical and lexico-semantic analyses) adapting to varying cognitive demands (Bressler & Menon, 2010; Bullmore & Sporns, 2009; Sporns, 2011; Sporns, Chialvo, Kaiser, & Hilgetag, 2004).
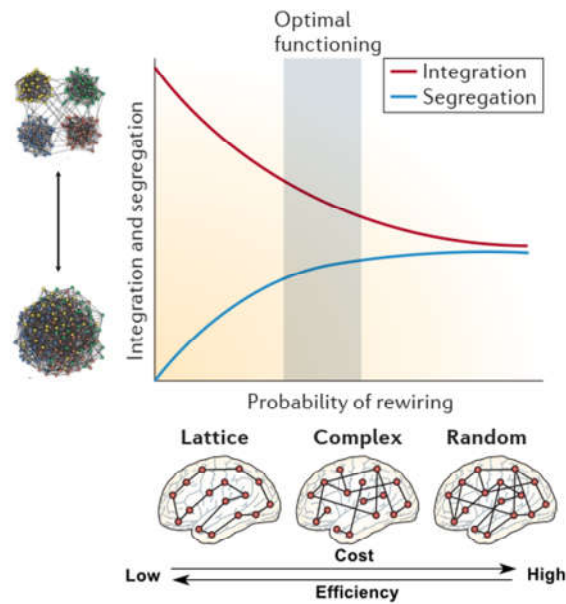
**Figure 2**. Segregation and integration in small-world network architectures. As the connectivity gradually changes from an ordered lattice to complete randomness, perturbational integration decreases, whereas perturbational segregation increases. The optimal function (that is, achieving a balance between segregation and integration) is obtained at an intermediate level of connectivity, between order and randomness. Adapted from Bullmore and Sporns (2012), Deco et al. (2015) and Shine and Poldrack (2018).

Recent developments in graph theory have enabled a mathematical description of large-scale brain networks, which has been translated to research on how (ab)normal brain functions arise from the interactions of neuronal ensembles and systems (Bullmore & Sporns, 2009; Sporns, 2011). Within this framework, a number of metrics can be used to quantify the way in which separate brain regions (i.e., nodes) are linked to each other (i.e., edges and their weights), as well as the cost-efficiency trade-off of the entire network (i.e., graph) and the local/global aspects of network attributes (see reviews in Bullmore & Sporns, 2009, 2012; Stam & van Straaten, 2012). It is suggested that healthy brain networks not only display small-world architectures, but are also characterized by highly specialized subsystems (i.e., modules) and a set of hub nodes (i.e., nodes occupying a central position in the network) that handle most of the information flow in the network (Stam, 2014; van den Heuvel & Sporns, 2013).

Across the life span, (structurally) interconnected brain networks and hubs emerge early since gestation (Fransson, Åden, Blennow, & Lagercrantz, 2011; Hoff, van den

Heuvel, Benders, Kersbergen, & de Vries, 2013; Shi et al., 2012), but do not reach a relatively mature functional state until adolescence or early adulthood (Cao et al., 2016; Hwang, Hallquist, & Luna, 2013; Uddin, Supekar, Ryali, & Menon, 2011). Aberrant network organization (both structural and functional) has been reported in a range of neurodevelopmental disorders including autism and dyslexia (Cao et al., 2016; Edwards et al., 2018; Uddin et al., 2011). A focus on global network organization provides a more holistic view beyond potential dysfunctions within single brain regions and recognizes the heterogeneous nature of these disorders (Menon, 2011). The most widely observed features of abnormal brain network organizations include (but are not limited to): disrupted global connectivity, the emergence of dysfunctional (and compensatory) subsystems and vulnerable hub nodes (for reviews, see Fornito, Zalesky, & Breakspear, 2015; Menon, 2011; Stam, 2014; van den Heuvel & Sporns, 2013).

Despite an increased understanding of the large-scale brain architecture obtained from conventional graph theoretical analyses, there is still a lack of consensus on dyslexia-related brain network malfunctions due to methodological issues that limit the comparability across studies, populations and functional states (Tewarie, Van Dellen, Hillebrand, & Stam, 2015). In particular, the connection strength of two nodes in a functional network is often defined as the statistical dependence of their time series (Bassett & Sporns, 2017; Deco et al., 2015; Sporns, 2014). Since the decision on whether a given connection is present in the network depends on an arbitrarily predetermined threshold, the resulting network structure (e.g., number of edges, overall connectivity strength) may vary largely across individuals and studies (Bressler & Menon, 2010). A special type of graph, the minimum spanning tree (MST), has been introduced to minimize biases in comparing network metrics between subject populations and/or experimental conditions that may differ in the overall strength of connectivity (Stam, 2014; Tewarie et al., 2015). MST is a loop-less graph containing the highest weights derived from the connectivity matrix between each pair of nodes, which thus leads to a fixed number of nodes and edges in the resulting MST graphs (Stam, 2014; Tewarie et al., 2015). In a large-sample ($n$ = 1675) EEG study on resting-state network topology, it has been shown that MST metrics undergo an inverted U-shaped developmental trajectory from childhood (~5 to 7 years of age) through middle adulthood (~50 years), with an estimated peak of network integration around an age of 40 years (Smit, de Geus, Boersma, Boomsma, & Stam, 2016), in line with

previous network studies using other algorithms for graph construction (Stam & van Straaten, 2012; Uddin et al., 2011). The MST approach has also been implemented in studies investigating the resting-state network topology associated with reading difficulties. For instance, reduced network integration in the theta- (4-8 Hz) and beta-band (13-30 Hz) networks were reported in children with dyslexia (Fraga-González et al., 2016; Xue et al., 2020), whereas dyslexic adults showed a more integrated alpha-band (8-13 Hz) network compared to their typically reading peers (Gonzalez, Smit, et al., 2018). Recent research has attempted to associate altered oscillatory network topologies to deficient visual processing (Dushanova & Tsokov, 2021; Taskov & Dushanova, 2020), speech tracking (Zhang, Riecke, Fraga-González, & Bonte, 2022) and letter-speech sound binding (Fraga-González et al., 2021) in dyslexia. Due to the limited number of prior investigations, which adopted different tasks, there is no general agreement about *where* (i.e., in which frequency band) and *how* (i.e., abnormally more integrated or more segregated) brain network organizations may differ between dyslexic and typical readers. Thus, the network organization of oscillatory activities underlying speech-structure tracking and its association with dyslexia are investigated in **Chapter 4** using the MST approach.

## 4 Overview

This doctoral dissertation presents the findings from one tACS and three EEG experiments investigating the cortical tracking mechanisms of spoken and written language, and their associations with (a)typical reading development. **Chapter 2** utilizes electrical brain stimulation to test the causal contribution of slow cortical oscillations to fine-grained auditory perception in a sub-syllabic time window in typical readers. In **Chapter 3**, a statistical learning paradigm combined with frequency-tagging techniques is adopted to track the temporal course of speech structure tracking (knowledge-driven) and learning (regularity-based) in both typical and dyslexic readers. **Chapter 4** employs graph theoretical analysis including MST to probe dyslexia-related alterations in brain network topology during speech tracking. Finally, extending findings from the auditory domain, **Chapter 5** investigates the modality-dependent and supra-modal cortical processes for both spoken and written language tracking.

# Chapter 2

# No evidence for modulation of sound rise-time perception by 4-Hz brain oscillations

Based on

Amplitude-rise time (ART), the duration from the onset of an acoustic signal to its maximum amplitude, is a major constituent of the amplitude envelope of auditory speech. ARTs spanning approximately one theta cycle (4-8Hz, corresponding to a period of approximately 200ms) are thought to play a key role in speech encoding and comprehension (Doelling, Arnal, Ghitza, & Poeppel, 2014), as well as phonological skills and reading dysfluency in dyslexic readers (Goswami, 2011). The amplitude envelope of speech conveys information about phrasal structures, word boundaries, speech prosody, and the identity of syllables and phonemes (Giraud & Poeppel, 2012). It has been suggested that low-frequency (theta) cortical oscillations may subserve the segmentation and identification of syllabic information by synchronizing their phases to peaks of the amplitude envelope that resemble the timing of syllables (Giraud & Poeppel, 2012). However, it is still unclear whether theta cortical oscillations contribute functionally to ART perception.

Transcranial alternating current stimulation (tACS) is a non-invasive technique that enables to modulate the excitability of neuronal ensembles by temporally aligning brain oscillations to the alternating current (Herrmann, Rach, Neuling, & Strüber, 2013), which can alter participants' perception of auditory input (Riecke & Zoefel, 2018). For instance, 40-Hz tACS applied over the auditory cortex may improve categorical phoneme perception in dyslexic readers (Rufener, Krauel, Meyer, Heinze, & Zaehle, 2019). Moreover, the relative timing between speech amplitude envelope and theta tACS over auditory cortex may affect recognition of the speech (Riecke, Formisano, Sorger, Baskent, & Gaudrain, 2018). Whether these effects are mediated by linguistic processes or lower-level, ART-related auditory processes is still unclear. To test the latter idea, we investigated whether tACS-modulated slow cortical oscillations can influence the perception of ART in non-speech sounds.

We applied 4-Hz tACS over the auditory cortices and assessed ART perception with a two-interval forced-choice task that required the 23 participants to identify which of two randomly ordered tones in noise had a longer ART (Figure 1a). The ART of the target tone was variable and always longer than that of the reference tone (62.5 ms). The relative timing of tACS and the tone on-ramps was varied across six phase lags spanning one tACS cycle (Figure 1b; see *Supplemental Material*). Hypothesizing that slow cortical oscillations contribute functionally to ART processing, we predicted that the experimental phase-lag changes induce cyclical changes in ART-discrimination performance. We included a sham-

stimulation condition to additionally test whether tACS irrespective of its phase influences ART perception.

ART-discrimination performance scores in the six phase-lag conditions were calculated and concatenated to construct a behavioral time series for each stimulation condition. To compensate for potentially confounding inter-individual brain-anatomy differences, the maximum of the time series (the 'best' lag, Figure S2) was aligned across participants and excluded from subsequent analyses (Asamoah, Khatoun, & Mc Laughlin, 2019).

A two-way repeated measures ANOVA including the *Type of stimulation* (tACS or sham) and the five *Phase lags* revealed no significant interaction ($F_{4,88}$ = .84, $p$ = .503) or main effect (*Phase lag:* $F_{4,88}$ = 1.6, $p$ = .181; *Type of stimulation:* $F_{1,22}$ = 3.3, $p$ = .083) (Figure 1c), suggesting that neither tACS nor its phase affected ART perception. To further test for a phase effect, we compared the average performance in phase-lag conditions around the best lag (-60° and 60°) vs. the opposite phase-lag conditions (120° and 240°), which revealed no significant difference either ($t_{22}$ = .20, $p$ = .422; Figure 1d). Similarly, regressing single-trial responses onto phase lags (Zoefel, Davis, Valente, & Riecke, 2019) revealed no reliable difference between participants' regression coefficients vs. zero (average beta value = 0.16, Fisher's $p$ = .449). Similar results were obtained when applying the same analyses to data stratified according to different ARTs (see Figure S4).

These results provide no evidence that slow cortical oscillations play a functional role in ART perception. One potential interpretation is that these oscillations affect ART perception as originally hypothesized, but we failed to detect this due to potential methodological limitations. The sensitivity of our measure of ART perception was perhaps suboptimal, as the onset of the first tone in a given trial might have phase-reset brain oscillations and consequently distorted any tACS-induced brain phase at the onset of the second tone. In anticipation of this risk, and to circumvent the use of a more criterion-dependent single-interval yes/no task, we presented tones at a low sound level (44 dB SPL) in continuous noise. However, whether these measures sufficed to prevent tone-induced phase resets remains unclear and would have required directly measuring brain oscillations. The strengths of our tACS and experimental manipulation were likely sufficient to modulate brain oscillations as they have proven effective in some, although not all, speech-perception studies with similar statistical power (Kösem, Bosker, Jensen,

Hagoort, & Riecke; Riecke et al., 2018). A perhaps more exciting interpretation is that slow cortical oscillations contribute less to the perception of ART, but more to its linguistic interpretation. The short tone stimuli in our experiment provided a continuum of basic acoustic differences without any linguistic information. When linguistic stimuli are used, subtle changes in ART or cortical phase have been observed to affect the categorical perception of phonemes (e.g., /d/ vs /t/, short /a/ vs long /a:/) (Kösem et al., 2020; Rufener et al., 2019). Thus slow cortical oscillations may adapt the boundaries of linguistic categories rather than the temporal representation of individual ARTs (Riecke et al., 2018). Even if slow cortical oscillations were not found to systematically affect ART perception here, it may be interesting to verify this in the future in a population with chronic ART-processing deficits, e.g., dyslexic participants with phonological impairment, who may be more susceptible to cortical phase modulations (Rufener et al., 2019).

In sum, the current study provides no evidence for a causal contribution of slow cortical oscillations to the perception of auditory ARTs. Together with positive findings from related speech-perception studies, our null finding suggests that slow cortical oscillations may contribute to linguistic categorization, rather than lower-level auditory processing of ART.
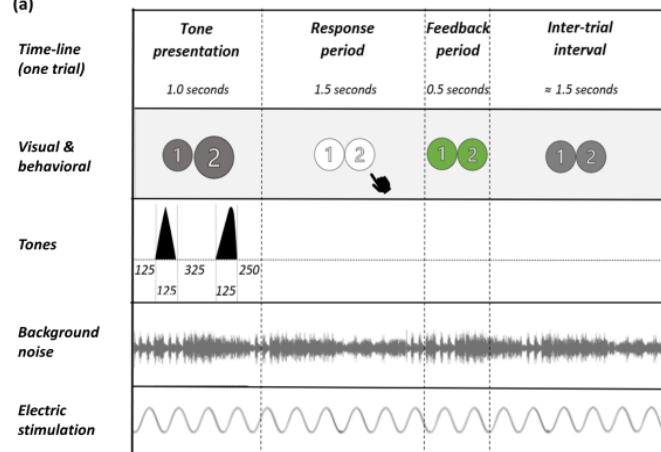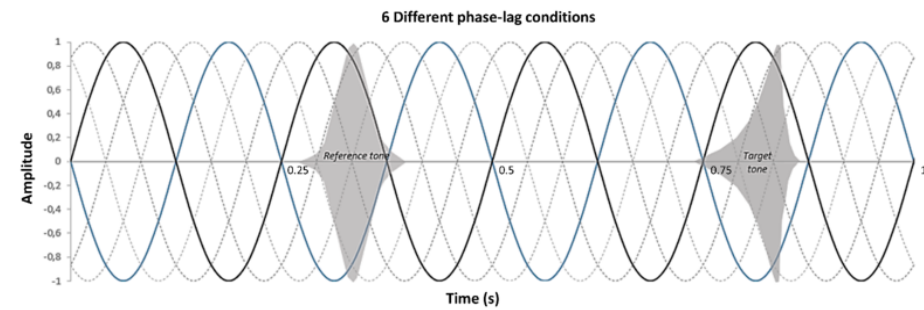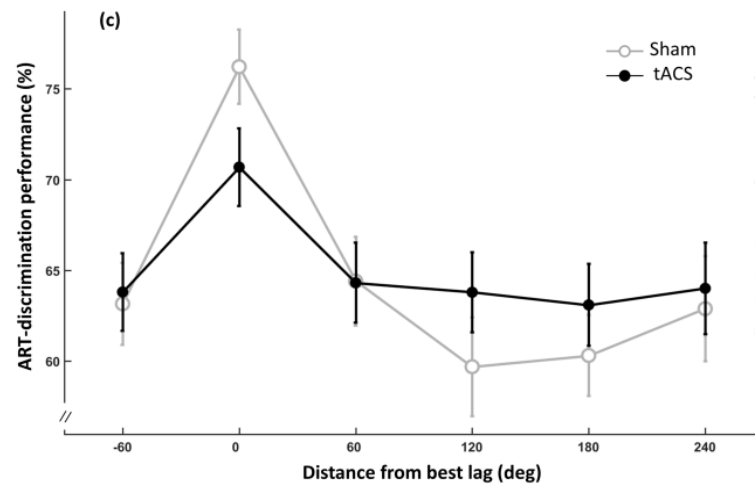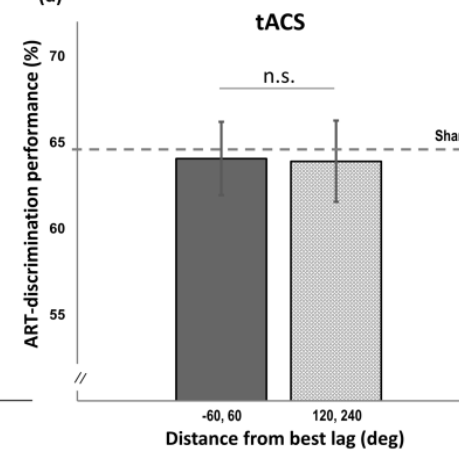
**Figure 1** (a) The time course of a single trial. Each trial involved four intervals: tone presentation, response period, feedback period and inter-trial interval. The width of the columns is proportional to the duration of each interval. The values in the third row represent durations in ms. The two digits "1" and "2" were shown continuously on the screen. During presentation of the first tone, the size of digit "1" was slightly increased, and analogously for the second tone/digit. The first tone was presented 125 ms after trial onset. The interval between two tones was fixed to 325 ms. Approximately 250 ms (jittered across trials) after the second tone was presented, both digits turned white, prompting participants to respond. Participants received feedback after each response coded by a change of color of the digits (green = correct, red = incorrect, pink = miss). The digits turned grey during the inter-trial interval, which varied in length. The background noise and the electric stimulation were continuously presented. (b) The relative timing between the tACS stimulation (i.e., sinusoidal curves) and the tones. Different sinusoidal curves represent the six phase lag conditions. In panel (c), ART-discrimination performance is shown as a function of distance from best lag during the tACS (black) and sham (grey) stimulation, and in panel (d) it was averaged across the best-lag distances presumed to resemble a positive (i.e., -60° and 60°; dark bar) and negative half-cycle (i.e., 120° and 240°; light bar). The grey dashed line corresponds to the average performance in the sham condition. Error bars represent the standard errors of mean. n.s. = non-significant.

## Supplementary Materials

### 1.1 Participants

Twenty-two healthy adults (16 females, age: $M$ = 23.74, $SD$ = 5.06) were included in the study. None reported prior diagnosis of hearing loss, developmental dyslexia or brain-related neurological illness. They were first tested for normal hearing by means of pure tone audiometry (*Maico MA30*), defined as hearing thresholds $\leqslant$ 25 dB HL at 0.25, 0.5, 0.75, 1, 2, 3, 4, and 6 kHz for both ears. Two participants showed mild (25-35 dB) to moderate (35-45 dB) hearing loss in one ear, for at most two frequency bands other than the test frequency (i.e., 1 kHz). Four other subjects were excluded from the analysis (three failed the behavioral pre-test described below, one did not tolerate tACS stimulation). All participants underwent a screening procedure to comply with the institutional safety criteria for non-invasive electrical brain stimulation. They received study credits or a monetary reward in the form of gift vouchers. Written informed consent form was signed by every participant prior to the measurement. The experimental protocol was approved by the institutional ethics committee (Ethical Review Committee Psychology and Neuroscience, Maastricht University). The present study was conducted in accordance with the principles of the Declaration of Helsinki.

### 1.2 Auditory stimuli

Pure tones with a frequency of 1 kHz and duration of 125 ms were created at a sampling rate of 16 kHz. The reference tone had linear on-ramp and off-ramps each lasting 62.5 ms (thus no plateau). The on- and off-ramp durations of the target tone varied between trials, such that the on-ramp of the target tone was always longer than that of the reference tone and the off-ramp of the target tone was correspondingly shorter. Seven on-ramp durations ranging from 62.5 to 120 ms (in steps of 9.6 ms) were used for the estimation of individual psychometric curves in a pre-test (see section 1.6). Broad-band noise with a 2-octave notch centered at the frequency of the tone was generated using a fourth-order Butterworth filter. The noise level was adjusted to yield a signal to noise ratio of 10 dB, and presented continuously throughout each run of the experiment. All sounds were digitally generated using MATLAB (*MathWorks, Inc.,* Natick, MA) and

diotically presented through a multi-channel D/A-converter (*National Instruments*) via earphones (*Etymotic Research, Inc.*) at a sound pressure level of 54 dB maximum intensity.

## 1.3 Electric stimulation

Electric currents were applied via rubber electrodes above the bilateral auditory cortices (i.e., T7 and T8, $5 \times 5$ cm$^2$), as well as the region centered around Cz (two electrodes of $5 \times 7$ cm$^2$ in each hemisphere), according to the 10/20 system. The 4-Hz sinusoidal current stimulation was delivered through two battery-driven transcranial current stimulators (*Neuroconn DC-Stimulator Plus*), with its intensity defined for each participant within a range of 0.5 to 1.0 mA in steps of 0.1 mA (peak-to-zero; see section 1.6 for details). Impedance was reduced as much as possible (< 10-15 kΩ, *M* = 6.55, *SD* = 4.47). Stimulation was ramped over the first and the last 10 s of each tACS run, while for the sham run, the stimulation had a 10 s on-ramp with a 70 s off-ramp at the beginning, and a 70 s on-ramp with a 10 s off-ramp at the end. The relative timing between the electric stimulation and auditory stimuli was controlled by a multi-channel D/A-converter (*National Instruments*; sampled at 16 kHz) and *Datastreamer* software (ten Oever et al., 2016).

## 1.4 Amplitude-rise time (ART) discrimination task

ART perception was assessed using a two-interval two-alternative forced choice (2I2AFC) task which required participants to identify the target from two tones and report via button press. The order of target and reference tones was randomized across trials. Additionally, visual cues (i.e., number "1" and "2", indicating the first and second tone, respectively) were given to visually indicate the presentation of each tone and provide feedback. To be more specific, there was a slight change in size of the digit when the corresponding tone was presented. Approximately 250 ms (jittered across trials) after the second tone was presented, both digits turned white, indicating to participants the onset of the response interval. Participants received visual feedback after each response coded by a change of color of the digits (green = correct, red = incorrect, pink = miss). The digits turned grey during

the inter-trial interval (≈ 1.5 s). Visual display and response recording were controlled using Presentation® software (*Neurobehavioral Systems, Inc.*, Berkeley, CA).

## 1.5 Experimental design

The influence of slow cortical oscillations on ART perception was tested taking into account two within-subject factors: (i) phase lag and (ii) type of stimulation (i.e., tACS vs. sham). The phase lag was defined as the delay between the positive peak of the electric stimulation and the midpoint of the on-ramp duration of the tones. Since the midpoints of the on-ramps of the two tones were separated by an integer number of tACS cycles, the phase lag relative to the first and second tone was always identical. In total, six phase lag conditions were created by varying the onset-timing of the auditory stimuli in six equidistant steps spanning a 4-Hz tACS cycle. During the main experiment, the order of different phase lags was randomized across trials.

As a secondary question, this study set out to examine whether 4-Hz tACS can enhance (or suppress) ART perception. To this end, a sham condition (i.e., without electric stimulation, see section 1.3 for details) was included to obtain a benchmark performance. Sham stimulation was presented throughout one of the five experimental runs.

## 1.6 Experimental procedure

Participants were seated in a sound-attenuated booth and took part in a series of procedural steps before the main experiment.

*Familiarization*
Participants were first presented with pairs of tones with varying ART differences. They were informed about the identity of the target tone. Subsequently, ART discrimination was practiced using a short version of the main 2I2AFC task (70 randomized trials, ≈ 5 min).

*Determination of individual on-ramp durations*

To obtain individual ART discrimination thresholds, participants were asked to perform the familiarization task again on an increased number of trials (N = 140). A psychometric curve was estimated based on the performance observed for the seven on-ramp durations. To allow testing tACS phase effects at multiple performance levels and creating some auditory variation to reduce the risk of fatigue or boredom, we extracted three thresholds, i.e., on-ramp durations yielding low, intermediate, and high performance levels on the psychometric curve. These three on-ramp durations, which we refer to as 'short, medium and long', respectively, were then used during the main experiment. Because participants reported the task at the initial thresholds (defined by 50%, 60% and 70% performance level) to be rather demanding, the majority of participants (*N* = 17) was tested at more relaxed thresholds defined by performance levels of 60%, 70% and 80%. For participants for whom no clearly monotonous psychometric function could be obtained (*N* = 6), the three on-ramp durations were defined by linearly interpolating between the low- and high-performance points on the curve.

*Determination of individual tACS intensity*
The peak TACS intensity was adjusted individually between 0.5 to 1.0 mA in steps of 0.1 mA (0.84 ± 0.18 mA peak-to-zero, mean ± SD across participants) to the maximum point for which participants reported no unpleasantness.

*Main experiment*
The experiment consisted of five 10-min runs. Participants received continuous electric stimulation in four tACS runs, and no stimulation in the sham run. The order of tACS and sham runs was counter-balanced across participants. Each run involved 144 trials (i.e., 24 trial per phase lag condition). The three thresholds were distributed uniformly across the phase lag conditions and randomly within each run. Participants were asked to take a break between each run. After the experiment, they completed a questionnaire inquiring their confidence on whether they received electric stimulation per run. Statistical analysis revealed that confidence ratings were not significantly higher after tACS runs (*M* = 54.95%, *SD* = 25.27%) than sham runs (*M* = 50.43%, *SD* = 36.99%; $t_{22}$ = .56, *p* = .58), indicating that participants did not reliably distinguish between real and sham stimulation.

## 1.7 Data analysis and supplementary results

Trials presented during the on-/off-ramps in the sham run were discarded from analysis. Performance in ART perception was computed as the proportion of correct responses. We first examined the effect of ramp durations by comparing performance across the presented on-ramp durations (i.e., short, medium or long; pooled across different types of stimulation), using a repeated measures ANOVA (Figure S1).
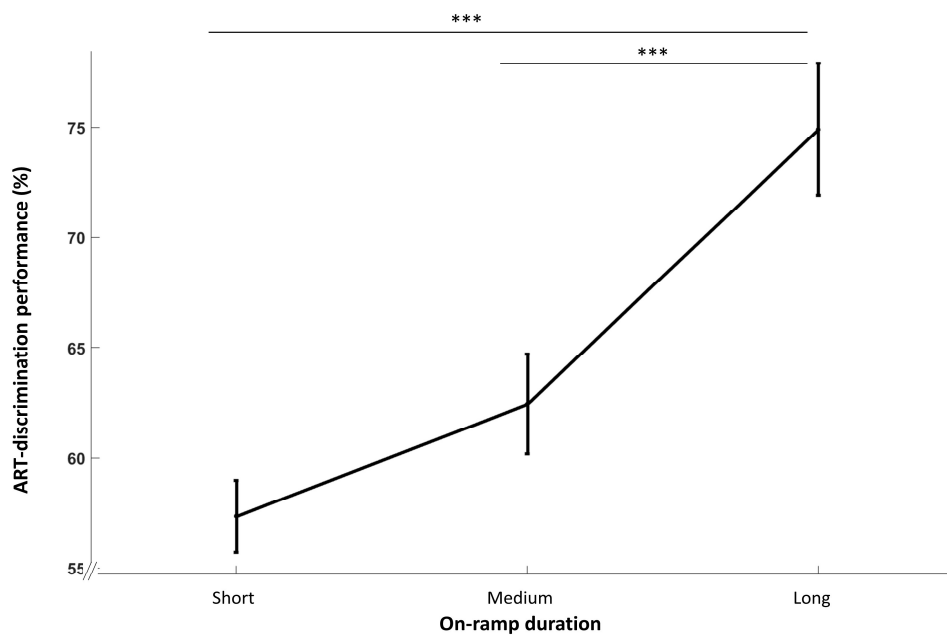


**Figure S1**. Effect of on-ramp duration on ART discrimination in the main experiment. The effect of on-ramp duration on ART perception was significant, showing better ART-discrimination performance for larger ART differences between the target and reference tones ($F_{2,44}$ = 36.6, $p$ < .001). The monotonic increase validates our selection of auditory stimuli. Error bars represent the standard errors of mean. *** $p$ < .001.

To test our main hypothesis, performance was computed per phase lag condition, for the tACS and sham stimulation separately. Afterwards, for each participant and each type of stimulation, the performance scores observed in the six phase lag conditions were concatenated to build a behavioral time series. Since individual differences in brain anatomy may cause inter-individual variations in tACS-effect polarity, the time series was aligned to the best lag (i.e., the phase lag that yielded

the best performance; excluded from subsequent analyses) across participants (Figure S2).

A two-way repeated measures ANOVA including within-subject factors *Phase lags* and *Type of stimulation* was applied to examine whether oscillatory phase and/or tACS per se (regardless of its phase; Figure S3) influenced ART perception (also see Figure 1c). To examine the potential influence of on-ramp durations, the same analyses were applied on data stratified by target performance levels (Figure S4).
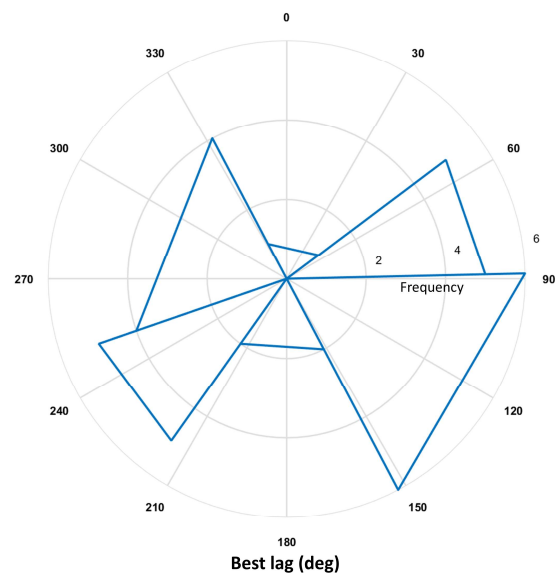


**Figure S2**. The phase angle histogram shows the distribution of participants' best lag for ART perception. The distribution did not deviate significantly from uniformity ($z$ = .20, $p$ = .82). On average, the participants' performance was best when the midpoint of the tone on-ramp lagged behind tACS stimulation by 58.95 ± 18.06 ms (or equivalently, preceded it by 191.05 ± 18.06 ms).
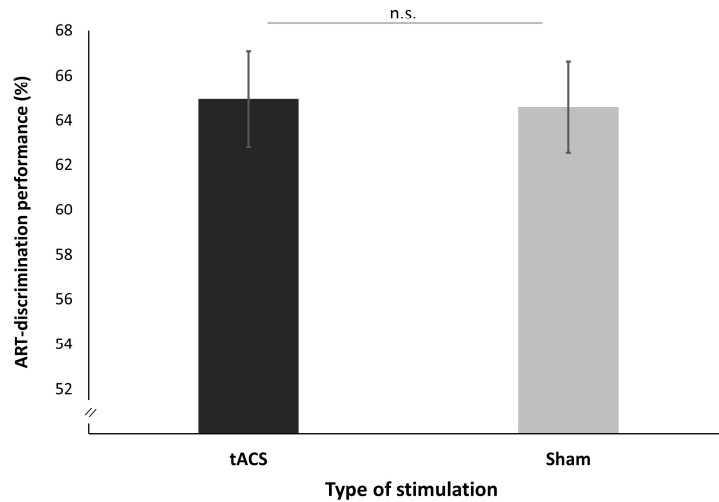
**Figure S3**. ART-discrimination performance averaged across best-lag distances in the tACS (black) and sham (grey) condition. The behavioral performance did not show a significant difference between tACS ($M$ = 64.95, $SD$ = 10.27) and sham ($M$ = 64.59, $SD$ = 9.84) stimulation, $t_{22}$ = .39, $p$ = .70. Error bars represent the standard errors of mean. n.s. = non-signficant.
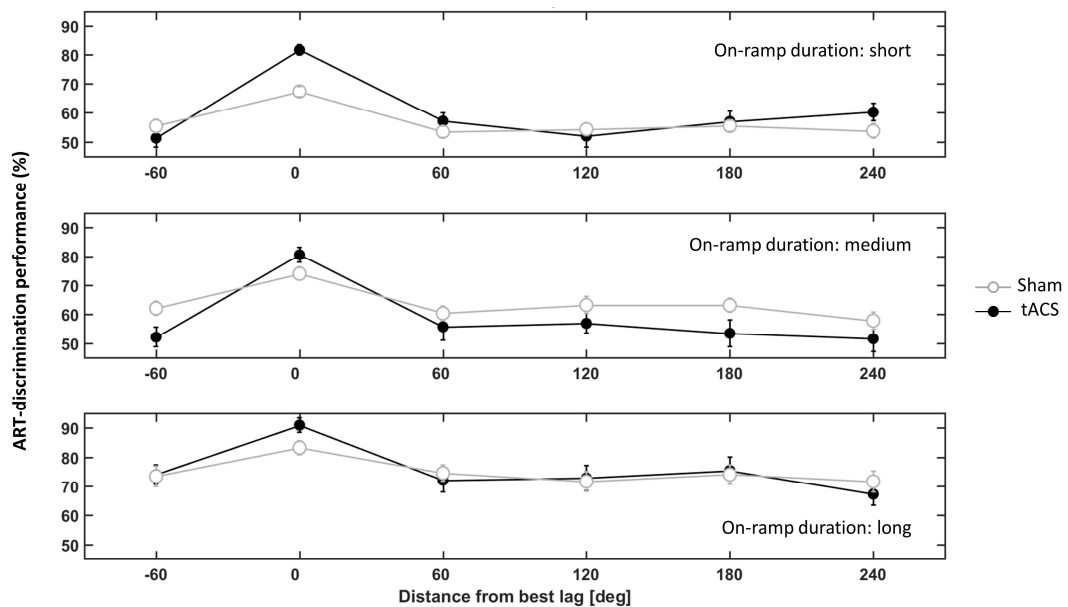


**Figure S4**. ART-discrimination performance on short (top), medium (middle) and long (bottom) on-ramp durations as a function of distance from best lag during the tACS (black) and sham (grey) stimulation. There was no significant main effect of *Phase lag* (*p*s > .114) or *Phase lag × Type of stimulation* interaction (*p*s > .183) for any of the three on-ramp durations.

Considering that ANOVA does not take into account the cyclical nature of the hypothesized phase effect, this putative effect was further tested in two alternative analyses. In the first analysis, participants' average performance at the two phase lags neighboring the best lag was compared with their average performance at the two 'opposite' (i.e., shifted by 180 deg) phase lags, using a one-tailed paired t-test. The rationale behind this analysis is that, under the hypothesis of a cyclical phase effect, performance at lags near the best lag should be better than at lags during the other half of the tACS cycle. In the second, theoretically optimal analysis (Zoefel, Davis, Valente, & Riecke, 2019), a logistic regression model (including the sine- and cosine transformed phase lag as predictors) was fitted to each participant's dichotomous (correct or incorrect) single-trial behavioral data. The resulting regression coefficients (beta values) were statistically compared to zero using an F-test. The resulting individual p values were submitted to a second-level group analysis using Fisher's test.

# Chapter 3

## Neurophysiological tracking of speech-structure learning in typical and dyslexic readers

## Abstract

Statistical learning, or the ability to extract statistical regularities from the sensory environment, plays a critical role in language acquisition and reading development. Here we employed electroencephalography (EEG) with frequency-tagging measures to track the temporal evolution of speech-structure learning in individuals with reading difficulties due to developmental dyslexia and in typical readers. We measured EEG while participants listened to (a) a structured stream of repeated tri-syllabic pseudowords, (b) a random stream of the same isochronous syllables, and (c) a series of tri-syllabic real Dutch words. Participants' behavioral learning outcome (pseudoword recognition) was measured after training. We found that syllable-rate tracking was comparable between the two groups and stable across both the random and structured streams of syllables. More importantly, we observed a gradual emergence of the tracking of tri-syllabic pseudoword structures that eventually approximated the neural tracking of real words in both groups. Compared to the typical readers, however, in the dyslexic readers this implicit speech structure learning seemed to build up at a slower pace. A brain-behavioral correlation analysis showed that slower learners (i.e., participants who were slower in establishing the neural tracking of pseudowords) were less skilled in phonological awareness. Moreover, those who showed stronger neural tracking of real words tended to be less fluent in the visual-verbal conversion of linguistic symbols. Taken together, our study provides an online neurophysiological approach to track the progression of implicit learning processes and gives insights into the learning difficulties associated with dyslexia from a dynamic perspective.

## Keywords

Developmental dyslexia, statistical learning, word segmentation, frequency-tagging, neural plasticity

# 1 Introduction

Developmental dyslexia (DD) is a learning disorder characterized by a specific impairment in accurate and/or fluent reading, despite adequate intelligence and conventional instruction, affecting approximately 5–12% of the population (Peterson & Pennington, 2012; Shaywitz & Shaywitz, 2005). A variety of deficiencies has been identified in dyslexic readers, including poor phonological processing (e.g., Ramus, 2003) and slowness in rapid automatized naming (RAN) (see Araújo & Faísca, 2019, for a recent meta-analysis). These deficiencies may hamper the formation of solid associations between orthographic (letters) and phonological (speech sounds) representations that are central to learning to read (Blau et al., 2010; Blau, van Atteveldt, Ekkebus, Goebel, & Blomert, 2009). There exists a vast body of over 8500 studies on the topic of "dyslexia" from the past two decades (Huettig, Lachmann, Reis, & Petersson, 2018); however, surprisingly few studies spotlighted potentially underlying learning difficulties by tracking the time course of learning. Instead, studies have mostly evaluated the learning ability based on changes before and after learning, often administered via memory tests or standardized assessments that usually cannot disentangle the contribution of online learning from that of memory storage, consolidation, and retrieval (Batterink & Paller, 2019). Moreover, since learning often progresses in a fluctuant fashion, and is susceptible to interference (Buiatti, Peña, & Dehaene-Lambertz, 2009), the learning process is difficult to model with behavioral responses, thus stirring growing interest in the development of learning-induced neural changes over time (Henin et al., 2019). Given that individual variability in cognitive-perceptual learning trajectories contributes to the heterogeneous patterns of language development observed in children (Saffran, 2018), combining learning tasks with simultaneous neuroimaging may provide a dynamic and objective measure of dyslexia as a learning disorder.

In the current study we employed a statistical learning (SL) paradigm as a tool for tracking the development of sensitivity to statistical regularities in the sensory environment (Batterink & Paller, 2017; Milne, Wilson, & Christiansen, 2018; Saffran, Aslin, & Newport, 1996). This paradigm has proven useful for assessing statistical learning within a few minutes of exposure (e.g., Saffran, Newport, Aslin, Tunick, & Barrueco, 1997), and can be combined with various stimulus types, sensory modalities and ages (Henin et al., 2019). Originally, it was used in 8-

month-old infants to show their ability to segment continuous syllable streams into repeating pseudowords by relying on the transitional probabilities between adjacent syllables, which were higher within words than across word boundaries (Saffran, Aslin, et al., 1996; Saffran, Newport, & Aslin, 1996). In behavioral studies, such extraction of statistical structures has been observed to be less efficient in individuals with dyslexia (Schmalz, Altoè, & Mulatti, 2017). For instance, children with dyslexia performed relatively poorly on SL tasks with syllable and tone sequences, as assessed with post-learning recognition tests (Gabay, Thiessen, & Holt, 2015). Neurophysiological studies further identified a reduced sensitivity to phonotactic probabilities, i.e., the distributional frequency of phoneme combinations in a given language, in both children (Bonte, Poelmans, & Blomert, 2007) and adults (Noordenbos, Segers, Mitterer, Serniclaes, & Verhoeven, 2013) with dyslexia. The online neural learning trajectory leading to this deviant tuning to statistical regularities, remains unclear, however, and is a focus of the current study.

The neural tracking of statistical regularities in speech-structures can be efficiently investigated by combining electroencephalographic (EEG) or magneto-encephalographic (MEG) measurements with a frequency-tagging technique (Batterink & Paller, 2017; Buiatti et al., 2009; Farthouat et al., 2017; Kabdebon, Peña, Buiatti, & Dehaene-Lambertz, 2015; Ordin, Polyanskaya, Soto, & Molinaro, 2020). This approach exploits the steady-state response which mirrors periodic changes in stimuli by oscillating at the same frequency (Buiatti et al., 2009). Frequency tagging has been combined with SL paradigms to show an incremental neural tracking of trisyllabic structures with accumulating exposure to trisyllabic pseudowords, but not for random syllable streams (Batterink & Paller, 2017, 2019; Henin et al., 2019; Kabdebon et al., 2015; Ordin et al., 2020). Furthermore, the frequency-tagging technique has been used to show that cortical tracking of phrasal and sentential structure in speech is coupled with the listener's knowledge of these structures (Ding et al., 2017; Ding, Melloni, Zhang, Tian, & Poeppel, 2016). Frequency tagging thus allows probing the neural integration of speech units driven by higher-level (e.g., statistical, lexical and syntactic) properties, and hence can provide useful metrics for SL and familiar word tracking.

Reduced behavioral and neural plasticity has been suggested as a potential signature of dyslexia. In addition to reduced sensitivity to transitional (Gabay et al., 2015; Menghini, Hagberg, Caltagirone, Petrosini, & Vicari, 2006; Schmalz et al.,

2017) and phonotactic probabilities (Bonte et al., 2007; Noordenbos et al., 2013), dyslexic readers may show a difficulty in dynamically constructing predictions based on stimulus-specific repetitions (Ahissar, Lubin, Putter-Katz, & Banai, 2006). Moreover, dyslexic individuals were found to benefit less from visual text input during short-term audiovisual learning (Keetels, Bonte, & Vroomen, 2018) and to show diminished neural adaptation to repeating visual and auditory stimuli (Perrachione et al., 2016; Peter, McCollum, Daliri, & Panagiotides, 2019). Nevertheless, to our knowledge no dyslexia research has yet set out to monitor neural responsivity while learning takes place, nor its potential association with various reading skills.

The present EEG study aimed to trace the online statistical learning of speech structures in both typically reading adults and those diagnosed with dyslexia. Participants were exposed to artificial speech streams composed of tri-syllabic pseudowords (structured condition), as well as a baseline condition in which the same set of syllables was presented randomly (random condition). The frequency-tagging approach was applied to assess the neural representation of speech units at (pseudo)word and syllable levels. Based on research reviewed above, we expected to observe a gradual establishment of steady-state responses at the frequency of the tri-syllabic pseudowords only in the structured condition and not in the random condition. Steady-state responses at the frequency of syllable occurrence were expected to remain stable and comparable in both conditions. To further examine whether the outcome of this learning process resembles the neural representation of familiar words, an additional condition involving tri-syllabic real words was included as a reference. Compared to the typical readers, we expected the participants with dyslexia to show a less efficient build-up of neural tracking of the structured pseudowords. Finally, we analyzed the relationship between the neural tracking of (pseudo)word structure and various behavioral performance measures to explore whether putative changes in brain responses are associated with individual differences in reading skills.

## 2 Methods

### 2.1 Participants

36 adults took part in the study. 18 of them were diagnosed with developmental dyslexia by a pediatrician or a psychologist (hereafter 'DD', mean age 23.9 ± 4.00 years; 12 females; 1 left-handed). The diagnosis was made at varying ages ranging from 6–13 years. The other 18 participants were typically reading adults (hereafter 'TR', mean age 20.8 ± 2.26 years; 14 females; all right-handed) and served as a control group. All participants were native Dutch speakers with no reported hearing loss, normal or corrected-to-normal vision, and no history of diagnosed neurological disorders. This study was approved by the ethics committee of the Faculty of Psychology and Neuroscience, Maastricht University. Written informed consent was obtained from each participant before conducting the experiment. Participants received either course credits or shopping vouchers as participation reward.

## 2.2 Behavioral measures

33 out of 36 participants (15 TRs and 18 DDs) also underwent a series of standardized tests on reading and phonological skills (see Table 1). First, word reading fluency was measured using a time-limited reading test consisting of 116 unrelated words that are arranged in ascending difficulty ("Een-Minuut-Test", or EMT) (Brus & Voeten, 1973). The reading fluency was calculated by subtracting the number of mistakes from the number of correctly read words. Second, a Rapid Automatized Naming (RAN) test (Van den Bos & Lutje Spelberg, 2007) was administered, which is composed of four subtests: colors, digits, objects, and letters. The participants were required to name the items as accurately and fast as possible. In each subtest, naming speed was quantified as the time needed to name all 50 items, divided by the associated accuracy, i.e., the accuracy-corrected naming time. We used the average RAN speed for colors and objects as an indicator of non-symbolic visual-verbal conversion (V-VC) skill, and the average RAN speed for digits and letters as an indicator of symbolic V-VC skill.  Third, Phonological Awareness (PA) was assessed with *Spoonerisms* and *Reversals* from the GL&SCHR test (Depessemier & Andries, 2009). In the *Spoonerisms* test, participants need to switch the first phonemes of two spoken words (e.g., Harry Potter becomes Parry Hotter), while in the *Reversals* test, participants have to judge whether the spelling of the second word in a sequence of two orally presented nonsense words is the reverse of the first word (e.g., gak - kag).

Accuracy (i.e., number of correct responses) and speed (in seconds) were measured for answering 20 items in each subtest after a brief practice of six examples. The accuracy-corrected response time was derived by the ratio of speed and accuracy times ten. The total accuracy of the two subtests was used to quantify individual performances in phonological awareness.

**Table 1**. Descriptive statistics and demographic information

| | TR | DD | Group differences | |
|---|---|---|---|---|
| | M (SD) | M (SD) | t | p-value |
| N (Female) | 18[f] (14) | 18 (12) | | |
| Age (years) | 20.78 (2.26) | 23.93 (4.01) | -2.91** | .007 |
| EMT[a] | 96.80 (10.87) | 77.67 (11.71) | 4.83*** | <.001 |
| RAN[b] letter | 18.89 (2.81) | 21.75 (4.61) | -2.18* | .037[g] |
| RAN[b] number | 19.60 (2.50) | 21.89 (4.11) | -1.96 | .059[g] |
| RAN[b] object | 35.28 (5.04) | 36.06 (4.65) | -.46 | .648 |
| RAN[b] color | 29.05 (4.15) | 31.22 (4.91) | -1.38 | .177 |
| Spoonerisms Acc.[c] | 17.53 (1.30) | 16.00 (2.85) | 2.04 | .052[g] |
| Spoonerisms RT[d] | 66.38 (15.63) | 117.30 (48.41) | -4.21*** | <.001[g] |
| Reversals Acc.[c] | 17.40 (1.45) | 15.28 (1.67) | 3.85*** | <.001 |
| Reversals RT[d] | 50.83 (12.92) | 68.42 (13.61) | -3.78*** | <.001 |
| Recognition Acc.[e] | 60.61 (15.71) | 55.67 (17.50) | .89 | .379 |
| Recognition RT | 835.89 (406.40) | 916.20 (400.76) | -.60 | .555 |

Note: [a] EMT = Een-Minuut-Test, number of correctly reading items; [b] RAN = Rapid Automatized Naming, accuracy-corrected response time (msec), i.e. reading time divided by accuracy; [c] Acc. = Accuracy, number of correct responses; [d] accuracy-corrected reaction time = total response time/score×10, in sec; [e] Acc. = Accuracy, percentage; [f] three out of 18 TR participants did not take the reading/phonological assessment; [g] Equal variances not assumed. * $p < .05$, ** $p < .01$, *** $p < .001$.

## 2.3 Stimuli

Twenty-three different syllables were adopted to develop three types of speech streams following the same procedure as Saffran, Aslin, et al. (1996). 12 consonant-vowel (CV) syllables were used in the random sequence (hereafter RS) and structured stream (hereafter SS), with the other 11 syllables forming four real Dutch words (RW condition, mostly CV syllables; one syllable appeared twice in two different words). The syllables were individually generated in Dutch with a female voice using Google TTS, an artificial speech synthesizer, with a sampling rate of 44100 Hz. Syllable sound files were edited in Praat (Boersma & Weenink, 2018) to flatten prosody and fix syllable length to 300 msec. Individual syllable sounds were concatenated in a predefined order in Matlab, containing no pauses in between.

Three types of continuous speech streams were generated. (1) In the SS, four tri-syllabic pseudowords (i.e., "*bidaku*", "*golabu*", "*padoti*" and "*tupiro*") were created and repeatedly presented within 2.5-minute exposure blocks. Therefore, the transitional probability between adjacent syllables was higher (i.e., 1.0) within words than between word boundaries (i.e., 0.33). (2) The RS was constructed by a pseudorandom concatenation of the same set of syllables used in SS, but without any higher-order structure. The transitional probability between neighboring syllables was 1/11, since an immediate repetition of the same syllable was avoided when generating the speech stream. (3) The RW stream was created based on a random repetition of four real Dutch words, i.e. "*radio*", "*camera*", "*lucifer*" (i.e., the noun "match" in English) and "*domino*".

A total of 14 different blocks of speech streams (i.e., six each for the RS and SS conditions, and two for the RW condition) were produced. Each block contained 480 syllables (corresponding to 160 pseudo- and real words in the SS and RW conditions respectively) presented at a rate of 3.3 Hz. To avoid potential cueing of word structures, a total of three to five random syllables were added to the start and end of each block. Moreover, the volume of the speech stream was ramped on and off, over the first and last 1500 msec, respectively, to ensure that participants could not make use of properties other than transitional probability to detect the precise beginning and end of each sound stream.

## 2.4 Procedure

A visual summary of the experimental design is shown in Figure 1. The experiment was run in an acoustically and electrically shielded room on a PC using Presentation Software (Version 20.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). Auditory stimuli were presented at a comfortable listening level (approximately 70 dB SPL) from two speakers placed approximately 120 cm in front of the participant.

### 2.4.1 Exposure task

During the experiment, participants were exposed to each of the three artificial speech streams. The order of RS and SS conditions was counterbalanced across individuals, while the RW condition was always presented at the end of the experiment. This is because the tri-syllabic structure in the RW condition was prominent due to prior knowledge, which would have prompted explicit prediction or strategy and hence attenuate implicit learning in any subsequent block. Participants were not informed of the hidden structure before exposure, nor were they instructed to give any explicit responses. Instead, they were asked to relax and listen attentively to an alien language. A brief break was given after each 2.5-min block.

### 2.4.2 Recognition task

After listening to the RS and SS streams (and before proceeding to the RW condition), a two alternative forced-choice auditory recognition test was carried out to determine whether the participants were able to identify the artificial words belonging to the SS they just heard. The test comprised 16 pairs of syllabic triplets of which one was always a structured pseudoword, while the other one was either a 'part-word' (i.e., a tri-syllabic sequence with lower transitional probability spanning word boundaries, such as '*butupi*') or a 'random-word' (i.e., three random syllables that never appeared as a chunk in the SS). In each trial, the two test items were separated by a 1500-msec ISI, with the presentation order counterbalanced across trials. Participants were asked to press one of two buttons

to indicate which of the two triplets sounded more familiar to them. The next trial automatically began about 500 msec after each response. No feedback was given.
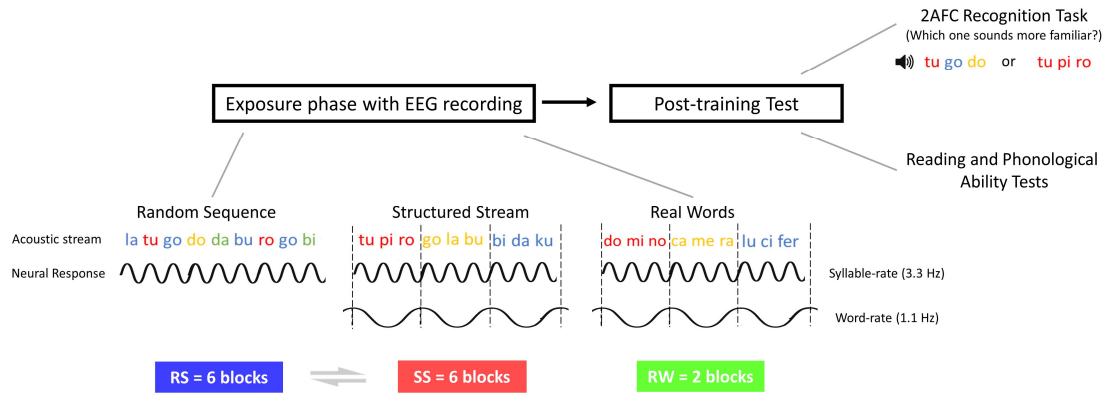


**Figure 1**. Schematic depiction of the experimental procedure and design. The exposure phase consisted of three conditions: the random sequences (RS), the structured streams (SS) and the real word (RW) condition. The order of RS and SS conditions was counterbalanced across participants, while the RW condition was always presented at the end of the exposure phase. The predicted neural response is shown below the sample piece of acoustic stream in each condition: neural tracking at the syllable-rate (3.3 Hz) was expected in all three conditions, whereas the word-rate tracking (1.1 Hz) was expected only in SS and RW conditions. After the exposure to RS and SS streams, explicit memory of the pseudowords in the SS condition was tested in an auditory recognition task. Finally, a battery of measurements on reading and phonological skills was performed.

## 2.5 Data acquisition and analysis

### 2.5.1 EEG recording and preprocessing

EEG was recorded with 64 Ag/AgCl active electrodes at a sampling rate of 2500 Hz, using the actiCAP according to the 10/20 system, and a 24-bit battery-supplied Brainvision actiCHamp amplifier (Brain Products GmbH, Germany). A ground electrode was located on the forehead, and the reference electrode was FCz. Electrode impedances were kept below 10 kΩ throughout the experiment. The first block of RS was excluded in one TR participant due to recording failure during the first minute of learning. Moreover, brain signals from two noisy channels (Pz and POz) in one DD participant were removed from the overall dataset based on visual inspection during the experiment and the impedance check afterwards. The

resulting channel-reduced dataset was excluded from spatial analyses (described below in section *Evaluation of the learning outcome*).

Using EEGLAB (Delorme & Makeig, 2004), the electrophysiological signals were subsequently down-sampled to 500 Hz, and re-referenced off-line to the algebraic average of the left and right mastoids. A band-pass filter of 0.1-30 Hz was applied. Independent Component Analysis was performed (63 estimated components per participant) to categorize brain activity versus stereotypical artifacts (including eye blinks and movements, heart beats, muscle activity, and channel noise) by visual inspection of the scalp topographies, time courses and activity power spectra of the independent components. After removing components representing non-brain artifacts, EEG data were reconstructed based on the remaining components (on average of $39.72 \pm 9.38$ components in the TR group and $42.94 \pm 8.92$ in the DD group; no group difference). The data were then baseline corrected for each individual block with a pre-stimulus interval of 5 sec.

### 2.5.2 EEG data analysis

Data from each block were time-locked to (pseudo)word (or triplet in the RS condition) onsets and extracted into non-overlapping epochs of 10.8 sec, corresponding to the duration of 12 (pseudo)words (or triplets), or 36 syllables. We analyzed neural responses elicited by both the individual syllable and (pseudo)word rate using inter-trial phase coherence (ITPC). The ITPC ranges from 0 to 1, and indicates the extent to which the EEG activity is phase-locked across single trials at a given frequency. ITPC was computed for each electrode using a fast Fourier transformation (frequency resolution = 0.0926 Hz) in Matlab, and then averaged across all electrodes.

## 2.6 Quantification of the learning process

In order to examine the time course of cortical tracking and statistical learning of hierarchical speech units, we plotted the word- (i.e., 1.1 Hz) and syllable- (i.e., 3.3 Hz) rate ITPC as a function of the temporal position of blocks. Figure 3 shows these time courses for each condition and each group. Among our two frequencies of interest (FOI), we focused on the word rate to assess implicit learning of the

pseudoword structure. We conducted a condition × block × group mixed factorial ANOVA to evaluate the learning trajectory of word-rate tracking. Visual inspection of individual learning curves revealed that the increase of word-rate ITPC tended to be most evident in the first few blocks of exposure. On average, the TR and DD group reached their maximum word-rate ITPC after approximately four (10 min) and five blocks (12.5 min), respectively (see Figure 3a and 3b). After that, gain in the neural tracking of triplets either continued or started to reduce, as also shown in previous EEG studies (Chen, Jin, & Ding, 2020; Choi, Batterink, Black, Paller, & Werker, 2020; Cunillera et al., 2009; Farthouat et al., 2017).

To further quantify the implicit learning of speech structures while considering individual variability in the learning courses, we identified the block showing the maximum ITPC value at the pseudoword rate in the SS condition (hereafter SSmax) for each participant. SSmax (reflecting the maximal learning gain) and the corresponding block number (indexing the learning speed) were compared between the two groups using an independent-sample $t$-test and a non-parametric Mann-Whitney $U$ test, respectively.

## 2.7 Evaluation of the learning outcome

The outcome of auditory statistical learning was assessed by comparing the neural representation of newly learned pseudowords vs. familiar real words. We first calculated the maximum word-rate ITPC of the two RW blocks (hereafter RWmax) for each participant as a benchmark for measuring individual learning outcome. This value was then compared against the SS block in which the maximal learning gain was observed for each individual (SSmax) via a condition × group mixed factorial ANOVA.

Regarding the spatial distribution of word-rate ITPC, we first examined whether it differed between the two groups in the RW condition. Based on Batterink and Paller (2017), word-rate ITPC was statistically analyzed by averaging across the two RW blocks (hereafter RW) and pooling electrodes within nine spatial clusters. The electrode clusters were located at left anterior (AF7, AF3, F7, F5 and F3), left central (FT7, FC5, FC3, T7, C5 and C3), left posterior (TP7, CP5, CP3, P7, P5, P3, PO7 and PO3), middle anterior (AFz, F1, Fz and F2), middle central (FC1, FCz, FC2, C1, Cz and C2), middle posterior (CP1, CPz, CP2, P1, Pz, P2 and POz), right anterior (AF4,

AF8, F4, F6 and F8), right central (FC4, FC6, FT8, C4, C6 and T8) and right posterior (CP4, CP6, TP8, P4, P6, P8, PO4 and PO8) scalp regions. These mean amplitudes were analyzed using a left-right region × anterior-posterior region × group mixed factorial ANOVA.

Furthermore, we plotted the group-averaged topographical maps for both the SS blocks and the average of the two RW blocks, and then quantified the topographic similarity between each SS block and the RW reference by calculating the Euclidean Distance (EucD) between each pair of those topographic matrices (i.e., $SS_k$ versus RW). In general, for an $n$-dimensional space the EucD is

$$EucD_{(p,q)} = \sqrt{(p_1 - q_1)^2 + (p_2 - q_2)^2 + \cdots + (p_i - q_i)^2 + (p_n - q_n)^2}$$
$$= \sqrt{\sum_{i=1}^{n} (p_i - q_i)^2}$$

Accordingly, the lower this value, the higher the spatial resemblance of pseudoword tracking to real word tracking.

## 2.8 Brain-behavior correlation

We computed Pearson correlation coefficients to examine whether the phase-locking to word(-like) structures (i.e., SSmax and RWmax) (1) were related to individual variability in word reading (i.e., EMT), phonological awareness and (non-)symbolic visual-verbal conversion skills and (2) predicted the behavioral outcome of the learning process (i.e., the recognition RT of pseudowords). The resulting one-tailed $p$ values were FDR corrected for multiple comparison.

## 2.9 Data and code availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request. The data and code sharing adopted by the authors comply with the requirements of the Faculty of Psychology and Neuroscience, Maastricht University and the funding bodies.

# 3 Results

## 3.1 Behavioral results

In the TR group, the mean accuracy in the recognition task was 60.6% (*SD* = 15.7%) and significantly above chance level (i.e., 50%) [*t*(17) = 2.87, *p* = .011]. In the DD group, it was 55.7% (*SD* = 17.5%) and not significantly different from chance level [*t*(17) = 1.37, *p* = .187]. The difference between the two groups was not statistically significant in terms of recognition accuracy [*t*(34) = .89, *p* = .379, Cohen's *d* = .295] or average reaction time (TR: 835.89 ± 406.40 msec; DD: 916.20 ± 400.76 msec; *t*(34) = -.60, *p* = .555, Cohen's *d* = -.199; Table 1).
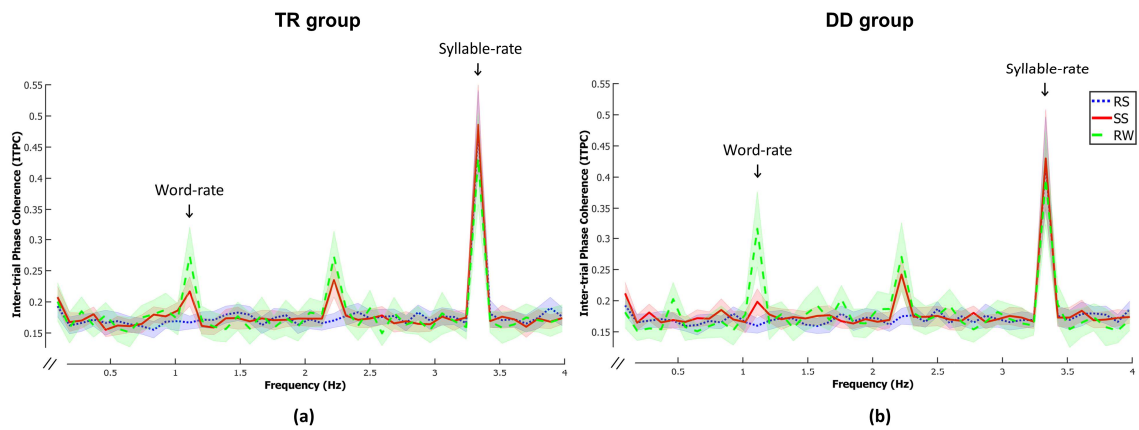


**Figure 2**. Average ITPC spectrum across all electrodes for each condition in typical readers (TR) and individuals with dyslexia (DD). The data show high ITPC at frequencies of interest as expected, including the individual syllable rate (3.3 Hz), syllable pair rate (2.2 Hz) and tri-syllabic word rate (1.1 Hz). RS = random sequence; SS = structured stream; RW = real word stream. The shaded area represents the 95% confidence interval.

## 3.2 EEG results

Consistent with our prediction, the inter-trial phase coherence (ITPC) data (Figure 2) showed clearly visible peaks at our frequencies of interest (FOIs), revealing neural tracking of speech units both at individual syllable (i.e., 3.3 Hz) and tri-syllabic (pseudo)word (i.e., 1.1 Hz) rate, as well as at an intermediate rate of syllable pairs (i.e., 2.2 Hz). In both groups, the peak of ITPC at the syllable-rate was

comparable across the random (RS), the structured (SS) and the real word (RW) conditions. In contrast, only RW and SS elicited peaks of ITPC at the word-rate.

## 3.3 Quantification of the learning process

ITPC data were plotted as a function of the temporal position of blocks in each condition and statistically tested at the two FOIs in both groups (Figure 3). We first investigated ITPC at the word-rate to quantify the tracking and chunking of syllable elements during the statistical learning of word(-like) structure. Overall, the typical readers required significantly less exposure [$M$ = 3.50 ± 1.098 blocks] to the syllables in the structured condition to reach a maximum word-rate ITPC (SSmax), compared to those with dyslexia [$M$ = 4.50 ± 1.465 blocks; Mann-Whitney $U$ = 231.00, one-sided $p$ = .015, Cohen's $d$ = -.722]. This result indicates that dyslexic readers learned the statistical word structure at a significantly slower pace. Moreover, the SSmax was significantly higher in the typical [$M$ = .397 ± .079] than dyslexic [$M$ = .348 ± .046] readers [$t(34)$ = 2.281, $p$ = .029, Cohen's $d$ = .758; Figure 4].

A repeated-measures ANOVA on word-rate ITPC with within-subjects factors condition (RS or SS) and block (1-6), and between-subjects factor group (TR or DD), showed a trend toward a three-way interaction [quadratic trend, $F(1, 33)$ = 4.03, $p$ = .053, $\eta^2_p$ = .109] and a significant group difference [$F(1, 33)$ = 4.58, $p$ = .040, $\eta^2_p$ = .122]. Overall, the DD group showed a reduced word-rate tracking compared with the TR group.

In the TR group, a repeated-measures ANOVA on word-rate ITPC with condition and block as within-subjects factors revealed a significant quadratic condition x block interaction [$F(1, 16)$ = 5.02, $p$ = .040, $\eta^2_p$ = .239] and a significant main effect of condition [$F(1, 16)$ = 13.62, $p$ = .002, $\eta^2_p$ = .460]. The main effect of block was not significant [$F(5, 80)$ = 1.83, $p$ = .117, $\eta^2_p$ = .103]. As predicted, the SS condition showed a significantly higher word-rate ITPC than the RS condition. This effect emerged quite rapidly (as early as Block 3) and progressively increased over time (up to Block 4), and then dropped off in the last two blocks (Figure 3a).

The DD group showed a different trajectory of learning gains. A repeated-measures ANOVA on word-rate ITPC showed a significant main effect of condition

[$F(1, 17) = 9.52$, $p = .007$, $\eta^2_p = .359$], but no significant main effect of block [$F(5, 85) = .74$, $p = .596$, $\eta^2_p = .042$] nor their interaction [$F(1, 17) = .48$, $p = .499$, $\eta^2_p = .027$]. Therefore, the DD group did not show a systematic enhancement in pseudoword tracking over time (Figure 3b). However, post-hoc comparisons did reveal a significantly higher word-rate ITPC in SS vs. RS conditions in only the two final blocks, not in any of the earlier blocks. This suggests that dyslexic readers started to learn the statistical word structure only toward the end of the experiment, in line with our result above indicating a slowed learning trajectory.
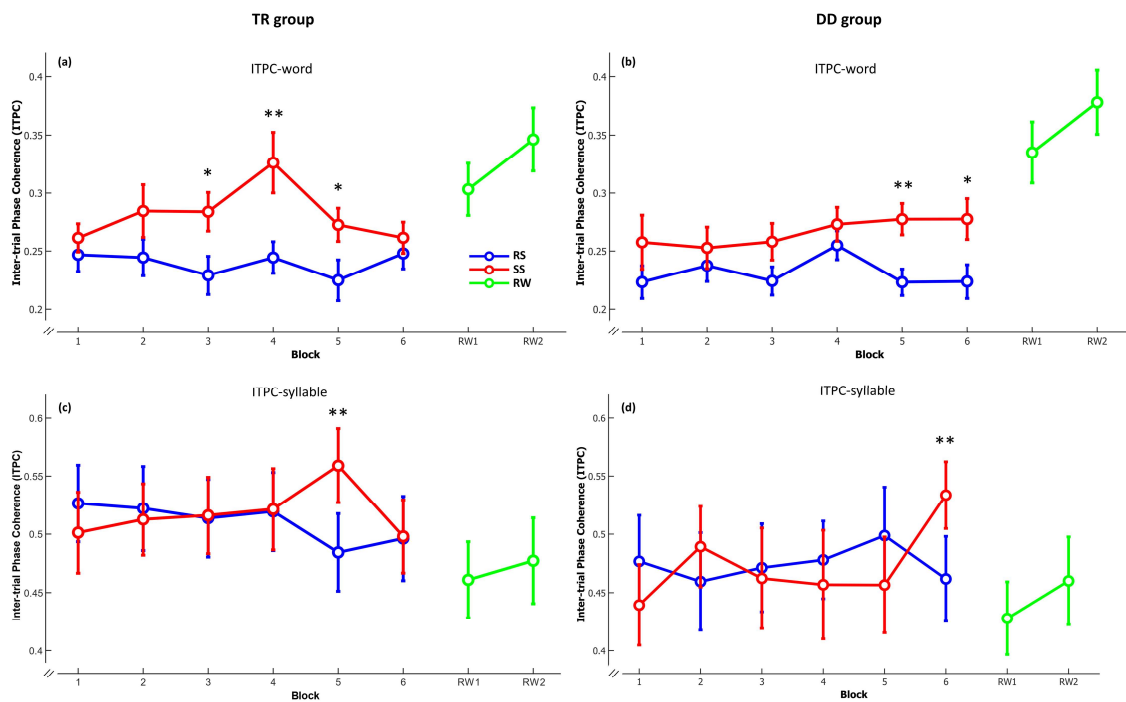


**Figure 3**. The time course of average ITPC in typical readers (TR, left column) and individuals with dyslexia (DD, right column) across all electrodes in the different conditions at the two frequencies of interest: word (1.1 Hz, top row) and syllable (3.3 Hz, bottom row) rate. RS = random sequence; SS = structured stream; RW = real word stream. Error bars = standard error of mean. Asterisks represent the post-hoc comparison on the condition difference at each block, * $p < .05$, ** $p < .01$, one-sided.

Syllable-rate ITPC showed a different pattern of results, with comparable and stable syllable-level tracking across blocks in TR and DD participants in both RS and SS conditions (Figure 3c and 3d). Accordingly, repeated measures did not show significant main effects for either condition [TR: $F(1, 16) = .67$, $p = .425$, $\eta^2_p = .040$;

DD: $F(1, 17) = .012$, $p = .912$, $\eta^2_p = .001$] or block [TR: $F(3.01, 48.14)$ = .40, $p = .755$, $\eta^2_p = .024$, Greenhouse-Geisser correction applied due to violation of sphericity; DD: $F(5, 85) = .96$, $p = .450$, $\eta^2_p = .053$], nor their interaction [TR: $F(1, 16) = .29$, $p = .597$, $\eta^2_p = .018$; DD: $F(1, 17) = .78$, $p = .389$, $\eta^2_p = .044$].

## 3.4 Evaluation of the learning outcome

Regarding the neurophysiological learning outcome, the maximum word-rate ITPC in the RW condition (RWmax) was used as a benchmark, in which no significant difference was found between the two groups [TR: $M = .379 \pm .092$, DD: $M = .389 \pm .109$; $t(34) = -.303$, $p = .763$, Cohen's $d = -.099$]. This benchmark was compared to the individually determined maximum word-rate ITPC in the SS condition (SSmax) [TR: $M = .397 \pm .079$, DD: $M = .348 \pm .046$] using a repeated measures ANOVA with factors of condition (SSmax or RWmax) and group (TR or DD). No significant main effects or interaction were found [$ps > .147$, $\eta^2_p < .061$] (Figure 4), suggesting that the learning outcome relative to the RW condition was not reduced in either group, but only acquired at a slower pace in the DD group.
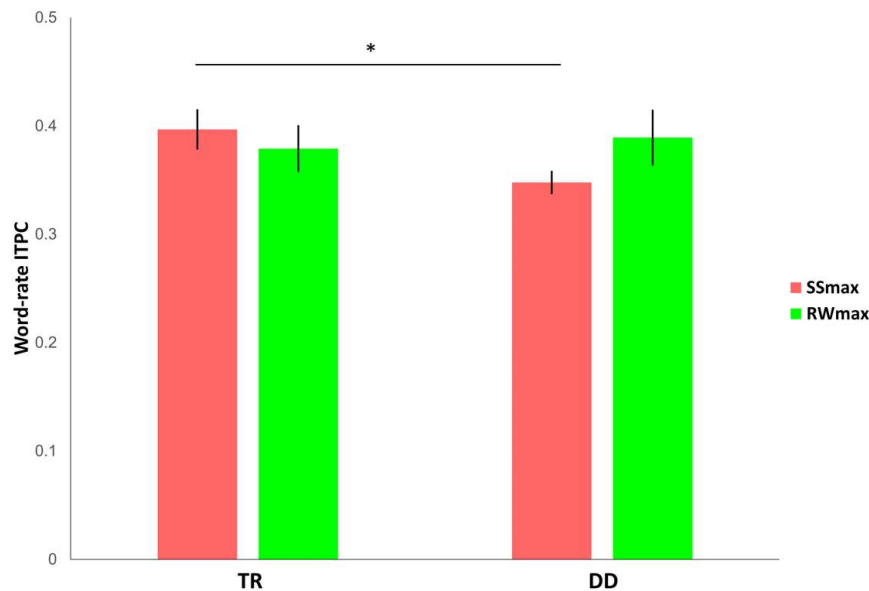


**Figure 4**. The maximum word-rate ITPC during the structured and real word conditions in typical readers (TR) and individuals with dyslexia (DD). The individually determined maximum word-rate ITPC in the structured condition (SSmax) and the real word condition (RWmax) are plotted in red and green, respectively. Error bars = standard error of mean. * $p < .05$.

The topographical distribution of word-rate ITPC in the RW condition (Figure 5, rightmost column) showed maximum word tracking over fronto-central regions in both groups, with a trend toward left-lateralization in the TR group, but not in the DD group. A repeated-measures ANOVA with left-right region (left, middle, and right channel groups) and anterior-posterior region (anterior, central, and posterior channel groups) as within-subjects factors, and group as a between-subjects factor, revealed a significant main effect of anterior-posterior region [$F$(1.30, 42.81) = 8.87, $p$ = .002, $\eta^2_p$ = .212, Greenhouse-Geisser correction applied due to violation of sphericity], with the posterior region [$M$ = .259 ± .092] showing significantly lower ITPC values than the anterior [$M$ = .314 ± .161, $t(34)$ = -2.29, $p$ = .028] and central [$M$ = .334 ± .154, $t(34)$ = -3.91, $p$ < .001] regions across groups. The main effect of left-right region was not significant [$F$(2, 66) = 1.02, $p$ = .366, $\eta^2_p$ = .030]. We did not find any significant group-related effects ($p$s > .170, $\eta^2_p$ < .047).

Comparison of the group-averaged scalp maps of each SS block to their RW reference revealed that the Euclidean Distance from the RW reference map reduced from SS1 (.61) to SS4 (.24) in the TR group, whereas it persisted at a relatively high level (>.67) over blocks in the DD group.

## 3.5 Brain-behavior correlation

To explore potential links between brain and behavior, we investigated the pairwise correlation between the maximum word-rate tracking in the RW and SS conditions and reading/phonological skills, as well as the post-exposure recognition RT of pseudowords (Table 2). Across all participants who took the behavioral assessment ($n$ = 33), a significantly positive correlation was observed between the maximum word-rate ITPC in the SS condition (SSmax) and the phonological awareness ($r$ = .401, $p_{FDR}$ = .050; Figure 6a), a composite measure of the performances in Spoonerisms and Reversals tests. This suggests that individuals who showed a stronger pseudoword tracking during the learning process tended to have better phonological skills. Additionally, there was a significantly positive correlation between the maximum word-rate ITPC in the RW condition (RWmax) and the symbolic RAN (i.e., digit and letter naming)

performance ($r$ = .401, $p_{FDR}$ = .050; Figure 6b). This associates a stronger neural tracking of real words with a less fluent visual-verbal conversion of symbols.

**Table 2**. Correlation matrix between the neurobehavioral indicators of (pseudo)word tracking and four reading/phonological measures

|  |  | EMT[a] | Non-symbolic RAN[b] | Symbolic RAN[c] | PA[d] | Recog. RT[e] |
|---|---|---|---|---|---|---|
| Word-rate | SSmax | .305 | .042 | -.117 | .401* | .028 |
| ITPC | RWmax | -.215 | .303 | .401* | -.005 | .295 |

Note: [a] Een-Minuut-Test; [b] the average accuracy-corrected naming time of color and object; [c] the average accuracy-corrected naming time of letter and digit; [d] Phonological awareness, the total score of Spoonerisms and Reversals; [e] Recognition reaction time; * FDR-corrected $p$ < .05.

## 4 Discussion

In the present EEG study, we investigated the neural dynamics underlying auditory statistical learning in typical and dyslexic readers. We measured frequency-tagged responses to speech syllables within structured streams of tri-syllabic (pseudo)words. In typical readers, learning was observed in the emergence of phase-locking to the pseudowords with increasing exposure (Batterink & Paller, 2019; Henin et al., 2019; Ordin et al., 2020) and these phase-locked responses gradually approximated those elicited by real words. Importantly, in the participants with dyslexia, this gradual build-up of pseudoword tracking occurred at a significantly slower pace and was characterized by more bilaterally distributed phase-locked responses in a fronto-central region. Pooled across groups, participants' maximum pseudoword tracking response was significantly related to their phonological awareness skills. Furthermore, participants' maximum neural tracking of familiar words was positively correlated with their symbolic RAN scores. These results suggest more efficient neurophysiological tracking of word(-like) structures in adults with better phonological awareness and symbolic visual-verbal conversion skills.
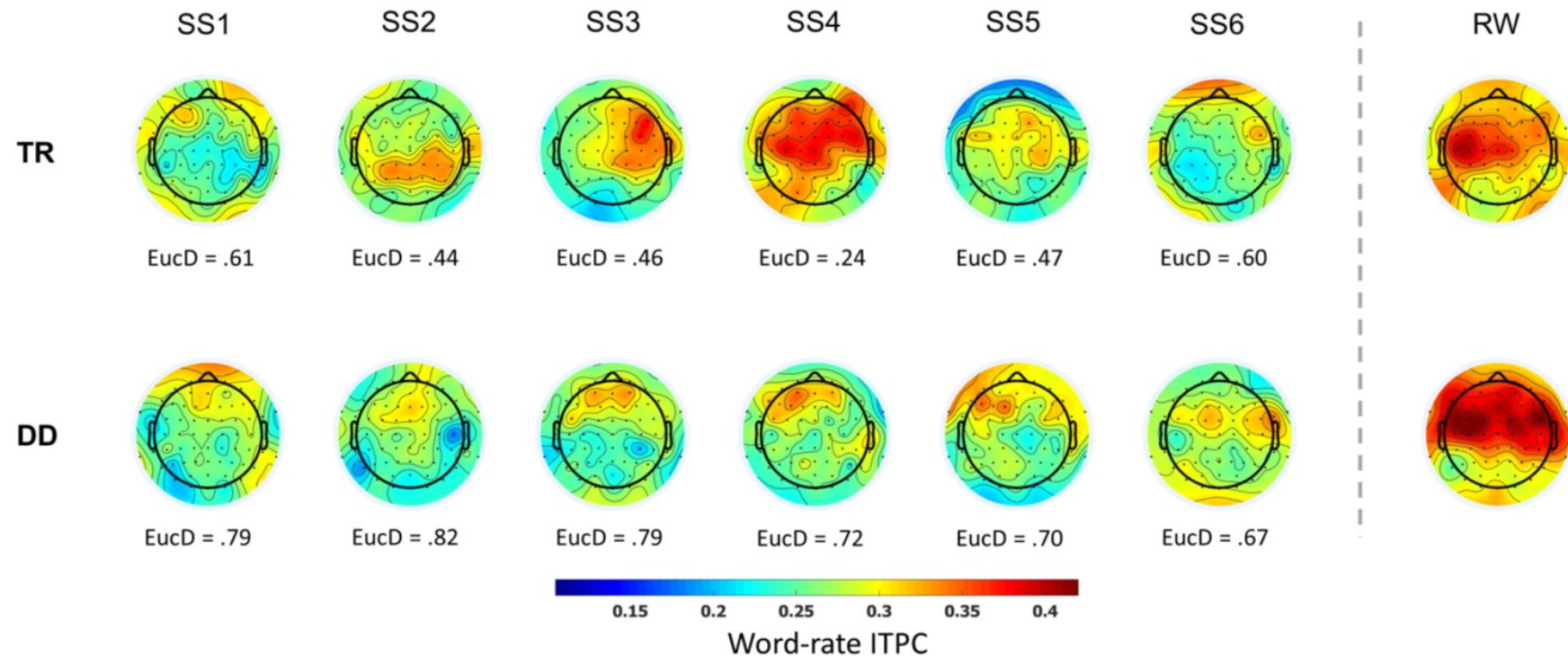
**Figure 5**. Topographic plots showing the spatial distribution of word-rate ITPC across structured stream (SS) blocks (column 1-6). The average of the two real word (RW) blocks is plotted in the rightmost column as a reference. The first row represents the TR group, and the second row represents the DD group. The Euclidean Distance (EucD) value under each subplot indicates the topographical dissimilarity between the group-averaged topography of SS block and the RW reference.
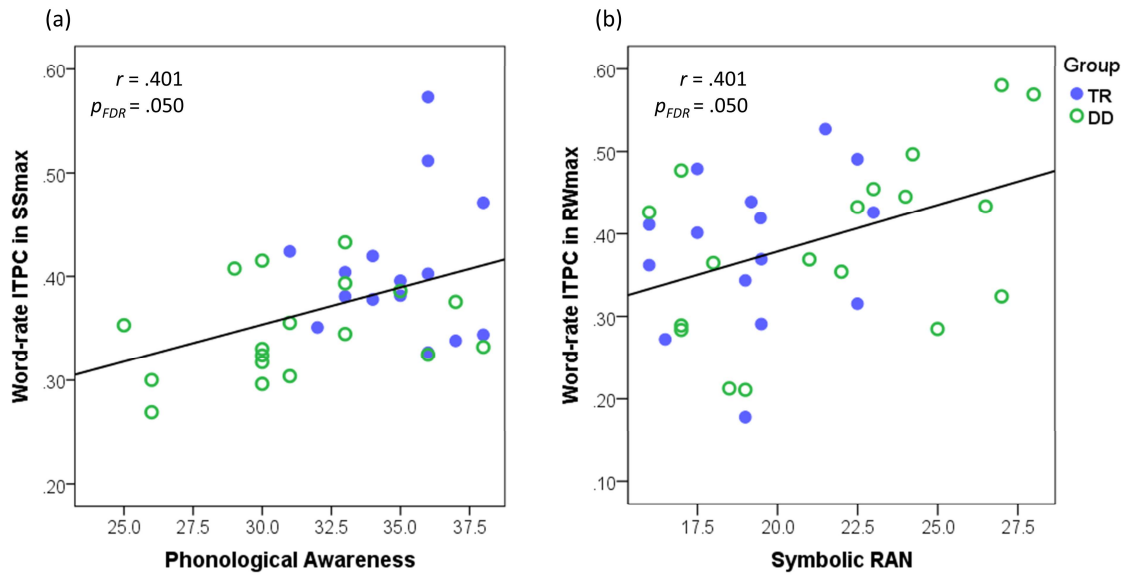
**Figure 6**. Scatterplots showing positive correlations between (a) the maximum word-rate ITPC in the structured condition (SSmax) and phonological awareness; (b) the average word-rate ITPC in the real word condition (RW) and symbolic rapid automatized naming (RAN) performance. Blue filled circles represent typical readers (TR), while green rings represent individuals with dyslexia (DD). The lines represent fitted simple linear regression models. A false discovery rate (FDR) correction was applied to *p* values for multiple comparison.

## 4.1 Neurophysiological mechanism underlying speech-structure tracking

In the typically reading adults, our results showed the expected stable neural tracking of syllables, next to an amplified brain synchronization to lower frequency information when neighboring syllables were integrated into words (Batterink & Paller, 2017; Henin et al., 2019; Ordin et al., 2020). Behavioral performance in a subsequent recognition task further confirmed a successful segmentation of pseudoword structures. Interestingly, synchronized neural responses to the newly learned pseudowords approximated those of familiar words. This was revealed by a gradual decrease in the difference between neural activity (i.e., the strength of word-rate phase locking and its fronto-central distribution) evoked in the SS and RW conditions. This effect may reflect the efficiency with which typically learning brains utilize existing speech recognition networks to incorporate new information. This interpretation is in line with previous results showing a similar fronto-central distribution of brain responses during knowledge-driven word decoding across languages (Ding et al., 2016; Sheng et al., 2018). Furthermore, it matches with the

results of a recent study that used electrocorticography (ECoG) to localize the enhanced pseudoword tracking as a result of statistical learning in inferior frontal gyrus, anterior temporal lobe and superior temporal gyrus (Henin et al., 2019).

It is noteworthy that at the group level, the pseudoword tracking of typical readers increased in the first 8.8 min of SS exposure (≈ 3.5 blocks), after which it started to decrease. While previous studies in typically reading participants have used exposure sessions of 10-12 min duration (Batterink & Paller, 2017; Henin et al., 2019), we decided for a prolonged exposure of 15 min (six blocks) in order to examine the learning course of dyslexic readers whom we expected to take longer time to attain a certain degree of improvement (Wang et al., 2014). In fact, our results indicate that the dyslexic readers reached their learning outcome on average 1.7 min later than the typical readers (4.17 blocks vs 3.5 blocks). The observed pattern of an initial increase in word-rate ITPC, followed by a subsequent decrease in the SS condition in both groups resembles the findings of two recent studies (Chen et al., 2020; Choi et al., 2020). Similar results were also reported by Abla, Katahira, and Okanoya (2009) and Cunillera et al. (2009), who used an event-related potential (ERP) component, the N400, to index statistical learning. These inverted U-shape curves may reflect two stages of learning: an initial phase involving adaptation or tuning to statistical information and a subsequent phase involving access to already-segmented, but not semantically intelligible pseudowords (Cunillera et al., 2009). It has been suggested that the brain responds more strongly if the representation of the target stimulus is yet to be built up, which then turns into a repetition suppression after a stable representation can be accessed (Nordt, Hoehl, & Weigelt, 2016). Otherwise stated, the late reduction in word-rate ITPC may indicate the emergence of neural adaptation to repetitive syllable input after the participants (both typical and dyslexic readers) reached a systematic phase-locked response to these repetitions. The decrease of neural responsiveness to repetitive sensory features has been associated with improvements in perception (Atiani, Elhilali, David, Fritz, & Shamma, 2009) and follows the same trajectory as behavioral habituation (Turk-Browne, Scholl, & Chun, 2008). The fact that the DD group did not show a clear sign to enter this suppression phase in the current study corroborates previous findings showing a sluggish neural adaptation in dyslexic readers across linguistic and non-linguistic stimuli, in both auditory and visual modalities (Perrachione et al., 2016; Peter et al., 2019).

## 4.2 Neural tracking during speech-structure learning in dyslexic readers

The participants with dyslexia failed to show above-chance recognition of the pseudowords after exposure. This may be due to a fast decay of implicit memory for pseudowords in dyslexic readers (Jaffe-Dax, Frenkel, & Ahissar, 2017; Lieder et al., 2019) or a reduced sensitivity of explicit recognition tasks for the detection of implicit learning effects (Batterink & Paller, 2017; Stanley, Mathews, Buss, & Kotler-Cope, 1989). In fact, next to developmental differences related to sensitive periods for language learning (Thiessen, Girard, & Erickson, 2016; Werker & Hensch, 2015), the use of implicit looking/listening time measures may also contribute to the strong pseudoword learning effects typically observed in infants using the same syllable/pseudoword tracking paradigm (e.g., Saffran, Aslin, et al., 1996).

The word-rate ITPC in the SS condition of the dyslexic readers did increase and approximated the neural tracking of real words, albeit at a significantly slower rate compared to the typical readers. Our observations may be explained by previous results showing less consistent neural responses to speech sounds in individuals with dyslexia compared with typical readers (Hornickel & Kraus, 2013) along with difficulties in forming perceptual anchors to stimulus statistics (Ahissar et al., 2006; Banai & Ahissar, 2010). Moreover, the brain-behavioral correlation analyses revealed that participants with stronger build-up of pseudoword tracking tended to be more proficient in phonological processing. Such finding may suggest a reduced capacity in dyslexic readers to dynamically fine-tune perception of auditory input and construct distinct phonemic categories (Vandermosten, Wouters, Ghesquière, & Golestani, 2019). One possible explanation is given by the so-called temporal sampling framework, which proposes that cortical oscillations in dyslexic individuals entrain inaccurately to slow-rate prosodic (delta band, 0.5-1 Hz) and syllabic (theta band, 4-8 Hz) information embedded in speech rhythm (Goswami, 2011; Goswami & Leong, 2013; Lallier, Molinaro, Lizarazu, Bourguignon, & Carreiras, 2017). Such deficits may impair the development of efficient phonological representations in infancy and may affect the audiovisual integration of letters and speech sounds when the child starts to learn to read (Goswami, 2011; Lallier et al., 2017). The observed reduced neural tracking of statistical information at the (pseudo)word level (1.1 Hz) suggests an inefficiency at a higher level beyond acoustic tracking of speech, and may relate to impaired phonological processing of speech at different levels of representation including individual syllables (Di

Liberto et al., 2018) and phoneme clusters (Bonte et al., 2007; Noordenbos et al., 2013).

Higher sensitivity to auditory word forms may help the formation of phonological representations. To learn phonological categories, phonotactic constraints and lexical-phonological knowledge, children need to extract discrete units, such as phonemes, syllables and words, from continuous speech. Thus, the sensitivity to sequential regularities and distributional patterns may be critical to the storage (and access) of phonological representations in the long-term memory (Bonte et al., 2005; Mainela-Arnold & Evans, 2014; Pavlidou & Bogaerts, 2019). In fact, auditory word segmentation based on statistical learning has been associated with phonological processing skills in typically developing children (Spencer, Kaschak, Jones, & Lonigan, 2015), while poor sensitivity to sound statistics may impair the acquisition of phonological representations in participants with dyslexia (Banai & Ahissar, 2018; Noordenbos et al., 2013; Vandermosten et al., 2019). Furthermore, the correlation between auditory word segmentation and nonword reading accuracy (as a measure of decoding ability; Qi, Araujo, Georgan, Gabrieli, & Arciuli, 2019) appears to be mediated by phonological abilities (Qi et al., 2019). These findings may thus indicate that efficient neural tracking of auditory word structures is important for the development of fine-grained phonological representations, which in turn could lead to better integration of letters and speech sounds during reading development (Gabay et al., 2015).

Participants with lower symbolic RAN scores showed a higher neural tracking response to real words. One possible explanation for this might be that participants with lower capacity for the visual-verbal conversion of symbols tend to rely more strongly on larger units in the phonological hierarchy, such as words, during speech processing. Such an effect might be interpreted as a compensatory mechanism (Hoeft et al., 2011; Peterson & Pennington, 2015; Shaywitz et al., 2002; Shaywitz & Shaywitz, 2005), as the observed positive correlation mainly resided in the dyslexic readers (DD: $r$ = .515, $p$ = .014; TR: $r$ = .289, $p$ = .148). This individual variability in real word tracking may also relate to a different balance between stimulus-driven (i.e., exogenous) versus knowledge-driven (i.e., endogenous) neural processing of speech signals. When learning to read, a bias toward knowledge-driven, e.g., word-level, processing may affect the perceptual tuning to the multisensory input, and the integration of letters and speech sounds (Hancock, Pugh, & Hoeft, 2017). Further (longitudinal) studies are thus required to

investigate the reciprocal relationship between hierarchical speech tracking and the acquisition and automatization of letter-speech sound mappings during reading development.

Although we obtained clear evidence for implicit pseudoword-structure learning in typical, but not dyslexic, readers, it should be noted that the condition × block × group interaction, as the most direct test of our hypothesis that pseudoword tracking establishes less efficiently in the DD group, did not reach significance ($p$ = .053). This may be due to a limited sample size in the current study. It has been suggested that the sample size required to detect a three-way interaction involving changes of measures over time is fourfold that required to detect the same effect size of a two-way interaction (Heo & Leon, 2010). Another possibility is that our participants with dyslexia (mostly university students) may have compensated, to a certain extent, for their less efficient statistical learning skills with other cognitive functions. For example, an implicit form of working memory may support the retention of statistical information, thereby enabling a better statistical learning performance as age increases (Arciuli & Simpson, 2012). In future studies, EEG research adopting a longitudinal approach and a larger sample size may investigate the neural tracking of speech structures by following the dynamic individual variability in various (non-)linguistic skills across different stages of reading development.


## 4.3 Conclusion

The present study shows a less efficient implicit learning of word-like structures in adults with dyslexia. In particular, dyslexic readers may take longer than typical readers to establish tracking of newly learned pseudowords. Moreover, the sensitivity of neural networks to realign the phase of their oscillatory activity to an (implicit) word rhythm was observed to correlate with individual variability in phonological awareness and symbolic visual-verbal conversion skills. The current findings suggest that inefficient low-frequency speech-brain synchronization may affect the extraction of hierarchical speech structures and hamper the development of phonological skills and, ultimately, reading fluency in individuals with dyslexia. Online neuroimaging techniques enable a sensitive and dynamic measure to zoom into the incremental learning gains that are otherwise difficult to

assess purely at the behavioral level, and thus help to reach a neuroscience-informed understanding of dyslexia as a learning disorder. Accordingly, further studies could use this methodology to trace the acquisition of auditory word forms and letter-speech sound associations in children, which may have profound implications for the development of early diagnosis tools and tailored intervention programs.

**Declaration of competing interest**:

The authors declare no competing interests.

**CRediT authorship contribution statement**

**Manli Zhang**: Conceptualization, Methodology, Software, Investigation, Formal analysis, Data Curation, Funding acquisition, Writing - Original Draft. **Lars Riecke**: Conceptualization, Methodology, Resources, Data Curation, Supervision, Writing - Original Draft, Writing - Review & Editing. **Milene Bonte**: Conceptualization, Methodology, Resources, Data Curation, Supervision, Funding acquisition, Project administration, Writing - Original Draft, Writing - Review & Editing.

# Chapter 4

# Altered brain network topology during speech tracking in developmental dyslexia

**Abstract**

Developmental dyslexia is often accompanied by altered phonological processing of speech. Underlying neural changes have typically been characterized in terms of stimulus- and/or task-related responses within individual brain regions or their functional connectivity. Less is known about potential changes in the more global functional organization of brain networks. Here we recorded electro-encephalography (EEG) in typical and dyslexic readers while they listened to (a) a random sequence of syllables and (b) a series of tri-syllabic real words. The network topology of the phase synchronization of evoked cortical oscillations was investigated in four frequency bands (delta, theta, alpha and beta) using minimum spanning tree graphs. We found that, compared to syllable tracking, word tracking triggered a shift toward a more integrated network topology in the theta band in both groups. Importantly, this change was significantly stronger in the dyslexic readers, who also showed increased reliance on a right frontal cluster of electrodes for word tracking. The current findings point towards an altered effect of word-level processing on the functional brain network organization that may be associated with less efficient phonological and reading skills in dyslexia.

**Keywords**

# 1 Introduction

Developmental dyslexia (DD) is a learning disorder with substantial and persistent reading and spelling difficulties despite adequate intellectual abilities and instruction, affecting approximately 5-17% of the population (Lyon, Shaywitz, & Shaywitz, 2003; Pennington & Peterson, 2015). It is neurobiological in nature (Ramus, 2004; Shaywitz & Shaywitz, 2005) and often associated with reduced brain activity in the left-hemispheric spoken (dorsal) and written (ventral) language networks (Richlan, 2012, 2020). DD is considered a multifaceted disorder manifested by various difficulties, such as a phonological deficit, e.g., poor phonemic/phonological awareness (Ramus, 2003; Snowling, 1980; Snowling & Stackhouse, 2013) and less efficient grapheme-to-phoneme conversion (Blomert, 2011).

Individuals with dyslexia may show a range of auditory- or speech-processing difficulties (Hämäläinen, Salminen, & Leppänen, 2013), including less accurate representations of speech units, e.g., phonemes (Goswami, Fosker, Huss, Mead, & Szucs, 2011), syllable stress (Leong, Hämäläinen, Soltesz, & Goswami, 2011), and reduced or slower build-up of sensitivity to phonological regularities in speech (Bonte, Poelmans, & Blomert, 2007; Noordenbos, Segers, Mitterer, Serniclaes, & Verhoeven, 2013; M. Zhang, Riecke, & Bonte, 2021). Underscoring the heterogeneity of dyslexia (Pennington, 2006; van Bergen, van der Leij, & de Jong, 2014), further associated deficits include a reduced sensitivity to low-spatial-frequency and high-temporal-frequency visual patterns (Livingstone, Rosen, Drislane, & Galaburda, 1991; Stein & Walsh, 1997), and a poor allocation of spatial attention (Vidyasagar & Pammer, 2010). Regardless of sensory modality, these difficulties have been linked to altered (spatio)temporal coding of sensory input via neural oscillations spanning multiple frequency bands (Goswami, 2011). According to the Temporal Sampling Framework of dyslexia for example, atypical temporal alignment of slow oscillatory activities (delta/theta) may hamper syllable parsing and eye saccades (Goswami, 2011; Lallier, Molinaro, Lizarazu, Bourguignon, & Carreiras, 2017). This in turn may affect the representation of phonemes and graphemes captured by fast oscillations (gamma) presumably via cross-frequency coupling (Archer, Pammer, & Vidyasagar, 2020; Lallier et al., 2017). Low-frequency oscillations that actively track the sequential structure of (supra)syllabic information (Doelling, Arnal, Ghitza, & Poeppel, 2014; Kosem et al., 2018) may

thus form a neural substrate for altered speech (and visuo-spatial) processing observed in dyslexia. At the same time, the exact oscillatory mechanisms involved may be shaped by the phonological and orthographic properties of a given language (Lallier et al., 2017).

Previous magnetoencephalography (MEG) and electroencephalography (EEG) work has examined the spontaneous oscillatory tracking of speech syllables and their higher-order chunks (e.g., words, phrases). It has shown that dyslexic readers may show an atypical right-hemisphere-dominant neural entrainment to slow-rate prosodic and syllabic amplitude modulations in speech (Goswami et al., 2011; Leong et al., 2011). Using a frequency tagging technique where cortical activity fluctuates at the same frequency as a periodic stimulus or perceived stimulus structure, recent studies found that the cortical tracking of higher-order speech structures is modulated by the listeners' word knowledge (Ding et al., 2017; Ding, Melloni, Zhang, Tian, & Poeppel, 2016) and gradually builds up with increasing exposure when learning pseudowords (Batterink & Paller, 2017; Buiatti, Pena, & Dehaene-Lambertz, 2009; Henin et al., 2021). Compared to typically reading controls, dyslexic readers have been found to show a slower buildup of word-rate tracking while learning pseudowords (M. Zhang et al., 2021). So far, this research has typically focused on stimulus- and/or task-related differences in oscillatory activity of individual cortical regions or their interactions. It remains unclear how large-scale inter-regional neural interactions are organized in the oscillatory brain responses during speech processing.

Inter-regional long-range oscillatory synchronization subserves the coordinated communication between anatomically distributed neuronal assemblies and gives rise to the emergence of complex cognitive functions (Fries, 2005; Schnitzler & Gross, 2005). Literacy acquisition not only relies on the specialization of existing brain circuits for speech and visual perception (Bonte, Correia, Keetels, Vroomen, & Formisano, 2017; Chyl et al., 2018; Cohen et al., 2002; Cone, Burman, Bitan, Bolger, & Booth, 2008; Dehaene, Cohen, Morais, & Kolinsky, 2015; van Atteveldt, Formisano, Goebel, & Blomert, 2004), but also involves communications among brain systems underpinning more general cognitive functions including attention, memory and executive control (Finn et al., 2014; Krishnamurthy et al., 2019). With time, these written and spoken language, and cognitive, functions interactively develop in a dynamic and inter-individually variable way, shaped by an individual's underlying strengths and weaknesses.

In the current study, we investigated whether this dynamic and multi-faceted development culminates into altered long-range oscillatory synchronization during speech processing in adults with dyslexia. To this end, we used a network approach that allows characterizing properties of a network (referred to here as 'graph') defined by a set of nodes (e.g., brain regions) and their connections (e.g., phase-based functional connectivity; defined here as weighted 'edges'). These properties are interpreted in terms of how efficiently information flows within the network; for example, whether there is more integration or intercommunication between the nodes or whether there are more segregated subnetworks (Bullmore & Sporns, 2009, 2012; Stam & van Straaten, 2012). It has been proposed that well-functioning brain network organization strives to balance between efficient information transmission and minimizing wiring costs by forming both densely, locally clustered connections, and longer-range connections that globally link these clustered nodes (Bullmore & Sporns, 2009, 2012; Sporns, 2011; Stam & van Straaten, 2012; van den Heuvel & Sporns, 2019).

Previous studies investigating large-scale network topologies in dyslexic readers have suggested alterations in the interplay within and between brain networks during resting state (Bailey, Aboud, Nguyen, & Cutting, 2018; Finn et al., 2014; Fraga-González et al., 2018; Fraga-González et al., 2016; Kershner, 2016; Schurz et al., 2015). In both structural (Qi et al., 2016) and functional networks at rest (Finn et al., 2014), children with dyslexia show lower local clustering of connections in the left hemisphere than typical readers. Moreover, the location of hubs, i.e., nodes that are centrally positioned and contribute strongly to global network function (van den Heuvel & Sporns, 2013), are distributed more bilaterally in dyslexic readers (Cao, Huang, Peng, Dong, & He, 2016; Finn et al., 2014; Qi et al., 2016). The organization of functional networks is not stationary over time and may be modulated by stimuli and/or task context (Bullmore & Sporns, 2012; Hutchison et al., 2013; van den Heuvel & Sporns, 2013). For instance, when performing orthographic judgments on Chinese characters (i.e., a logographic script), children with reading difficulties were found to display reduced global connections along with increased local clustering in the bilateral visual cortices, compared to the typical readers. In contrast, no group differences in network topology were found for a homophone judgment task, suggesting a relatively intact functional organization for phonological processing in Chinese poor readers (Yang & Tan, 2020).

An interpretational problem may arise when comparing networks across groups and/or experimental conditions involving an overall difference in the strength of connectivity, as this can result in comparison between networks of a different number of nodes or edges. As a solution for this, some studies have used a minimum spanning tree (MST), which is a loop-less graph containing the highest weights derived from the connectivity matrix between each pair of nodes (Stam, 2014; Tewarie, van Dellen, Hillebrand, & Stam, 2015). Assuming all connectivity weights are unique, this leads to a fixed number of nodes and edges in the resulting MST graphs. A large-sample ($n$ = 1675) study applying this approach to resting-state EEG data found that MST metrics characterizing the network integration gradually increase as the brain matures through middle adulthood (Smit, de Geus, Boersma, Boomsma, & Stam, 2016). Prior research on resting state also reported a close correlation between abnormalities in MST-based network topology and reading difficulties. Fraga-González et al., (2016, 2018) found a significantly less integrated topology in the theta-band (4-8 Hz) network in Dutch children with dyslexia. Moreover, a reduced network integration was also observed in the theta- and beta-band (13-30 Hz) networks in dyslexic children speaking Chinese (Xue et al., 2020). In contrast, significant group differences were reported in the alpha band (8-13 Hz) for adults, with dyslexic readers showing a more interconnected topology, which in turn may indicate a reduction in specialized sub-networks (Fraga-González et al., 2018). To date, however, there exist no clear findings on how these oscillatory network topologies may relate to specific reading/language processes and deficits in dyslexia.

Combining EEG measurements with graph-theoretic MST analyses, the current study aimed to examine the large-scale brain network topology for speech tracking in dyslexic and typically reading adults. We focused on network metrics during the neural tracking of spoken words and syllables to explore how functional brain network topology adapts to the processing of different speech structures. Participants were passively exposed to artificial speech streams composed of real trisyllabic words, as well as a control condition comprising random syllable sequences. MST graphs were constructed upon phase-based connectivity matrices in the delta, theta, alpha and beta frequency bands separately. The functional organization of such oscillatory networks was quantified in terms of connectivity strength, network topology and cost-efficiency trade-off. Node-level analysis was carried out to further identify EEG channels whose connectivity with other

channels was modulated by speech structures and differed between the two groups. Finally, we assessed whether word processing-triggered modulations in brain network topology are associated with individual differences in reading and phonological skills. Given the relatively small number of prior studies, with variable results, we did not formulate specific prior hypotheses about where (i.e., in which frequency band) we expected speech structure modulations or how these may differ between dyslexic and typical readers.

## 2 Methods

### 2.1 Participants

In total, 36 native Dutch speakers participated in the present study of whom 18 were diagnosed with developmental dyslexia ('DD', mean age ± SD = 23.9 ± 4.01 years; 12 females; 1 left-handed; age of dyslexia diagnosis ranged between 6 and 13 years old). The other 18 typically reading adults ('TR', mean age ± SD = 20.8 ± 2.26 years; 14 females; all right-handed) were allocated to a control group. While all participants were between 18-32 years old, on average the TR group was significantly younger than the DD group ($t_{34}$ = -2.91, $p$ = .007). All participants reported having a normal or corrected-to-normal vision, no hearing loss, and no history of diagnosed neurological disorders. This study was approved by the ethics committee of the Faculty of Psychology and Neuroscience, Maastricht University. Written informed consent was obtained from each participant before the experiment. Most participants were university students and received either course credits or gift vouchers as compensation for their participation.

### 2.2 Behavioral measures

Participants performed standardized Dutch tests of word reading and phonological skills (15 TRs and 18 DDs; 3 TRs who were our first three participants, did not complete these tests). First, word reading fluency was calculated based on the number of correctly read Dutch words within one minute (i.e., the "Een-Minuut-Test", or EMT) (Brus & Voeten, 1973). The test consists of 116 unrelated words, listed in order of ascending difficulty. Next, we administered a Rapid Automatized Naming (RAN) test (involving four subtests: colors, digits, objects, and letters, each

contains 50 items) (van den Bos & Lutje Spelberg, 2007), in which, participants are required to name the items as accurately and quickly as possible. In each subtest, the accuracy-corrected naming speed was computed as the ratio between the time taken to name the 50 items and the associated accuracy. Principal component analysis with varimax rotation was used to compute a composite RAN score for our correlational analysis. This score was calculated by multiplying the resulting coefficient matrix with the original variables after standardizing (using the *z*-transformation) the latter across participants. As such, the accuracy-corrected color (with a factor loading of 0.54), digit (0.54), object (0.64) and letter (0.73) naming times were combined into a RAN score, with an eigenvalue of 2.46, explaining 61.40% of the variance. Third, *Spoonerisms* and *Reversals* from the GL&SCHR test (Depessemier & Andries, 2009) were selected to assess phonological skills. In the *Spoonerisms* test, participants need to switch the first phonemes of two spoken words (e.g., "Harry Potter" becomes "Parry Hotter"). In the *Reversals* test, participants need to judge whether the spelling of the second word in a pair of orally presented nonsense words is the reverse of the first word (e.g., gak - kag). Accuracy and speed (in seconds) were measured for answering 20 items in each subtest after a brief practice of six examples with feedback. Following the same procedure as for RAN, the accuracies of the two phonological tests (with a factor loading of 0.69) were combined into a standardized factor score of "Phonological Awareness", with an eigenvalue of 1.37, explaining 68.59% of the variance.

## 2.3 Stimuli

Twenty-three Dutch syllables were selected to generate two types of speech streams. Twelve of these syllable were consonant-vowel (CV) syllables and used to construct a random sequence (hereafter RS). The other 11 syllables were used to construct four tri-syllabic real words (hereafter RW; mostly CV syllables, one syllable appeared twice in two different words). EEG data of both types of speech streams were obtained in a previous investigation of speech structure learning (M. Zhang et al., 2021). This previous study additionally included a learning condition involving the presentation of fixed combinations of tri-syllabic pseudowords (structured syllable stream (SS)) that was not analyzed in the present study. An artificial speech synthesizer (Google TTS, female voice) was used to generate the syllables with a sampling rate of 44100 Hz. The sound files were equalized in

length (i.e., 300 msec) and matched for prosody (i.e., with equalized pitch contour, thereby carrying no explicit prosodic information about the word boundaries) using *Praat* software (Boersma & Weenink, 2018). Individual syllable sounds were concatenated in a predefined order in *Matlab* (*MathWorks, Inc.,* Natick, MA), containing no pauses in between. The RS was constructed by a pseudorandom concatenation of 12 syllables ("go", "la", "bu", "bi", "da", "ku", "pa", "do", "ti", "tu", "pi", "ro") without any higher-order structure. Since an immediate repetition of the same syllable was avoided, the resulting transitional probability (TP) between neighboring syllables was 1/11. Similarly, the RW stream was created based on a pseudorandom repetition of four real Dutch words: "radio", "camera", "lucifer" (i.e., the noun "match" in English), and "domino". These words were selected from the book "Streeflijst Woordenschat Voor Zesjarigen" (Target Vocabulary List for Six-year-olds) (Schaerlaekens, Kohnstamm, & Lejaegere, 1999), with medium to high word frequencies in the SUBTLEX-NL database (Keuleers, Brysbaert, & New, 2010). Immediate repetitions were avoided during concatenation (Figure 1), and thus resulted in a TP of 1 within each word, and a TP of 1/3 across word boundaries.

In the original study, we presented six RS blocks and two RW blocks (M. Zhang et al., 2021). Here we focused the analysis on the first two blocks of the RS condition (RS1 and RS2) and the two blocks of the RW condition (RW1 and RW2). Note that RS2 and RS3 were used for one TR participant whose RS1 was not recorded, while RS5 and RS6 were used for one DD participant who showed low concentration (i.e., apparent from eye and body movements) during the first RS blocks. Each block lasted approximately 2.5 min and contained 480 syllables (corresponding to 160 real words in the RW condition), presented at a rate of 3.3 Hz. In order to prevent the potential cueing of triplet structures, a total of three to five random syllables were added to the start and end of each block. Moreover, the volume of the speech stream was ramped on and off, over the first and last 1500 ms, respectively.

## 2.4 Task

Participants were seated in a sound-proofed booth with the auditory stimuli presented at a comfortable listening level (approximately 70 dB SPL) from two speakers placed approximately 120 cm in front of the participant. During the

experiment, participants were exposed to each type of speech stream without being instructed to give any explicit responses. Instead, they were asked to relax and listen attentively to an alien language. The order of RS and SS conditions was counterbalanced across participants, while the RW condition with its most apparent word structure was always presented at the end of the experiment. The stimulus delivery was controlled by *Presentation* software (*Neurobehavioral Systems,* Inc., Berkeley, CA).
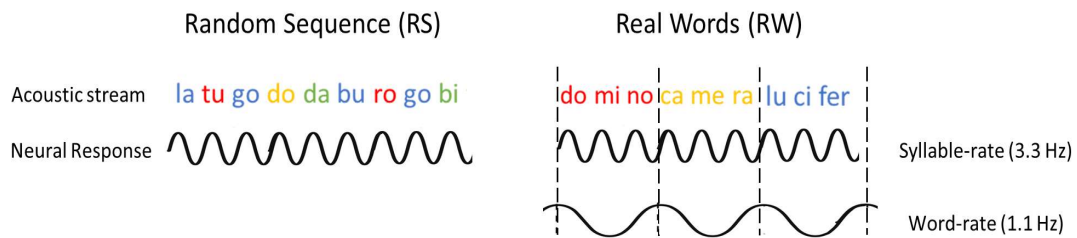


**Figure 1**. Schematic depiction of the stimuli and experimental design. The predicted neural response is shown below the sample sequence of stimuli (acoustic stream) in each condition: neural tracking at the syllable rate (3.3 Hz) was expected in both the random sequence and real word conditions, whereas the word-rate tracking (1.1 Hz) was expected only in the real word condition.


## 2.5 Data acquisition and analysis

### 2.5.1 EEG recording and preprocessing

EEG was recorded with 64 Ag/AgCl active electrodes, using the actiCAP according to the 10/20 system, and a 24-bit battery-supplied Brainvision actiCHamp amplifier (Brain Products GmbH, Germany). The sampling rate was 2500 Hz. A ground electrode was located on the forehead, and the reference electrode was FCz. Electrode impedances were kept below 10 kΩ throughout the experiment.

Using EEGLAB (Delorme & Makeig, 2004), the electrophysiological signals were subsequently down-sampled to 500 Hz, and re-referenced off-line to the arithmetic mean of all channels. A zero-phase Hamming-windowed sinc finite impulse response (FIR) bandpass filter of 0.1-30 Hz was applied. This was implemented in EEGLAB using the function *pop_eegfiltnew*, which automatically chooses the optimal filter order and transition bandwith, and corrects for phase

distortion by passing the signal forward and backward through the filter, achieving zero-lag phase in the overall process (Hulsemann, Naumann, & Rasch, 2019; Widmann, Schröger, & Maess, 2015). Due to low test-retest reliability of graph metrics in the gamma band (> 30 Hz) reported in previous studies (Kuntzelman & Miskovic, 2017; Velde, Haartsen, & Kemner, 2019), the gamma band was excluded from the current analysis. Channels with excessive artifacts were removed and reconstructed from the nearby channels using spline interpolation in 5 TR participants (a maximum of 2 electrodes) and 3 DD participants (a maximum of 3 electrodes). After removing the non-experimental time periods (e.g., the breaks between blocks), Independent Component Analysis was performed (on all channels, resulting in 64 estimated components per participant) on the remaining continuous dataset to categorize brain activity versus stereotypical artifacts (including eye blinks and movements, heartbeats, muscle activity, and channel noise) by visual inspection of the scalp topographies, time courses, and activity power spectra of the independent components. After removing components representing artifacts, EEG data were reconstructed based on the remaining components (on average of 48.5 ± 4.19 components in the TR group and 47.3 ± 4.00 in the DD group; $t_{34}$ = .85, $p$ = .399, no group difference). The data were then baseline corrected for each block with a pre-stimulus interval of 5 sec. For each block, the first and last 3 sec (with sound-level ramps) were not included in the analysis. Moreover, noisy time intervals containing irregular artifacts that the removed ICs did not capture (< 2% of the entire dataset) were rejected by visual inspection before extracting epochs. On average, in the TR group, there were 140.1 ± 0.62 sec remaining in each RS block and 140.5 ± 0.83 sec remaining in each RW block. In the DD group, there were 140.8 ± 0.48 sec remaining in each RS block and 140.5 ± 1.04 sec remaining in each RW block. No statistical condition ($F_{1,34}$ = .08, $p$ = .773, $\eta^2_p$ = .002) or group ($F_{1,34}$ = 2.07, $p$ = .160, $\eta^2_p$ = .057) difference was observed in the amount of time remaining in each block. Data were then segmented into non-overlapping epochs of 4 sec.

### 2.5.2 Spectral power

To examine potential group differences in the participants' attentional states during the tasks, we first calculated the power spectrum for each channel in the RS and RW conditions, using Fast Fourier Transformation with a frequency resolution

of 0.25 Hz. Then the power spectra were averaged across all channels and epochs. We computed the relative power as the ratio of power values at each frequency bin and the total power (Figure 2), and extracted the relative power values at four frequency bands: delta (0.5-4 Hz), theta (4-8 Hz), alpha (8-13 Hz) and beta (13-30 Hz).

### 2.5.3 Functional connectivity

As a first step towards quantifying brain network topology for speech tracking, we calculated functional connectivity measures in the RS and RW conditions. We adopted the Phase Lag Index (PLI) to quantify the functional connectivity between all pairs of 64 channels in each epoch and for each frequency band, separately. PLI is a measure of phase synchronization exploiting the asymmetry of the distribution of instantaneous phase differences between two time series (Stam, Nolte, & Daffertshofer, 2007). This distribution is expected to be symmetric if no phase synchronization exists between two signals, while any deviation from a symmetric distribution indicates interdependency between sources (Stam, Nolte, & Daffertshofer, 2007). Moreover, by discarding phase differences that center around 0 (mod $\pi$), it is less sensitive to the influence of volume conduction and electrode montage (Stam et al., 2007).

To obtain PLI values, we first determined the instantaneous phase differences $\Delta\varphi(t_k)$, $k = 1 \dots N$, between the EEG signal at two channels using the Hilbert transformation (Stam et al., 2007). PLI was quantified using the following formula:

$$PLI = |\langle sign[\,\Delta\varphi(t_k)\,]\rangle|$$

Here, *sign* is the signum function. The PLI ranges between 0 and 1. A value of 0 indicates either no coupling or coupling with a phase difference centered around 0 (mod $\pi$). A value of 1 indicates a perfect phase locking at a value $\Delta\varphi$ different from 0 (mod $\pi$). Thus, a larger PLI suggests stronger nonzero phase locking (Stam et al., 2007). The resulting 63 × 63 weighted connectivity matrices were used in the later analysis to construct graphs in each frequency band for both RS and RW conditions. Moreover, we calculated the overall connectivity strength as the average PLI across all channel-pairs.

## 2.5.4 Network topology

To quantify brain network topology, we constructed a minimum spanning tree (MST) for each PLI matrix derived per epoch. MST is an undirected graph derived from a weighted connectivity matrix that connects all nodes of the network by selecting only the smallest edge weights (i.e., the strongest connections) while avoiding loops (Smit et al., 2016; Stam et al., 2014). Hence, MST may be regarded as a "backbone" structure that captures the fundamental attributes of a complex network (Stam et al., 2014; Van Mieghem & Magdalena, 2005). In principle, brain networks are expected to display an intermediate topology between two extreme cases (see Figure 2): (1) a path-like topology (corresponding to maximal segregation) consists of a series of successively connected nodes, and (2) a star-like topology (corresponding to maximal integration) characterized by one central node to which all other nodes are connected with only one edge (Stam et al., 2014; Stam & van Straaten, 2012). An MST contains $m = N - 1$ edges, where $N$ is the number of nodes in the network. The weights of all possible connections were defined as $1 - PLI$, and sorted in ascending order (Fraga-González et al., 2016). Kruskal's algorithm (Kruskal, 1956) was used to iteratively add the edge with the lowest weight to the tree (or skip it, if adding this link resulted in the formation of a loop), until all nodes were connected in a loop-less network (Stam et al., 2014). The root node, i.e., the first node entering MST, was set to FP1.
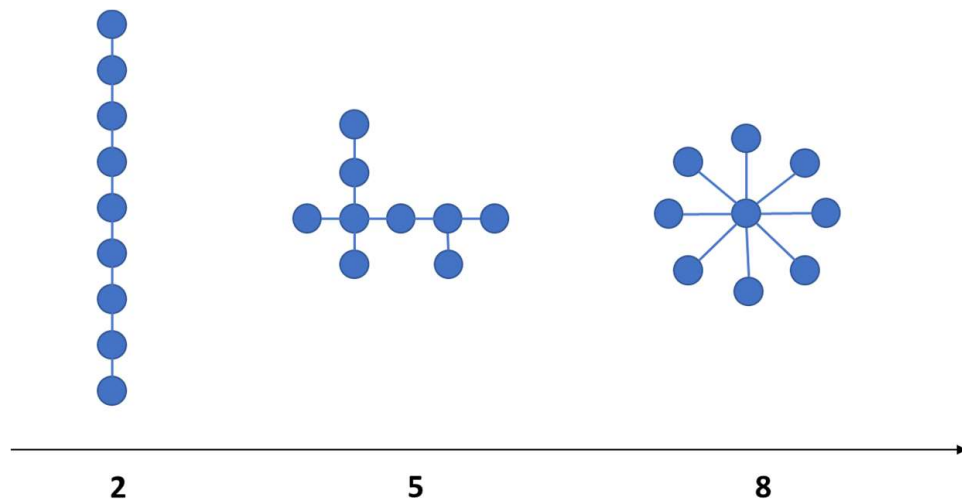


**Figure 2**. Examples of tree structures with increasing number of leaf nodes from a path-like tree (left) to a star-like tree (right). All three examples include 9 nodes (circles) and 8 edges (lines). Adapted from Fraga-González et al. (2016).

The following measures were computed for each epoch to characterize the topological properties of the MST network: degree, leaf fraction (*LF*), diameter, eccentricity (*Ecc*), betweenness centrality (*BC*), tree hierarchy ($T_h$), Kappa, and mean connectivity (*MC*) (Table 1; see Stam et al., 2014 for a detailed description). The *degree* of a node is its number of connections with other nodes. The maximum degree of all constituent nodes was used to quantify the degree of the MST. The *LF* represents the fraction of leaf nodes (i.e., with *degree* = 1) in the MST, and hence characterizes the tree topology. In a graph, the distance between two nodes is the sum of the weights of edges in the shortest path connecting them. The *diameter* of a graph is thus the maximum distance between any two nodes, and its upper limit ($D_{max}$) is determined by the number of leaf nodes (*L*) as $D_{max} = m - L + 2$. The *Ecc* of a node is the longest distance between it and any other nodes, and is low if this node is central in the tree. The *BC* (betweenness centrality) of a node *u* is the number of shortest paths between any pair of nodes *i* and *j* that pass through *u*, divided by the total number of shortest paths between *i* and *j*. This calculation can be rescaled by dividing by the number of node pairs that do not contain *u*, which is (*N* - 1)(*N* - 2)/2 for undirected graphs. The resulting *BC* ranges between 0 and 1, with higher values suggesting a relatively more central role in the network. In short, *degree*, *Ecc,* and *BC* are different measures characterizing the importance of a given node in an MST (Stam et al., 2014). The $T_h$ is defined as $L / 2mBC_{max}$, where $BC_{max}$ is the maximal *BC* for any tree node. It quantifies the balance between efficient communication and prevention of elevated wiring cost in a network (Boersma et al., 2013). Another metric, *Kappa*, is a measure of the broadness of the degree distribution (Stam & van Straaten, 2012). High *Kappa* indicates the presence of high-degree nodes and hence the more efficient spread of information across the tree. However, it also renders the network more vulnerable if those high-degree nodes are damaged (Otte et al., 2015). Finally, we computed the *MC*, i.e., the mean weight of all edges in the MST.

## 2.5.5 Statistical analysis

Group differences in reading and phonological skills were tested by comparing the behavioral performances on the EMT, RAN, Spoonerisms and Reversals tests between the TR and DD groups using independent sample *t*-tests. For the EEG data, to rule out potential bias on MST construction due to differences in the number of

epochs generated per individual (61 to 70 epochs per condition; no overall differences across groups/conditions), we randomly selected 60 epochs for each participant and condition. This procedure was repeated 1000 times, then repeated-measures ANOVAs were performed on the grand average of 1000 randomly selected sets of 60 epochs in each frequency band. These ANOVAs included a within-subjects factor *Condition* (two levels: RS and RW), and a between-subjects factor *Group* (two levels: TR and DD) to compare spectral power, connectivity measure PLI and eight MST metrics. Shapiro-Wilk tests revealed that most PLI and MST metrics were not normally distributed; thus, a natural log transformation was applied prior to the analysis to achieve normality as implemented in previous studies (Fraga-González et al., 2018; Fraga-González et al., 2016; Xue et al., 2020). The resulting *p*-values were corrected for multiple comparisons via false discovery rate (FDR) (Benjamini & Hochberg, 1995) at a moderate threshold of *q* < .10 (two-sided).

**Table 1.** MST measures summary

| | | |
|---|---|---|
| $N$ | Nodes | Number of nodes in the MST |
| $m$ | Edges | Number of edges in the MST |
| | Degree[a] | The number of neighbors for a given node |
| $LF$ | Leaf fraction | Fraction of nodes with degree = 1 |
| | Diameter | Largest distance between any two nodes |
| $Ecc$[b] | Eccentricity | Largest distance between a given node and any other nodes |
| $BC$[b] | Betweenness centrality | Fractions of all shortest paths that pass through a given node |
| $T_h$ | Tree hierarchy | A hierarchical metric that quantifies the trade-off between the large scale integration in the MST and the overload of central nodes |
| | Kappa | Measure of the broadness of the degree distribution |
| $MC$ | Mean connectivity | Mean weight of all edges included in the MST |

For an MST: [a] the *degree* is the maximum degree of its nodes. [b] the *Ecc* and *BC* are the average across all nodes.

As *Group*-related effects were found only in the theta band (see Results and Table S1), we focused the analysis on the theta-band network. Within the theta-band network, we investigated influences of individual nodes on information flow, and tested for group (DD vs. TR) and condition (RS vs. RW) differences. We performed permutation tests on the *Condition × Group* factorial model for the three local graph metrics that measure the importance of a given node in the network: nodal *degree*, *Ecc,* and *BC*. Since it is not possible to construct an exact permutation test for an interaction term using the *F*-statistic, we adopted an alternative approach to permute the residuals under a reduced model. It has been suggested that the residual-based approximate permutation comes closest to a conceptually exact test (Anderson & Robinson, 2001). At each node (i.e., EEG electrode), the observations were replaced by residual values to control for main effects when testing the interaction term. Residualized observations in the RS and RW conditions were randomly shuffled within each individual, then half of the participants were randomly assigned to the TR group, and the other half to the DD group. Subsequently, we calculated an *F*-value for the interaction term on the permuted data. This procedure was repeated 1000 times and pooled across all nodes to acquire a permutation distribution. We obtained the permutation *p*-value at each node by computing the proportion of *F*-values which were larger than that in the original residualized data. All nodes with permutation *p*-values lower than 0.01 were selected and clustered into connected sets based on their spatial adjacency. Then we calculated the cluster-level *F*-statistics (i.e., cluster weights) by taking the sum of the *F*-values within each cluster. The largest cluster weight for every randomization was selected to obtain a null distribution. The permutation *p*-value for each cluster was estimated as the proportion of elements in this null distribution exceeding the observed cluster-level *F*-statistic (Maris & Oostenveld, 2007; Suckling & Bullmore, 2004). FDR-correction was applied at $q < 0.05$.

To quantify the topological organization induced by the extraction of word versus random syllable structures in the speech signals, we calculated the difference value between the RW and RS conditions for each MST metric. Finally, we investigated the relation between MST metrics and participants' phonological and reading skills. To this end, we performed permutation-based correlation analyses (number of permutations = 10000) with the PERMUTOOLS toolbox in Matlab (https://github.com/mickcrosse/PERMUTOOLS) to explore the associations between the *Condition*-modulated theta-network measures (i.e., the difference

values between RW and RS) and participants' reading, RAN and phonological awareness skills. The resulting *p*-values were FDR-corrected for multiple comparisons at $q < .10$.

## 2.6 Data and code availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request. The data and code sharing adopted by the authors comply with the requirements of the Faculty of Psychology and Neuroscience, Maastricht University, and the funding bodies.

## 3 Results

### 3.1 Behavioral results

The results of the independent sample *t*-tests for EMT, RAN, and phonological skills are shown in Table 2. The participants with dyslexia (DD) performed significantly worse than the typical readers (TR) on word reading, RAN of letters, Spoonerism test (speed), and Reversals test (both accuracy and speed).

**Table 2.** Descriptive statistics and demographic information

| | TR | | DD | | Group differences | |
|---|---|---|---|---|---|---|
| | *M (SD)* | *Range* | *M (SD)* | *Range* | *t* | *p*-value |
| N (Female) | 18[f] (14) | | 18 (12) | | | |
| Age (years) | 20.78 (2.26) | 18.18 – 26.04 | 23.93 (4.01) | 18.92 – 32.10 | -2.91[**] | .007 |
| EMT[a] | 96.80 (10.87) | 78 – 115 | 77.67 (11.71) | 59 – 99 | 4.83[***] | <.001 |
| RAN[b] letter | 18.89 (2.81) | 15 – 25 | 21.75 (4.61) | 15 – 32 | -2.18[*] | .037[g] |
| RAN[b] number | 19.60 (2.50) | 17 – 24 | 21.89 (4.11) | 17 – 30 | -1.96 | .059[g] |
| RAN[b] object | 35.28 (5.04) | 29 – 45 | 36.06 (4.65) | 26 – 42 | -.46 | .648 |
| RAN[b] color | 29.05 (4.15) | 24 – 35 | 31.22 (4.91) | 23 – 42 | -1.38 | .177 |
| Spoonerisms score[c] | 17.53 (1.30) | 15 – 19 | 16.00 (2.85) | 9 – 20 | 2.04 | .052[g] |
| Spoonerisms RT[d] | 66.38 (15.63) | 45 – 107 | 117.30 (48.41) | 52 – 228 | -4.21[***] | <.001[g] |
| Reversals score[c] | 17.40 (1.45) | 15 – 18 | 15.28 (1.67) | 13 – 18 | 3.85[***] | <.001 |
| Reversals RT[d] | 50.83 (12.92) | 36 – 86 | 68.42 (13.61) | 53 – 101 | -3.78[***] | <.001 |

*Note.* [a] EMT = Een-Minuut-Test, number of correctly reading items; [b] RAN = Rapid Automatized Naming, accuracy-corrected response time (sec), i.e. reading time divided by accuracy; [c] number of correct responses; [d] accuracy-corrected reaction time = total response time/score×10, in sec; [e] Acc. = Accuracy, percentage; [f] three out of 18 TR participants did not take the reading/phonological assessment; [g] Equal variances not assumed. * *p* < .05, ** *p* < .01, *** *p* < .001.

## 3.2 Spectral power

As shown in Figure 3, the power spectra of EEG activity during the random sequence (RS) and the real word (RW) conditions did not indicate group differences in participants' overall attentional state or activity strength. Accordingly, a repeated-measures (RM) ANOVA showed no significant *Group* difference or *Group × Condition* interaction in any of the four frequency bands (*p*s > .089). A further RM ANOVA comparing the visually diverging maximum alpha peaks between the two groups, did not show a significant difference between the TR (RS: 9.90 ± 1.13 Hz, RW: 9.53 ± 1.09 Hz) and DD (RS: 10.19 ± 1.37 Hz, RW: 9.75 ± .96 Hz) groups ($F_{1,34}$ = .71, *p* = .405, $\eta^2_p$ = .021).
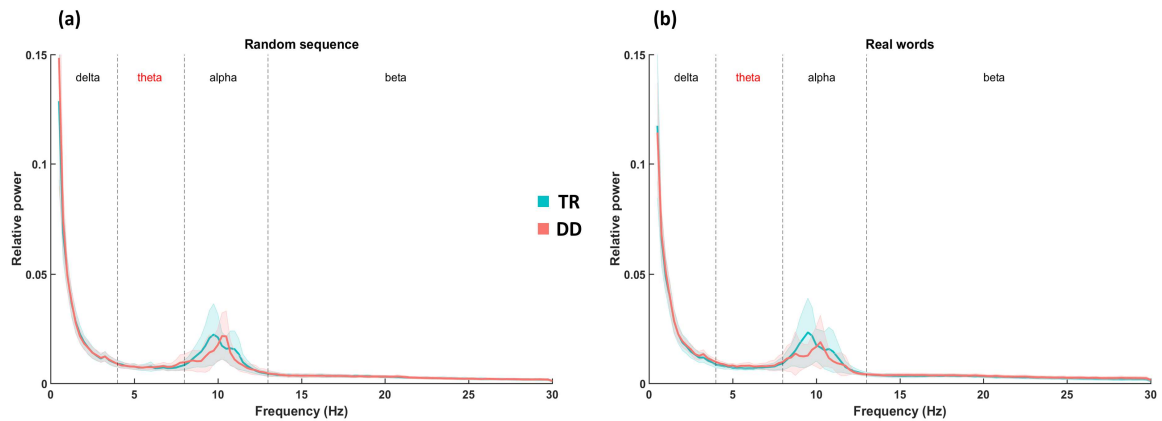


**Figure 3**. Power spectra averaged across all channels in (a) the random sequence (RS) condition and (b) the real word (RW) condition. TR = typical reader, DD = developmental dyslexia. Shaded error bars represent the 95% confidence interval.

## 3.3 Functional connectivity

An RM ANOVA of overall connectivity strength, i.e., the average Phase Lag Index (PLI), revealed no statistically significant *Condition* effect (*p*s > .058), *Group* difference (*p*s > .410), or interaction of these factors (*p*s > .261) in any of the four frequency bands (Table S1).

## 3.4 Network topology

Our analysis (RM ANOVAs) of network topology yielded significant *Condition* effects and *Group × Condition* interactions (after FDR correction at *q* < .10) only in the theta band (Table 3). First, results indicated a more integrated network topology when the speech stream contained real words. Thus, compared to the RS (syllable) condition, the brain network for RW (word) tracking showed higher *Degree* ($F_{1,34}$ = 8.05, FDR-corrected *p* = .072, $\eta^2_p$ = .191; Figure 4a) and *Kappa* ($F_{1,34}$ = 7.37, FDR-corrected *p* = .045, $\eta^2_p$ = .178; Figure 4b).

Interestingly, related MST measures indicated a larger shift towards a more integrated topology during word processing, relative to the perception of random syllables, in dyslexic readers than in typical readers. First, there was a significant *Group × Condition* interaction in leaf fraction (*LF*: $F_{1,34}$ = 9.56, FDR-corrected *p* = .036, $\eta^2_p$ = .220; Figure 4c). A simple main effect analysis for *Condition* revealed that for the TR group, *LF* was not significantly different between RS and RW tracking ($F_{1,17}$ = .21, *p* = .654, $\eta^2_p$ = .012). Conversely, for the DD group, *LF* was significantly increased during RW compared to RS tracking ($F_{1,17}$ = 21.24, *p* < .001, $\eta^2_p$ = .555). Second, there was a significant *Group × Condition* interaction in tree hierarchy ($T_h$: $F_{1,34}$ = 6.00, FDR-corrected *p* = .09., $\eta^2_p$ = .150; Figure 4d). A main effect analysis for *Condition* again found a higher $T_h$ in the RW compared to RS condition solely in the DD group (DD: $F_{1,17}$ = 5.34, *p* = .034, $\eta^2_p$ = .239; TR: $F_{1,17}$ = 1.34, *p* = .264, $\eta^2_p$ = .073). *Group* and *Condition* effects in all other measures (including the *mean connectivity*) and frequency bands were not statistically significant (FDR-corrected *p*s > .113; Table 3 and Table S1). For illustration purposes, the MST trees constructed from the group average PLI in the RS and RW conditions are presented in Figure 5. In the Supplementary information, we additionally provide the ANCOVA results on connectivity strength and network metrics with age as a covariate. The age-related effects were not significant (main effect of Age: *p*s > .164; Age × Condition: *p*s > .069; Table S2). Furthermore, most of the reported *Condition* effects and *Group × Condition* interactions in theta-band MST measures remained significant after controlling for age, although the *Group × Condition* interaction on theta *LF* and *Th* no longer survived FDR correction. Furthermore, the exclusion of one DD participant for whom the RS5 and RS6 were used did not impact on the conclusions that can be drawn from the results (Table S3).

**Table 3.** Group and condition comparisons of network metrics in the theta band

| | Condition | | | Group | | | Condition × Group | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F_{1, 34}$ | $p$ | $\eta_p^2$ | $F_{1, 34}$ | $p$ | $\eta_p^2$ | $F_{1, 34}$ | $p$ | $\eta_p^2$ |
| PLI | 3.21 | .082 | .086 | .01 | .922 | .000 | .50 | .485 | .014 |
| *Degree* | **8.05**[a] | **.008\*** | **.191** | .99 | .326 | .028 | .15 | .699 | .004 |
| *LF* | **5.56** | **.024** | **.140** | .51 | .479 | .015 | **9.56** | **.004\*** | **.220** |
| *Diameter* | 1.79 | .190 | .050 | .75 | .394 | .021 | 4.13 | .050 | .108 |
| *Ecc* | 2.13 | .154 | .059 | .68 | .416 | .020 | 4.20 | .048 | .110 |
| *BC* | 1.87 | .180 | .052 | 2.95 | .095 | .080 | 3.39 | .074 | .091 |
| $T_h$ | .66 | .423 | .019 | .25 | .621 | .007 | **6.00** | **.020** | **.150** |
| *Kappa* | **7.37**[a] | **.010\*** | **.178** | 1.06 | .309 | .039 | .49 | .488 | .014 |
| *MC* | 3.87 | .057 | .102 | .19 | .670 | .005 | .91 | .347 | .026 |

*Note.* PLI = Phase Lag Index; *Degree* = maximum nodal degree; *LF* = leaf fraction; *Ecc* = eccentricity; *BC* = betweenness centrality; $T_h$ = tree hierarchy; *MC* = mean connectivity in the MST. $p$ represents uncorrected $p$-values. Bold text represents significant effects after FDR correction at $q$ = 0.10; \* represents significant effects after FDR correction at $q$ = 0.05. [a] Random sequence (RS) < real words (RW). The statistical results for MST metrics in all frequency bands are summarized in Table S1.
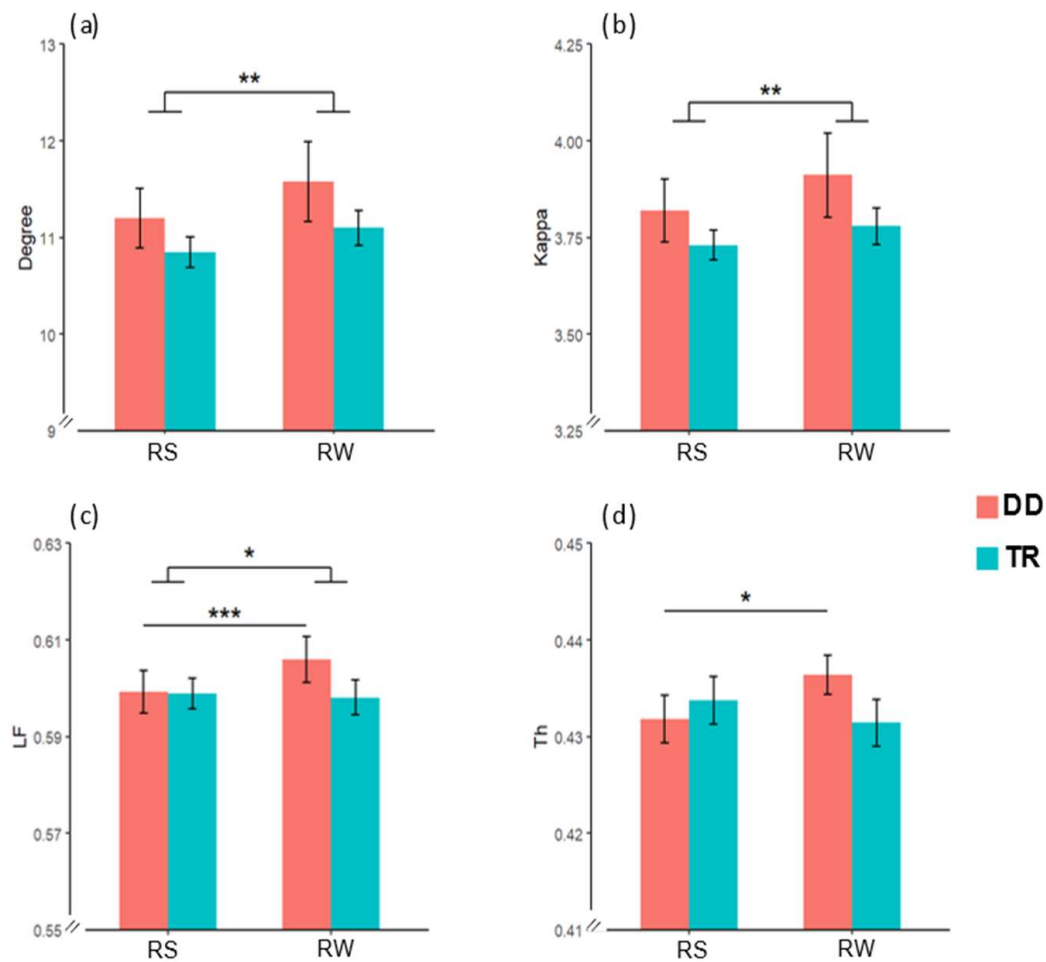
**Figure 4**. Group averages for the theta-band MST metrics (a) *Degree*, (b) *Kappa*, (c) leaf fraction (*LF*) and (d) tree hierarchy (*Th*) in the random sequence (RS) condition and the real word (RW) condition. TR = typical reader, DD = developmental dyslexia. Error bars represent the standard errors of mean. * $p < .05$, ** $p < .01$, *** $p < .001$, uncorrected.
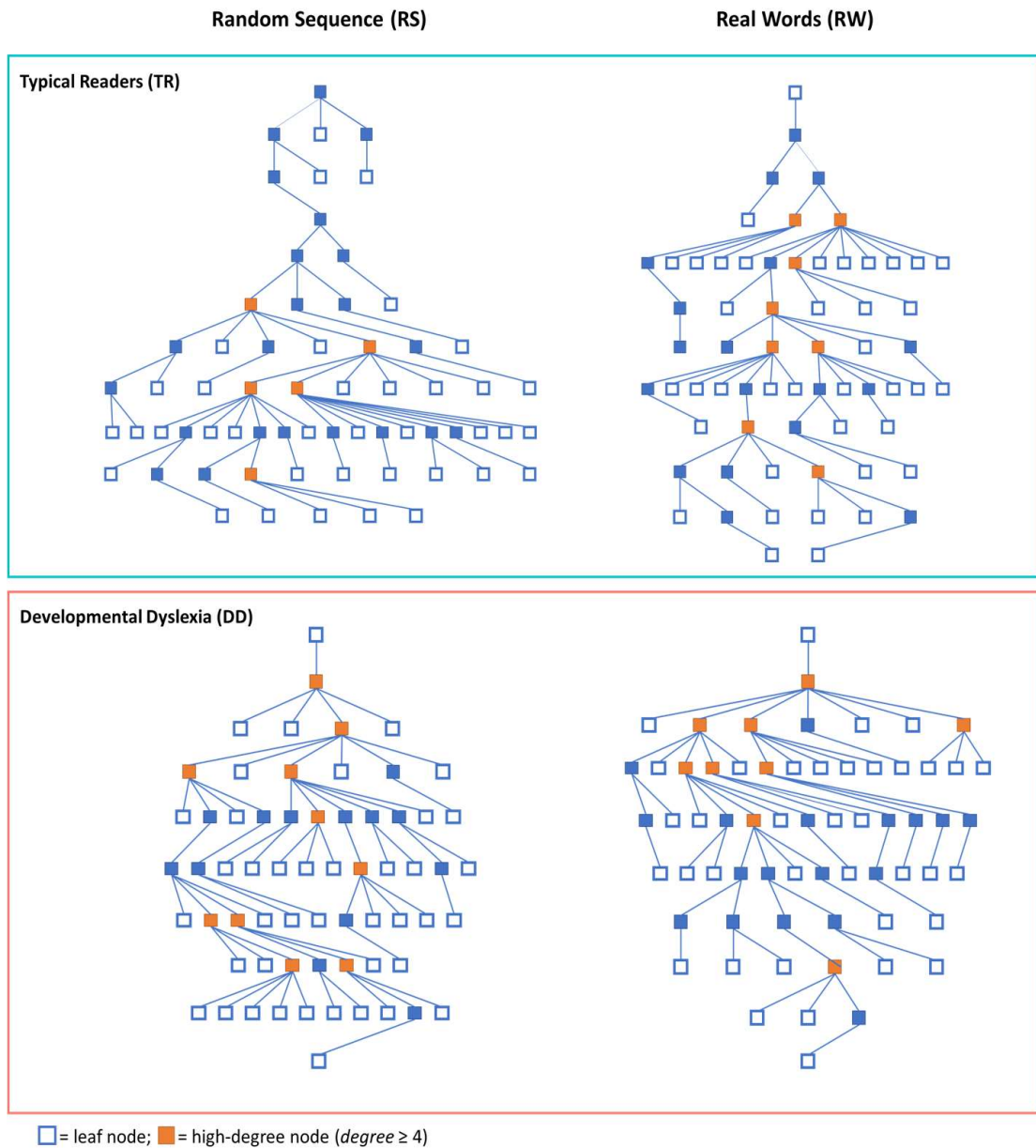
**Figure 5**. An illustration of theta-band MSTs (generated using the Matlab function *treeplot*) constructed from the group average PLI of the typical readers (above) and dyslexic readers (below) in the random sequence condition (left panels) and real word condition (right panels).

## 3.5 Nodal properties

Our analysis of local network measures indicated an increased reliance on a right frontal cluster of electrodes for word tracking in dyslexic as compared to typical

readers. In particular, the cluster-based permutation tests on the nodal metrics in the theta-band network revealed a significant *Group × Condition* interaction on eccentricity (*Ecc*) at right frontal electrode sites (i.e., AF8, F4, F6, and F8; $F_{cluster}$ = 39.33, $p_{perm}$ < .001; Figure 6). The theta-band *Ecc* at this region was significantly reduced during RW compared to RS tracking in the DD group ($F_{1,17}$ = 10.34, $p$ = .005, $\eta^2_p$ = .378), but there was no significant condition difference in the TR group ($F_{1,17}$ = 1.97, $p$ = .179, $\eta^2_p$ = .104). No *Group* or *Condition* effects were found for the other local measures, nodal *Degree* and betweenness centrality (*BC*).
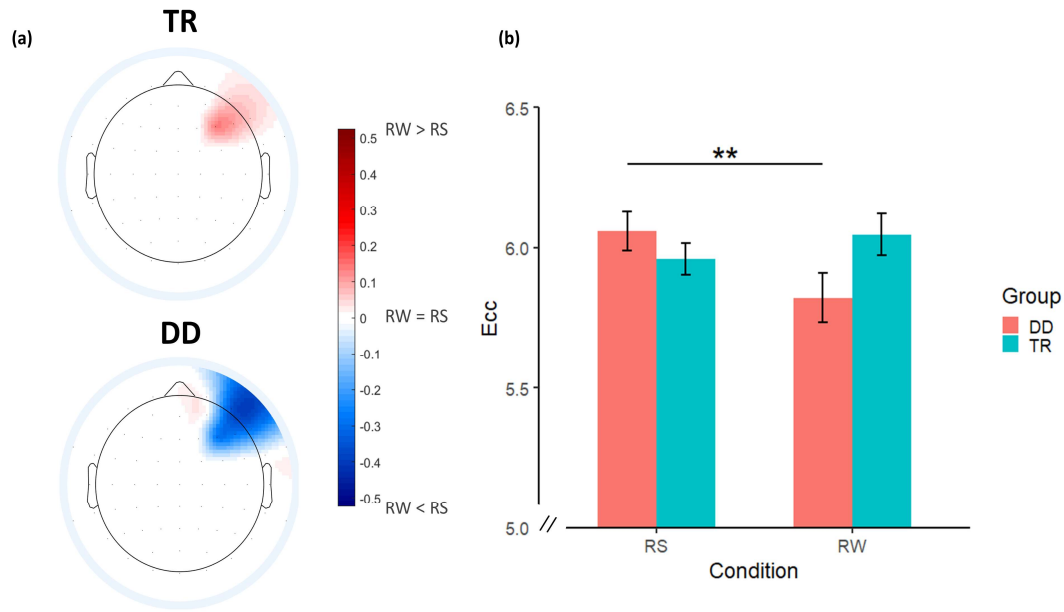


**Figure 6**. Right frontal electrodes (nodes) showing a *Group × Condition* interaction on nodal Eccentricity (*Ecc*) in the theta-band network. TR = typical reader, DD = developmental dyslexia. (a) Topographic maps of the difference in theta-band *Ecc* between the random sequence (RS) and real word (RW) conditions. (b) The theta-band *Ecc* averaged across four electrodes: AF8, F4, F6, and F8. Error bars represent the standard errors of the mean. ** $p$ < .01.

## 3.6 Brain-behavior correlation

We examined whether the reorganization of theta-band network topology induced by the extraction of word structure was associated with individual differences in reading and phonological skills. Results suggested a negative correlation between the difference value of tree hierarchy (*ΔTh*; RW versus RS) and the composite score of phonological awareness (i.e., the summary measure of

Spoonerisms and Reversals), $r$ = -.385, $p_{perm}$ = .025 (Figure 7), which was not significant when correcting for multiple comparisons. This trend suggests that individuals with poorer phonological awareness skills might show a larger shift toward a more integrated, star-like topology in the theta-band network during real word versus random syllable perception. An additional analysis using an independent-samples t-test confirmed a larger $\Delta Th$ (i.e., a greater shift toward a more integrated topology) in the DD (.005 ± .008) than the TR group (-.002 ± .009; $t_{34}$ = 2.42, one-sided $p$ = .011). None of the other correlations was statistically significant.
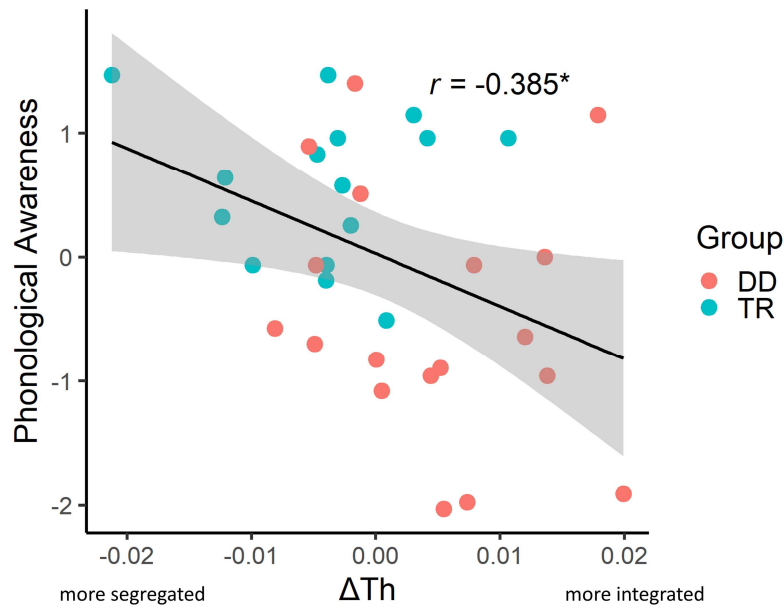


**Figure 7**. Correlation between phonological awareness scores and the change in tree hierarchy ($\Delta Th$; real word minus random sequence condition) in the theta-band network. Positive $\Delta Th$ values indicate a shift toward a more integrated (star-like) network topology, whereas negative values indicate a shift toward a more segregated (path-like) topology, during real word compared to random syllable tracking. TR = typical reader, DD = developmental dyslexia. * $p_{perm}$ < .05.

## 4 Discussion

The present study investigated the brain network topology of oscillatory activity during speech processing in typical and dyslexic readers and its modulation by speech structure. To this end, we applied MST-based graph theoretical analysis to EEG data in response to streams of random syllables and real words. In both typical and dyslexic readers, we found that the neural tracking of real words elicits

a more interconnected topology in theta-band oscillations, compared to that of syllables. Notably, this effect was larger, and accompanied by an increased reliance on sites above the right frontal cortex in dyslexic readers than in typical readers.

## 4.1 Theta oscillatory activity during speech tracking

The MST analysis indicated a more integrated network topology (higher tree degree and kappa) in the theta-band network during the tracking of real words compared to that of random syllables, in both groups. This is in line with the fact that word, compared to syllable processing, requires more coordinated communication across multiple systems, including the phonological, orthographic, and the lexical-semantic system (Gow Jr., 2012; Hickok & Poeppel, 2007; G. Zhang, Si, & Dang, 2019). In particular, increased tree degree indicates that certain nodes have an increased number of connections with the rest of the network (Bullmore & Sporns, 2009; Tewarie et al., 2015), and may thus reflect a shift from a more decentralized path-like topology, towards a more interconnected, star-like topology. Relatedly, the increased kappa, or degree diversity, during word processing indicates an increased prevalence of interconnected, or high-degree, nodes (Stam & van Straaten, 2012).

The observed shift towards a more integrated topology when the speech stream contained words was only found in the theta band (4-8 Hz). Because the theta band differs from the presentation rates of the syllables (3.3 Hz) and words (1.1 Hz), this functional shift may not merely reflect stimulus-driven entrainment, but rather (or at least partly) originates from an intrinsic mechanism for speech processing. Corresponding to the average syllabic rate of speech across many languages (Pellegrino, Coupé, & Marsico, 2011), theta band oscillations are thought to represent an optimal brain rhythm for the temporal tracking of speech structures (Ding et al., 2017; Giraud & Poeppel, 2012). In particular, the phase alignment of theta band oscillations may subserve the active chunking of speech information ranging across a broad timescale (Riecke, Formisano, Sorger, Baskent, & Gaudrain, 2018; Teng, Tian, Doelling, & Poeppel, 2018). Accordingly, phase and power modulations of theta-band oscillations have been linked to a large range of speech perception functions (Peelle, Gross, & Davis, 2013), including acoustic

speech decoding (Hickok & Poeppel, 2007; Luo & Poeppel, 2007; Riecke et al., 2018), speech segmentation (Ding & Simon, 2014; Doelling et al., 2014; Teng et al., 2018), and the retrieval of lexical-semantic information (Bastiaansen, van der Linden, ter Keurs, Dijkstra, & Hagoort, 2005; Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008). In addition, theta oscillations are considered to be related to other non-language-specific executive functions that regulate speech tracking, such as (verbal) working memory (Fell & Axmacher, 2011; Jensen & Tesche, 2002; Klimesch, 1999; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010) and attention control (Song, Meng, Chen, Zhou, & Luo, 2014; Viswanathan, Bharadwaj, & Shinn-Cunningham, 2019). Regarding the general properties of the oscillatory brain network, the "traveling wave" framework proposes that theta (and alpha) oscillations propagate progressively across the cortex carrying temporally segmented information, and hence support the neural communication across distant cortical areas (von Stein & Sarnthein, 2000; H. Zhang, Watrous, Patel, & Jacobs, 2018).

## 4.2 Network topology for speech tracking in dyslexia

As compared to typical readers, dyslexic readers showed a larger shift towards a more integrated network topology (higher leaf fraction and tree hierarchy) for words versus syllables. Analogous to this finding, a previous study found increased network integration (i.e., a more star-like topology) in dyslexic adults in the alpha-band network during resting-state (Fraga-González et al., 2018). The fact that only leaf fraction led to this significant *Group × Condition* interaction, may relate to increased sensitivity of this metric, compared to e.g., degree or kappa, in detecting subtle shifts in network topology. One possible reason for such increased sensitivity, could be that leaf fraction is less influenced by confounding factors such as volume conduction (Lai, Demuru, Hillebrand, & Fraschini, 2018). We further observed a trend toward a negative correlation between participants' phonological processing performance and the word versus syllable change in tree hierarchy of the theta-band network. In other words, participants with lower phonological awareness seemed to exhibit a greater shift toward a more integrated network topology for word tracking. It is noteworthy that overall spectral power and connectivity strength (i.e., PLI and mean connectivity in the MST) did not show any group or condition differences. This suggests that during

speech tracking, only the pattern, rather than the strength, of functional connectivity was altered in dyslexic readers.

A more integrated network topology may reflect reduced recruitment of functionally specialized subnetworks in dyslexic readers (Fraga-González et al., 2018). Previous EEG studies similarly indicated a more integrated MST topology (as reflected by higher leaf fraction, tree hierarchy, and kappa, and a lower diameter) in the theta-band network (and also beta- and gamma-band), in dyslexic compared to typically reading children during a word reading (Taskov & Dushanova, 2020) and a visual word/pseudoword task (Dushanova & Tsokov, 2021). Interestingly, the leaf fraction and kappa in the theta-band network during word/pseudoword discrimination decreased after a three-month remediation program on visual perception (Dushanova & Tsokov, 2021). Post-training, the dyslexic group demonstrated a more specialized network similar to the typical readers, characterized by increased connectivity between nodes on the major language pathways in the left hemisphere, e.g., middle and inferior temporal cortex, prefrontal cortex, and the rest of the network (Berwick, Friederici, Chomsky, & Bolhuis, 2013; Dushanova & Tsokov, 2021; Saur et al., 2008). Meanwhile, the observed trend toward a more integrated network topology for word (versus syllable) tracking in participants with poorer phonological awareness skills may further suggest a less specialized brain network organization, and/or a (compensatory) bias to semantic word-level information during speech perception. Although speculative at this point, this putative effect may be associated with less accurate representations of auditory word forms and the constituent phonemes (Bonte et al., 2007; Goswami et al., 2011; Noordenbos et al., 2013; M. Zhang et al., 2021), accompanied with deficits in slow temporal sampling via delta/theta oscillations as observed in previous research (Goswami, 2011; Hämäläinen et al., 2013; Lallier et al., 2017). Note that our paradigm involved the presentation of unambiguous and clearly distinguishable speech syllables; therefore, it was not designed to also test these more subtle auditory/speech processing difficulties.

A more integrated star-like topology in dyslexic readers may also reflect a more costly functional organization responding to a potentially increased cognitive demand for word compared to syllable tracking. It has been shown that when encountering demanding tasks, the global network topology shows enhanced interconnectivity and an increased number of connector hubs (Finc et al., 2017;

Shine et al., 2016; Vourkas et al., 2014). Our results did not indicate group differences in overall oscillatory activity or connectivity strength, nor in behavioral accuracy of word recognition in the behavioral post-test. They did indicate an increased leaf fraction in the theta-band network, along with lower eccentricity at right frontal electrodes (nodes) for word relative to syllable tracking especially in the dyslexic readers. Such increase in leaf fraction may be indicative of the presence of highly connected hub nodes and shortened path length (i.e., more efficient information flow) in the network (Stam, 2014; Tewarie et al., 2015). With reduced eccentricity, the right frontal nodes of dyslexic readers exhibited shorter distance (i.e., functionally closer) with other nodes, and hence played a more central or hub-like role in the theta-band network for word perception (Stam et al., 2014; van Dellen et al., 2014). Bilateral frontal cortex has been identified in a multiple-demand system subserving various domain-general functions, including working memory, mental programming and executive control (Diachek, Blank, Siegelman, Affourtit, & Fedorenko, 2020; Duncan, 2010; Duncan & Owen, 2000; Fedorenko, Duncan, & Kanwisher, 2013). Dyslexic readers may recruit the right fronto-parietal regions to enhance large-scale neural communication and counterbalance language processing deficits in the left hemisphere (Kershner, 2020; Ligges, Ungureanu, Ligges, Blanz, & Witte, 2010). In the current study, participants with dyslexia may have engaged the right hemisphere during word tracking to help retaining verbal information in working memory (Beneventi, Tønnessen, Ersland, & Hugdahl, 2010; Gerton et al., 2004; Vasic, Lohr, Steinbrink, Martin, & Wolf, 2008; Xu, Yang, Siok, & Tan, 2015) or resolve competing phonological activations (Maisog, Einbinder, Flowers, Turkeltaub, & Eden, 2008; Margolis et al., 2020; Shaywitz & Shaywitz, 2005), resulting in a more interconnected, star-like topology compared to syllable processing. Such more bilaterally distributed activations and interconnections have been widely reported as a compensatory strategy in previous dyslexia studies investigating both the structural (Hosseini et al., 2013; Qi et al., 2016) and functional (Dimitriadis, Simos, Fletcher, & Papanicolaou, 2019; Finn et al., 2014; Spironelli, Penolazzi, & Angrilli, 2008) networks. Taken together, the tendency for dyslexic adults to engage a more integrated theta-band network with increased reliance on nodes in the right frontal site for word versus syllable tracking may serve to compensate for reduced sensitivity to speech sound structures (Hornickel & Kraus, 2013; M. Zhang et al., 2021). Nevertheless, this finding should be interpreted with caution as the analyses were conducted in the sensor space. Additional studies with clearer

assumptions/models to perform source-level analysis are needed to further identify the neural neural correlates subserving an altered network topology (and information flow) during speech processing in dyslexia.

Our findings highlight the relevance of synchronized theta oscillations between distant brain regions/functional hubs in speech tracking. In future studies, it would be interesting to investigate how this relates to potentially atypical temporal alignment of slow oscillatory activities (delta/theta) to the speech envelope in individuals with dyslexia (Goswami, 2011; Lallier et al., 2017; Hämäläinen et al., 2013). In particular, a reduction in speech-brain phase alignment widely reported in previous studies (Hämäläinen, Rupp, Soltész, Szücs, & Goswami, 2012; Leong & Goswami, 2014; Leong et al., 2011) does not necessarily result in diminishing synchrony across brain regions. Hence, additional studies are needed to probe into the interaction between local and large-scale oscillatory activities during speech processing, and its association with (a)typical reading development. Another interesting lead for future studies is our focus beyond the syllable level towards oscillatory network dynamics for higher-order chunks such as syllable clusters and words. This is especially meaningful for the investigation on (spatio)temporal sampling deficits of dyslexia in the visual domain, as the mental parsing of written language is governed by the ability to consistently sweep the attentional spotlight over a series of graphemes (e.g., about 23 letters per second in English) (Vidyasagar, 2013). Finally, a methodological limitation should be noted. The manual rejection of artefactual ICs in the current study (on average 23% of the components) might be too conservative and thus may result in a risk of losing actual brain signal and reducing the sensitivity to detect group differences in brain network topology. An alternative approach could be a wavelet enhanced ICA method to threshold the decomposed ICs before the removal of artifacts (Castellanos & Makarov, 2006). Alternatively, when employing our paradigm with MEG data, the temporal Signal Space Separation algorithm could be used to minimize the influence of artifacts, as it models brain signals while filtering out the external noises that oscillate at the same frequency (Taulu & Hari, 2009). A systematic evaluation of these and other alternative methods for artifact rejection could be useful to specify their potential influence on network topology.

## 5 Conclusion

To summarize, we observed a more interconnected topology in the theta-band network during word versus syllable tracking in both typical and dyslexic readers. Spoken word perception elicited a different brain network organization in adults with dyslexia compared with typical readers. In particular, the theta-band oscillatory network revealed a greater shift toward a more integrated, star-like topology with an over-reliance on the nodes in the right frontal site for word tracking in dyslexic readers. Furthermore, individuals with poorer phonological skills were more inclined to show a more integrated brain network topology during word processing. Notably, such altered functional organization of oscillatory networks in dyslexic readers was not accompanied by changes in the strength of oscillatory activity or inter-channel connectivity. Within the framework of graph theory, the current findings corroborate that dyslexia is accompanied by reduced sensitivity to speech structures and altered theta-band functions. As large-scale network topology may change with brain maturation, accumulating experience and increasing cognitive capacity (Bullmore & Sporns, 2012; Cao et al., 2016; Smit et al., 2016; Thatcher, North, & Biver, 2008), developmental studies are needed to shed light on the developmental trajectory of brain network organization, and its association with a variety of language and general cognitive functions as a child learns to read.

## Declaration of competing interest

The authors declare no competing interests.

**CRediT authorship contribution statement**

**Manli Zhang**: Conceptualization, Methodology, Software, Investigation, Formal analysis, Data Curation, Funding acquisition, Writing - Original Draft. **Lars Riecke**: Conceptualization, Methodology, Resources, Data Curation, Supervision, Writing - Original Draft, Writing - Review & Editing. **Gorka Fraga-González**: Methodology, Software, Writing - Review & Editing. **Milene Bonte**: Conceptualization, Methodology, Resources, Data Curation, Supervision, Funding acquisition, Project administration, Writing - Original Draft, Writing - Review & Editing.

**Table S1.** Group and condition comparisons of network metrices

| | Condition | | | Group | | | Condition × Group | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F_{1,\,34}$ | $p$ | $\eta_p^2$ | $F_{1,\,34}$ | $p$ | $\eta_p^2$ | $F_{1,\,34}$ | $p$ | $\eta_p^2$ |
| *Delta*: PLI | .98 | .330 | .028 | .34 | .562 | .010 | .34 | .565 | .010 |
| *Degree* | .26 | .616 | .007 | .09 | .771 | .003 | .13 | .726 | .004 |
| *LF* | .08 | .783 | .002 | .17 | .688 | .005 | 1.54 | .223 | .043 |
| *Diameter* | .51 | .482 | .015 | .56 | .458 | .016 | .35 | .561 | .010 |
| *Ecc* | .67 | .421 | .019 | .56 | .459 | .016 | .36 | .554 | .010 |
| *BC* | .13 | .726 | .004 | .72 | .402 | .021 | .16 | .697 | .005 |
| $T_h$ | .05 | .829 | .001 | .06 | .815 | .002 | .66 | .423 | .019 |
| *Kappa* | .04 | .846 | .001 | .16 | .690 | .005 | .10 | .751 | .003 |
| *MC* | 1.54 | .223 | .043 | .17 | .684 | .005 | .22 | .639 | .007 |
| *Theta*:PLI | 3.21 | .082 | .086 | .01 | .922 | <.001 | .50 | .485 | .014 |
| *Degree* | **8.05**[a] | **.008**[*] | **.191** | .99 | .326 | .028 | .15 | .699 | .004 |
| *LF* | **5.56** | **.024** | **.140** | .51 | .479 | .015 | **9.56** | **.004***| **.220** |
| *Diameter* | 1.79 | .190 | .050 | .75 | .394 | .021 | 4.13 | .050 | .108 |
| *Ecc* | 2.13 | .154 | .059 | .68 | .416 | .020 | 4.20 | .048 | .110 |
| *BC* | 1.87 | .180 | .052 | 2.95 | .095 | .080 | 3.39 | .074 | .091 |
| $T_h$ | .66 | .423 | .019 | .25 | .621 | .007 | **6.00** | **.020** | **.150** |
| *Kappa* | **7.37**[a] | **.010**[*] | **.178** | 1.06 | .309 | .039 | .49 | .488 | .014 |
| *MC* | 3.87 | .057 | .102 | .19 | .670 | .005 | .91 | .347 | .026 |
| *Alpha*:PLI | .18 | .674 | .005 | .70 | .410 | .020 | .11 | .738 | .003 |
| *Degree* | .13 | .721 | .004 | .05 | .825 | .001 | .002 | .962 | <.001 |
| *LF* | .01 | .907 | <.001 | .13 | .725 | .004 | .56 | .459 | .016 |
| *Diameter* | .50 | .485 | .014 | .72 | .402 | .021 | .03 | .875 | .001 |
| *Ecc* | .25 | .618 | .007 | .70 | .410 | .020 | .08 | .784 | .002 |
| *BC* | .71 | .405 | .021 | .02 | .902 | <.001 | .001 | .981 | <.001 |
| $T_h$ | .51 | .481 | .015 | .54 | .468 | .016 | 2.82 | .103 | .076 |
| *Kappa* | .38 | .544 | .011 | .02 | .895 | .001 | .05 | .829 | .001 |
| *MC* | .51 | .482 | .015 | 1.13 | .295 | .032 | .25 | .624 | .007 |
| *Beta*:PLI | 3.84 | .058 | .101 | .14 | .715 | .004 | 1.31 | .261 | .037 |
| *Degree* | 1.90 | .177 | .053 | .39 | .538 | .011 | .04 | .837 | .001 |
| *LF* | 1.48 | .233 | .042 | .01 | .922 | <.001 | 3.12 | .086 | .084 |
| *Diameter* | .86 | .360 | .025 | .20 | .657 | .006 | 3.81 | .059 | .101 |
| *Ecc* | .78 | .384 | .022 | .23 | .637 | .007 | 2.65 | .113 | .072 |
| *BC* | .16 | .694 | .005 | .55 | .465 | .016 | 1.60 | .214 | .045 |
| $T_h$ | 2.74 | .107 | .075 | .02 | .896 | .001 | .95 | .337 | .027 |
| *Kappa* | 1.99 | .167 | .055 | .19 | .670 | .005 | .23 | .638 | .007 |
| *MC* | 4.66 | .038 | .120 | .26 | .615 | .008 | .27 | .608 | .008 |

*Note.* PLI = Phase Lag Index; *Degree* = maximum nodal degree; *LF* = leaf fraction; *Ecc* = eccentricity; *BC* = betweenness centrality; $T_h$ = tree hierarchy; *MC* = mean connectivity in the MST. *p* represents uncorrected *p*-values. Bold text represents significant effects after FDR correction at *q* = 0.10; * represents significant effects after FDR correction at *q* = 0.05. [a] Random sequence (RS) < real words (RW).

**Table S2.** Group and condition comparisons of network metrices <u>after controlling for age</u>

| | Condition | | | Group | | | Condition × Group | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F_{1, 34}$ | $p$ | $\eta_p^2$ | $F_{1, 34}$ | $p$ | $\eta_p^2$ | $F_{1, 34}$ | $p$ | $\eta_p^2$ |
| *Delta*:PLI | .95 | .336 | .028 | .55 | .465 | .016 | .51 | .482 | .015 |
| *Degree* | .25 | .619 | .008 | .34 | .565 | .010 | .39 | .535 | .012 |
| *LF* | .77 | .783 | .002 | .86 | .360 | .025 | 2.57 | .118 | .072 |
| *Diameter* | .50 | .485 | .015 | .82 | .373 | .024 | .72 | .401 | .021 |
| *Ecc* | .66 | .424 | .019 | .75 | .392 | .022 | .73 | .400 | .022 |
| *BC* | .12 | .727 | .004 | 1.54 | .224 | .044 | .60 | .443 | .018 |
| $T_h$ | .05 | .829 | .001 | .72 | .402 | .021 | 1.53 | .225 | .044 |
| *Kappa* | .04 | .848 | .001 | .59 | .449 | .017 | .32 | .576 | .010 |
| *MC* | 1.51 | .228 | .044 | .19 | .666 | .006 | .41 | .525 | .012 |
| *Theta*:PLI | 3.13 | .086 | .087 | <.01 | .970 | <.001 | .55 | .462 | .017 |
| *Degree* | **7.88** | **.008** | **.193** | .94 | .338 | .028 | .35 | .557 | .011 |
| *LF* | **5.44** | **.026** | **.141** | .72 | .403 | .021 | 6.26 | .017 | .159 |
| *Diameter* | 1.74 | .196 | .050 | .61 | .439 | .018 | 3.32 | .078 | .091 |
| *Ecc* | 2.07 | .160 | .059 | .61 | .439 | .018 | 3.43 | .073 | .094 |
| *BC* | 1.83 | .185 | .053 | 2.35 | .135 | .066 | 1.95 | .172 | .056 |
| $T_h$ | .64 | .430 | .019 | .42 | .521 | .013 | 4.51 | .041 | .120 |
| *Kappa* | **7.21** | **.011** | **.179** | 1.02 | .321 | .030 | .73 | .401 | .021 |
| *MC* | 3.77 | .061 | .103 | .06 | .806 | .002 | .96 | .334 | .028 |
| *Alpha*:PLI | .19 | .663 | .006 | .68 | .415 | .020 | 1.33 | .258 | .039 |
| *Degree* | .13 | .725 | .004 | <.01 | .947 | <.001 | .003 | .960 | <.001 |
| *LF* | .01 | .908 | <.001 | <.01 | .954 | <.001 | .67 | .419 | .020 |
| *Diameter* | .51 | .479 | .015 | .57 | .456 | .017 | .57 | .457 | .017 |
| *Ecc* | .26 | .612 | .008 | .56 | .460 | .017 | .81 | .376 | .024 |
| *BC* | .70 | .411 | .021 | .12 | .727 | .004 | .043 | .837 | .001 |
| $T_h$ | .50 | .485 | .015 | .56 | .458 | .017 | 3.11 | .087 | .086 |
| *Kappa* | .36 | .550 | .011 | .02 | .882 | .001 | .06 | .814 | .002 |
| *MC* | .53 | .473 | .016 | 1.07 | .308 | .031 | 1.31 | .261 | .038 |
| *Beta*:PLI | 3.73 | .062 | .101 | .15 | .700 | .005 | 1.11 | .301 | .032 |
| *Degree* | 1.86 | .182 | .053 | .45 | .508 | .013 | .19 | .665 | .006 |
| *LF* | 1.43 | .240 | .042 | .05 | .819 | .002 | 2.74 | .107 | .077 |
| *Diameter* | .84 | .367 | .025 | .39 | .538 | .012 | 2.56 | .119 | .072 |
| *Ecc* | .76 | .390 | .022 | .37 | .547 | .011 | 1.71 | .200 | .049 |
| *BC* | .15 | .697 | .005 | .63 | .435 | .019 | .71 | .405 | .021 |
| $T_h$ | 2.67 | .112 | .075 | <.01 | .985 | <.001 | .52 | .476 | .016 |
| *Kappa* | 1.95 | .172 | .056 | .25 | .621 | .007 | .36 | .554 | .011 |
| *MC* | 4.53 | .041 | .121 | .30 | .591 | .009 | .31 | .584 | .009 |

*Note.* Bold text represents significant effects after FDR correction at *q* = 0.10

**Table S3.** Group and condition comparisons of network metrics in the **theta** band (<u>excluding one DD participant</u>)

| | Condition | | | Group | | | Condition × Group | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F_{1, 33}$ | $p$ | $\eta_p^2$ | $F_{1, 33}$ | $p$ | $\eta_p^2$ | $F_{1, 33}$ | $p$ | $\eta_p^2$ |
| PLI | 3.05 | .090 | .085 | .003 | .960 | .000 | .48 | .495 | .014 |
| *Degree* | **8.44** | **.007** | **.204** | .50 | .487 | .015 | .26 | .614 | .008 |
| LF | 4.79 | .036 | .127 | .27 | .610 | .008 | **8.45** | **.006** | **.204** |
| *Diameter* | 1.88 | .180 | .054 | .46 | .503 | .014 | 4.18 | .049 | .112 |
| *Ecc* | 2.26 | .143 | .064 | .40 | .530 | .012 | 4.32 | .046 | .116 |
| *BC* | 2.15 | .153 | .061 | 1.99 | .168 | .057 | 3.71 | .063 | .101 |
| *Th* | .38 | .543 | .011 | .19 | .665 | .006 | 5.00 | .032 | .131 |
| *Kappa* | **6.89** | **.013** | **.173** | .58 | .453 | .017 | .45 | .507 | .013 |
| MC | 3.63 | .065 | .099 | .13 | .717 | .004 | .85 | .364 | .025 |

*Note.* Bold text represents significant effects after FDR correction at $q$ = 0.10

# Chapter 5

## Cortical tracking of language structures:
## Modality-dependent and supra-modal responses

Based on

Zhang, M., Riecke, L., & Bonte, M. (Under review). Cortical tracking of language structures: Modality-dependent and supra-modal responses.

# Chapter 6

## General Discussion

The human brain aligns its intrinsic rhythmic activity, i.e., neural oscillations, to track the hierarchical temporal structures of (non-)linguistic signals. This dissertation aimed to investigate the cortical tracking of spoken and written language structures by measuring and modulating slow cortical oscillations, as well as their association with (a)typical reading development (in terms of both the temporal and spatial aspects). We first applied tACS over the bilateral auditory cortices to examine the causal role of slow cortical oscillations for sound rise-time perception in a sub-syllabic time window (**Chapter 2**). In the next three empirical studies, we employed EEG to track oscillatory responses to varying structures when native Dutch speakers were exposed to auditorily and visually presented language streams. In **Chapter 3**, we adopted a statistical learning paradigm to investigate the temporal course of speech structure learning (regularity-based) and real word tracking (knowledge-driven) in adults with dyslexia and their typically reading peers. **Chapter 4** further investigated how dyslexic readers differ in the topological organization of oscillatory networks during speech tracking. Finally in **Chapter 5**, we made a step towards written language processing, where we investigated the commonalities and differences in the cortical tracking mechanisms of written versus spoken language structures. The present chapter contains a summary and discussion of the findings presented in this dissertation.

## 1 Summary

Human language is a complex, hierarchically organized structure that unfolds over time (Greenfield, 1991; Kotz & Schwartze, 2010). Our brain is capable of tracking such quasi-rhythmic patterns in speech on a real-time basis via neural oscillations spanning across multiple timescales (Giraud & Poeppel, 2012; Peelle & Davis, 2012), see Meyer (2018) for recent review. Such oscillatory mechanisms are suggested to be likewise at play for written language processing (e.g., Bastiaansen, van Berkum, & Hagoort, 2002; Vignali, Himmelstoss, Hawelka, Richlan, & Hutzler, 2016), although a systematic understanding of how individual linguistic units are represented and incrementally integrated into higher-order structures during reading is still lacking. Developmental dyslexia, a reading-specific learning disorder, has been suggested to be associated with deficient temporal sampling of auditory and visual information (Archer, Pammer, & Vidyasagar, 2020; Goswami, 2011; Lallier, Molinaro, Lizarazu, Bourguignon, & Carreiras, 2017) and abnormal

functional organization of brain networks for language and general cognitive control (Bailey, Aboud, Nguyen, & Cutting, 2018; Finn et al., 2014; Richlan, 2012). It is therefore of great importance to investigate whether and how the oscillatory mechanisms subserving the temporal tracking of hierarchical linguistic structures are altered in individuals with dyslexia. To this end, this dissertation measured (via EEG) and modulated (via tACS) the stimulus-brain phase synchronization in (a)typical readers when they received auditorily or visually displayed (non-)linguistic input varying in structure.

In **Chapter 2**, we set out to examine whether slow cortical oscillations contribute functionally to the perception of sound onset. According to the temporal sampling framework of dyslexia (Goswami, 2011; Lallier et al., 2017), aberrant neural sampling of acoustic signals at slow temporal rates (delta/theta) may directly (Di Liberto, O'Sullivan, & Lalor, 2015) and/or indirectly (Giraud & Poeppel, 2012; Lehongre, Ramus, Villiermet, Schwartz, & Giraud, 2011; Peelle & Davis, 2012) affect the fine-grained representation of auditory information at the phonemic scale, albeit empirical evidence for such a causal link is still scarce. Exploiting non-invasive brain stimulation, we applied 4-Hz tACS over the bilateral auditory cortices and assessed the perception of amplitude rise time (ART) in typically reading adults. The relative timing of brain stimulation and the sound on-ramps was cyclically varied across six phase lags, and a sham-stimulation condition was included to test whether tACS influences ART perception irrespective of its phase. We observed neither cyclical changes in participants' ART discrimination performance induced by the experimentally modulated stimulus-brain phase lags, nor general differences between the tACS and sham conditions. These results thus failed to provide evidence for a functional role of slow cortical oscillations in sound onset perception in a sub-syllabic time window. Considering positive findings from previous (correlational) speech-based studies (e.g., Hämäläinen, Leppänen, Torppa, Müller, & Lyytinen, 2005; Kösem, Bosker, Jensen, Hagoort, & Riecke, 2020), especially those that applied gamma-rate tACS (Marchesotti et al., 2020; Rufener, Krauel, Meyer, Heinze, & Zaehle, 2019), our null finding suggests that slow cortical oscillations may contribute to the (categorical) perception of phonemes and syllables, rather than lower-level processing of basic acoustic differences related to ART. To be more specific, we reason that slow cortical oscillations may influence phoneme/syllable level representations indirectly (Giraud & Poeppel, 2012; Peelle

& Davis, 2012) through low-gamma oscillations and cross-frequency coupling (Lallier et al., 2017).

In **Chapter 3**, our aim was to investigate the neural grouping of speech units driven by higher-level lexical and statistical properties in typical and dyslexic readers. It has been found that the cortical tracking of higher-order linguistic units in speech, such as words, phrases and sentences, is coupled with the listeners' knowledge (Ding et al., 2017; Ding, Melloni, Zhang, Tian, & Poeppel, 2016). Moreover, statistical learning, i.e., the ability to extract statistical regularities from the sensory environment (Saffran, Aslin, & Newport, 1996), is suggested to be crucial for acquiring such hierarchical structures (Buiatti, Peña, & Dehaene-Lambertz, 2009; Saffran, Newport, & Aslin, 1996). Given that dyslexic readers showed reduced perceptual sensitivity to statistical regularities in (non-)speech sequences (for review, see Lee, Cui, & Tong, 2022; Schmalz, Altoè, & Mulatti, 2017), we predicted that they would show a less efficient build-up of neural tracking of novel word structures. Therefore, a statistical learning paradigm was adopted in combination with EEG recordings, where participants with and without dyslexia were exposed to continuous speech streams of (1) tri-syllabic pseudowords (structured condition; statistical learning), (2) tri-syllabic real words (real word condition; knowledge-based) and (3) randomly ordered syllable sequences (random condition; control). The frequency-tagged cortical responses at the syllable- and (pseudo)word-rate were assessed in each block. As expected, the syllable-rate tracking was stable and comparable between the two groups, irrespective of the type of speech streams. More importantly, in typical readers the cortical tracking of pseudowords gradually increased and approached that of real words, whereas this establishment of pseudoword tracking was slower in the dyslexic readers. Correlational analyses further revealed that slower learners tended to have poorer phonological awareness. Moreover, those who showed stronger responses for real word tracking were less fluent in the visual-verbal conversion of linguistic symbols. In summary, these findings corroborate results from prior studies suggesting a statistical learning difficulty associated with dyslexia and poorer phonological/reading skills. They further shed new light on dyslexia research from an incremental learning perspective by utilizing an online neurophysiological approach combined with an implicit learning task.

**Chapter 4** extended the investigations on speech-structure tracking in (dys)fluent readers by examining the large-scale functional organization of oscillatory networks during the passive tracking of real words and random syllables. Previous research has reported dyslexia-related alterations in the spatial organization of structural and functional brain networks (Cui, Xia, Su, Shu, & Gong, 2016; Finn et al., 2014; Fraga-González et al., 2016; Qi et al., 2016; Schurz et al., 2015). However, it remains unclear how large-scale inter-regional interactions between oscillatory brain responses are organized to represent the incremental integration of speech units. In each of the four frequency bands of interest (i.e., delta, theta, alpha and beta), we used a graph-theoretical approach named "minimum spanning tree" (MST) to construct loop-less graphs of functionally inter-connected nodes (i.e., EEG channels) quantified by phase-based connectivity. These network properties were characterized during the neural tracking of spoken syllables and words, and compared between dyslexic and typically reading adults. In both groups, we found a more integrated theta-network topology elicited by words compared to that elicited by syllables. Furthermore, this effect was stronger in dyslexic readers, who also demonstrated an increased reliance on the right frontal site for word tracking. Intriguingly, there was no group difference in the overall spectral power or connectivity strength, suggesting that only the pattern, rather than the strength, of functional connectivity was altered during speech tracking in dyslexic readers. During word (relative to syllable) tracking, we additionally observed a trend toward a more integrated topology in the theta-band network in participants who were less skilled in phonological processing. This may point to a less specialized brain organization and/or a (compensatory) bias to familiar lexico-semantic information during speech perception, an idea that requires further investigation in dyslexia research.

Based on our findings in the auditory modality, we proceeded to investigate the cortical tracking of hierarchical structures in written language in **Chapter 5**. Previous neurophysiological research has tended to focus on the end-product of written text processing, e.g., text comprehension and the resolution of semantic/syntactic ambiguities (Bastiaansen et al., 2002; Osterhout, Holcomb, & Swinney, 1994), even though the incoming linguistic information is suggested to be incrementally integrated into high-order structures during reading comprehension (Perfetti & Helder, 2021). In order to reveal the online process in which visual letter strings are chunked into meaningful word structures, and compare it with

spoken language processing, we recorded EEG responses while typically reading participants were exposed to streams of random syllables and real words (as in Chapter 2 and 3), displayed either verbally or visually. Focusing on the spatial distribution of frequency-tagged responses in different sensory modalities, we expected the neural tracking of physically presented syllables to be relatively modality-dependent, while the neural tracking of mentally constructed words was expected to involve a (partially) shared supra-modal mechanism. As expected, we found that anterior and posterior scalp regions were selectively more sensitive to the spoken and written syllables, respectively. Meanwhile, the neural tracking of spoken and written words was observed to overlap in the anterior region. Two non-mutually exclusive working models, namely an "early integration" and a "late co-activation" model, were proposed to interpret the supra-modal effect of word tracking. These models fit well with a dual-route theory, i.e., an indirect grapho-phonological route and a direct lexico-semantic route, on reading development (Forster & Chambers, 1973), and thus may help explain the engagement of these two routes during online reading. To sum up, chapter 5 has attested a partially shared mechanism for hierarchical language tracking across modalities, and thus made a step forward in understanding the incremental processes of natural reading.

## 2 General discussion

Sensory input is processed by the brain on multiple temporal scales. For spoken language specifically, there is spontaneous oscillatory activity at frequencies of gamma (>30 Hz), theta (4-8 Hz) and delta (0.5-4 Hz) tracking the acoustic and linguistic information at the phonemic, syllabic and supra-syllabic (e.g., syllable stress, higher-order structures) scale, respectively (Ding et al., 2016; Giraud & Poeppel, 2012; Meyer, 2018). Among these scales, the syllable scale is considered a critical transition point where the encoded low-level sensory attributes are integrated and combined across chunks of syllables for further phonological and (pre-)lexical analysis (Carreiras, Riba, Vergara, Heldmann, & Münte, 2009; Hickok & Poeppel, 2007). Intriguingly, sensitivity to the rhythmic organization of syllable(-stress) patterns not only plays a pivotal role in early language acquisition (Geiser, Zaehle, Jancke, & Meyer, 2008; Goswami, 2019), but is also suggested to be crucial for phonological and reading development (Goswami, 2011, 2018). Prior research

extensively investigated the neural representation of isolated linguistic units such as phonemes and syllables (e.g., Boets et al., 2013; ten Oever & Sack, 2015), emphasizing the low-level sensory processing of incoming auditory and visual signals. Investigations on how discrete units are represented and integrated into meaningful chunks (e.g., words, phrases), presumably via synchronized slow oscillations (Ding et al., 2016; Henin et al., 2021; Roux & Uhlhaas, 2014), may help uncover the coordination of the two mechanisms, i.e., low-level sensory sampling and higher-level cognitive parsing, during language processing. Furthermore, it may expand our understanding of hierarchical language tracking and comprehension (both spoken and written), by taking into account the associations between slow cortical language tracking responses and (a)typical reading abilities.

## 2.1 No evidence for direct modulation of slow cortical oscillations on sub-syllabic sensory sampling

It is established that during speech perception, low-frequency cortical oscillations primarily aid the extraction and identification of syllable(-stress) patterns and the constituting phonemes (Di Liberto et al., 2015; Giraud & Poeppel, 2012; Poeppel, 2003). Deficient slow temporal sampling and cortical oscillations are thought to indirectly affect the representation of phonemic constituents by either disrupting precise syllable segmentation (Goswami, 2011; Peelle & Davis, 2012), or a developmental increase in the inherent sampling rate of the auditory system, which would lead to an oversampling of information at the phonemic scale (Giraud & Poeppel, 2012; Lehongre et al., 2011). Recent studies showed that in addition to the encoding of syllable(-stress) patterns, low-frequency cortical oscillations may also directly reflect processing at the phonemic scale (Di Liberto et al., 2015), and that such slow oscillation-based cortical tracking of phonetic features may be impaired in dyslexic readers (Di Liberto et al., 2018). Nevertheless, there remains a paucity of empirical evidence on whether slow cortical oscillations contribute functionally to the temporal sampling of acoustic information in a sub-syllabic time window.

In **Chapter 2**, we applied 4-Hz tACS over the bilateral auditory cortices while typically reading adults discriminated the ART of non-speech sounds. Contrary to our expectation and previous studies (e.g., Di Liberto et al., 2015; Goswami &

Leong, 2013), the experimentally controlled stimulus-brain phase lags did not induce cyclical changes in the behavioral performance of ART discrimination and thus provided no evidence for a causal role of slow cortical oscillations in sensory sampling at a sub-syllabic temporal scale. This absence of phase-dependent modulation of slow cortical oscillations on ART perception could be due to potential methodological limitations. For instance, the onset of the first tone in a given trial might have phase-reset brain oscillations and distorted the tACS-induced brain phase at the onset of the second tone. Moreover, the low-frequency tACS effect on the ART discrimination of single sound pairs may be less readily observable compared to that when target stimuli are embedded in a (quasi)rhythmic sound sequence, because external stimulation may more strongly affect neural rhythms that are already entrained by sensory input (Kösem et al., 2020; Reato, Rahman, Bikson, & Parra, 2010). On the other hand, assuming that the stimulation/assessment protocols were sufficiently effective, our observed lack of an effect of theta phase coupling on ART discrimination could also imply that slow cortical oscillations do not causally modulate the auditory temporal perception in a sub-syllabic time window. This could also explain why it was found in previous studies that theta oscillations were not strictly time-locked to the fine-grained temporal structure of acoustic information (Will & Berg, 2007), but rather reflected the brain activity induced by the sequence of stimuli (Riecke, Sack, & Schroeder, 2015; Will & Berg, 2007). Accordingly, theta oscillations were suggested to be associated with the between-units parsing (instead of within-unit sampling) of sensory input (Lallier et al., 2017; Teng, Tian, Doelling, & Poeppel, 2018).

However, it is worth noting that slow cortical oscillations may still induce long-term plasticity in the temporal processing of auditory (phonological) information (Giraud & Poeppel, 2012; Lehongre et al., 2011; Rufener & Zaehle, 2021). Since learning to read arguably shapes the brain by modifying its structural and functional organization of auditory, visual and other functionally specialized subsystems (e.g., attention, cognitive control) (Dehaene, Cohen, Morais, & Kolinsky, 2015; Romanovska & Bonte, 2021), the observed sensory dysfunctions in dyslexia could be a result of diminished reading experience, rather than being its cause (Bishop, Hardiman, & Barry, 2012; Goswami, Power, Lallier, & Facoetti, 2014). To rule out the influence of reduced reading experience and altered phonological representations in dyslexia, we carried out the experiment in

typically reading adults using non-linguistic stimuli. Therefore, in contrast to the positive association reported in previous speech-based (dyslexia) research (Hämäläinen et al., 2005; Kösem et al., 2020), our null result may suggest that slow cortical oscillations contribute less to the temporal sampling of low-level sensory information, but more to the phonological representations that are acquired through long-term practice. In other words, slow cortical oscillations may adapt the boundaries of categorical phoneme representation over language and reading development.

A putative explanation for such (long-term) effects is through an indirect regulatory mechanism termed cross-frequency coupling (CFC). That is, the phase of low-frequency oscillations (e.g., theta) can modulate the amplitude of higher-frequency oscillations (e.g., gamma), and thus enable the coordination of fast, spike-based computation and communication with slower state events (both external and internal) (Canolty & Knight, 2010). Recent studies that applied gamma-rate tACS (30-40 Hz) over the (bilateral) auditory cortices in dyslexic readers observed improved behavioral performances in voice onset time (VOT) discrimination (Rufener et al., 2019), phoneme awareness and (pseudo)word reading fluency (Marchesotti et al., 2020) compared to a sham condition. Moreover, bilateral 40-Hz tACS induced an increased auditory P50-N1 response in adolescents with dyslexia during VOT discrimination (Rufener et al., 2019), confirming a causal link between low-gamma oscillations and fast temporal sampling of acoustic information at the phonemic scale (Giraud & Poeppel, 2012; Poeppel, 2003). Meanwhile, theta-gamma phase-amplitude CFC has been widely observed across multiple (sub)cortical sites and under various experimental conditions (for review, see Canolty & Knight, 2010), including auditory perception (Canolty et al., 2006; Lakatos et al., 2005). The computational role of such CFC could be interpreted as (1) a long-range spatial integration (via theta-band oscillations) of local fast spikes (gamma-band oscillations) (Jensen & Colgin, 2007) (also see Section 2.2.2); and/or (2) a shift of attention (via theta-band oscillations) for subsequent temporal sampling (encoded by gamma-band oscillations) (Lallier et al., 2017). Accordingly, we reasoned that slow cortical oscillations may not directly affect fast sensory sampling in a cyclic manner, but they may still assert influences on gamma-band oscillations via phase-amplitude CFC. Deficient theta-gamma CFC could hamper the fine-grained phoneme representation on a long run and manifest as persistent phonological difficulties in dyslexia. Future studies on

phonological speech perception combining tACS and EEG (Rufener et al., 2019) to directly measure stimulation-induced changes in CFC, or those applying cross-frequency tACS (i.e., co-stimulation of theta and gamma frequencies) (Alekseichuk, Turi, Amador de Lara, Antal, & Paulus, 2016) are needed to test our hypothesis.

## 2.2 Contribution of slow cortical oscillations to supra-syllabic language parsing

The current dissertation extends prior work showing synchronized slow cortical oscillations tracking the hierarchical structure in speech based on existing lexical/syntactic knowledge (Ding et al., 2017; Ding et al., 2016; Sheng et al., 2018) and statistical regularities (Batterink & Paller, 2017; Buiatti et al., 2009; Choi, Batterink, Black, Paller, & Werker, 2020; Getz, Ding, Newport, & Poeppel, 2018; Henin et al., 2021). Specifically, we found that (1) the cortical tracking of newly learned pseudowords approximated that of familiar words, in terms of both the strength and scalp distribution of word-rate responses (**Chapter 3**); (2) the cortical tracking of familiar words elicited a more integrated network topology in theta-band oscillations compared to random syllable tracking (**Chapter 4**); and (3) hierarchically organized cortical tracking was also seen for written language, with a modality-specific processing of physically presented syllables, in addition to a relatively supra-modal tracking of internally constructed word structures (**Chapter 5**). The neurocognitive mechanisms suggested by these findings are discussed in the next section.

### 2.2.1 Learning to track the supra-syllabic structures

Consistent with findings from earlier studies (e.g., Ding et al., 2016; Henin et al., 2021; Sheng et al., 2018), we observed cortical tracking of tri-syllabic structures at fronto-central sites in the (pseudo)word conditions in **Chapters 3 and 5**, next to a stable and widespread cortical tracking of syllables in all types of language streams. EEG activity at fronto-central electrode sites is thought to be critical for speech processing, including higher-order structural analysis (Fedorenko, Duncan, & Kanwisher, 2012; Friederici, 2002; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Hagoort & Indefrey, 2014; Henin et al., 2021), as well as the

processing and storage of lexico-semantic information (Lau, Phillips, & Poeppel, 2008; Saur et al., 2008; Vigneau et al., 2006). The fact that the cortical tracking of pseudowords gradually built up at the same electrode sites showing familiar word tracking corroborates a growing body of evidence suggesting statistical learning as an innate domain-general mechanism that is closely tied to the detection of statistical patterns in language and the implicit acquisition of linguistic knowledge (Aslin, 2017; Christiansen, Conway, & Onnis, 2012; Clerget, Poncin, Fadiga, & Olivier, 2012; Daikoku, 2018; Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006; Kuhl, 2004).

In **Chapter 3**, we observed a rapid establishment of pseudoword tracking followed by an immediate decrease in neural responsiveness, resembling the inverted U-shaped learning curves reported in previous studies using similar learning paradigms (Abla, Katahira, & Okanoya, 2009; Chen, Jin, & Ding, 2020; Choi et al., 2020; Cunillera et al., 2009). Since attending to a certain event can produce higher amplitudes and/or phase synchronizations of oscillatory response as compared to when that event is ignored (Joon Kim, Grabowecky, Paller, Muthu, & Suzuki, 2007; Müller, Teder-Sälejärvi, & Hillyard, 1998), our results may reflect dynamic (and potentially adaptive) allocation of attention in two learning stages. In the initial phase, increased attention may be implicitly directed to the tri-syllabic pseudoword structures while the brain is tuning to the statistical regularities. After the participants achieved a systematic cortical tracking and improved perception of the pseudowords, their attention may have drifted away and thus resulted in reduced tracking responses and/or repetition suppression in a later phase (Atiani, Elhilali, David, Fritz, & Shamma, 2009; Nordt, Hoehl, & Weigelt, 2016). This aligns with the expansion-renormalization model of skill learning, which suggests an initial increase followed by a decrease (or "selective pruning") in brain structure and/or regional activity during continued practice (Lövdén, Garzón, & Lindenberger, 2020; Wenger, Brozzoli, Lindenberger, & Lövdén, 2017). The same inverted-U-trajectory has also been observed in behavioral and/or neural changes associated with habituation (Turk-Browne, Scholl, & Chun, 2008), math learning (Shrager & Siegler, 1998) and reading acquisition (Dehaene-Lambertz, Monzalvo, & Dehaene, 2018; Fraga-González et al., 2021; Fraga-González, Žarić, Tijms, Bonte, & Van Der Molen, 2017; Maurer et al., 2006).

What type of information is represented during statistical learning and how does it contribute to the successful segmentation of connected speech? It has been suggested that hierarchical structures are represented at multiple levels, from simple and local properties (e.g., the transitional probability between discrete elements) to relatively complex forms (e.g., the co-occurrence and ordinal position of multiple elements; the identity of recurrent chunks) (Henin et al., 2021; Ordin, Polyanskaya, Soto, & Molinaro, 2020). Moreover, the representation of simple properties was found to engage modality-specific sensory circuits, while that of complex forms was observed in relatively heteromodal (e.g., the inferior frontal gyrus) and memory-related brain regions (e.g., the anterior temporal lobe and hippocampus) (Henin et al., 2021). Put differently, with increasing exposure, the sensory input is segmented into recurrent chunks via a statistical computation of troughs in transitional probabilities (i.e., a "boundary-finding" mechanism), while an extraction of meaningful fragments (i.e., a "clustering" mechanism, based on e.g., temporal dependence) simultaneously serves to generate more concrete representations (Ordin et al., 2020; Perruchet & Pacton, 2006). It has been suggested that boundary-finding is a dominant mechanism for the statistical learning of speech segmentation (Ordin et al., 2020), whereas clustering is closely related to the formation of conscious knowledge (Meulemans & Van Der Linden, 2003; Perruchet & Vinter, 1998; Thiessen, 2017) and rule generalization (Aslin, 2017; Frost, Armstrong, Siegelman, & Christiansen, 2015; Goldstein et al., 2010). Thus, in our studies, the pseudo- and real word tracking may primarily reflect the strategies of boundary-finding and clustering, respectively. Further research is needed to identify the neurophysiological indicators of different components (i.e., from simple local to complex global features) encoded during statistical learning, as well their temporal evolution. This may be especially helpful for a deeper understanding of specific learning difficulties associated with neurodevelopmental disorders such as dyslexia.

## 2.2.2 Oscillatory networks underlying supra-syllabic tracking

In addition to the time course across which slow cortical oscillations gradually build up to track the hierarchical language structure, the current dissertation also investigated how such cortical responses are organized across the brain. It is thought that slow rate temporal information, such as (supra-)syllabic linguistic

information, is predominantly processed in the right-sided auditory cortex (Boemio, Fromm, Braun, & Poeppel, 2005; Poeppel, 2003), where the precise lateralization and/or spatial pattern is modulated by linguistic processing demands (Overath, McDermott, Zarate, & Poeppel, 2015; Peña & Melloni, 2012; Santoro et al., 2014). Meanwhile, it is suggested that the lexico-semantic speech processing engages a heteromodal anterior/inferior frontal system (Booth et al., 2002; Deniz, Nunez-Elizalde, Huth, & Gallant, 2019; Lau et al., 2008). Our results in **Chapter 4** revealed that the neural tracking of speech input also engaged long-range synchronization between spatially distributed regions/systems. Adopting a network-based perspective, we found that when individual syllables could be chunked into meaningful word structures, the theta-band network shifted to a more integrated topology. This accords with prior research indicating that in comparison to the representation of single syllables, word processing requires more coordinated brain function to link the phonological, orthographic, and lexico-semantic information (Gow, 2012; Hickok & Poeppel, 2007; Zhang, Si, & Dang, 2019). Our observation is also consistent with a global workspace theory (Dehaene & Naccache, 2001), which argues that the processing of perceptually salient stimuli or cognitively effortful tasks requires an integrated "workspace" where distant neuronal ensembles are globally connected via synchronized oscillations to enable rapid information exchange throughout the network (Baars, 2002; Bullmore & Sporns, 2012). In other words, a transition of network topology from a relatively segregated state during syllable tracking to a more integrated state for word tracking may reflect the emergence of more active processes (e.g., cognitive parsing, lexical retrieval) in the brain (Shine et al., 2016). It is noteworthy that the current results highlight a spontaneous reconfiguration of network topology (but not the overall spectral power or connectivity strength) during speech processing even in the absence of specific task demands. This points to the dynamic and flexible nature of human brain, and underlines the importance of taking a system-level perspective in understanding the manner in which the human brain organizes its activity while adapting to an ever-changing environment.

Intriguingly, the observed change in network topology triggered by syllable-to-word integration was restricted to synchronized brain activities in the theta range. This may highlight the functional role of theta-band oscillation as a "backbone" rhythm that modulates the temporal and spatial organization of information flow in the brain's (spoken) language system. On one hand, the phase alignment of

theta-band oscillations is found to subserve the active chunking of (speech) information operating across a broad timescale (Riecke, Formisano, Sorger, Baskent, & Gaudrain, 2018; Teng et al., 2018). That is, the theta cycle may provide a "temporal packet" to carry the individual items coded by higher-frequency oscillations (Jensen, 2006). Therefore, phase (and power) modulations of theta-band oscillations are associated with a number of speech functions, including acoustic decoding (Hickok & Poeppel, 2007; Luo & Poeppel, 2007), speech segmentation (Ding & Simon, 2014; Doelling, Arnal, Ghitza, & Poeppel, 2014; Teng et al., 2018), and the activation of lexico-semantic representations (Bastiaansen, Linden, Keurs, Dijkstra, & Hagoort, 2005; Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008). On the other hand, theta-band oscillations can propagate progressively across the cortex owing to inter-regional phase-locking (Canolty & Knight, 2010). These coupled activities between multiple sites may regulate the fast spiking of single neurons, and hence give rise to coordinated, long-range communication across anatomically dispersed cortical areas (Canolty & Knight, 2010; Jensen & Colgin, 2007; von Stein & Sarnthein, 2000; Zhang, Watrous, Patel, & Jacobs, 2018). The current dissertation further revealed that theta-band oscillations can spontaneously adjust their large-scale functional organization adapting to the structure of language input. Together, theta-band oscillations may have broad impact on language (and other general cognitive) processing at multiple temporal and spatial scales, presumably via phase-amplitude CFC with higher-frequency oscillations (see Section 2.1 for the temporal aspects of CFC). Thus, the contribution of CFC on (continuous) spoken and written language processing needs to be drawn into attention in future research.

### 2.2.3 Supra-modality of supra-syllabic tracking

Despite a growing understanding of the functional relevance of slow cortical oscillations for hierarchical speech processing, our knowledge of oscillatory activities during reading is still limited. Therefore in **Chapter 5**, we set out to investigate the cortical tracking of hierarchical structures in written language, and compared it with spoken language processing. As predicted, the cortical tracking of physically presented syllables revealed a modality-dependent spatial distribution of responses. That is, the anterior scalp regions were more sensitive to the spoken than written syllables, while the posterior part of the brain showed

stronger cortical tracking of written compared to spoken syllables. These findings reflect a sensory entrainment to the rhythmic input and align with prior research considering syllables as building blocks to encode and integrate low-level sensory features for further language-specific analyses, such as phonological and lexical processing (Carreiras et al., 2009; Hickok & Poeppel, 2007). We also noticed that the syllable-rate tracking at a few parietal channels situated between the two modality-selective regions was comparable across sensory modalities. Since the inferior parietal cortex has been associated with cross-modal sensory integration (Rohe, Ehlis, & Noppeney, 2019; Senkowski, Schneider, Foxe, & Engel, 2008), it could be one of the sites storing heteromodal linguistic representations (Binder, Desai, Graves, & Conant, 2009; Pei et al., 2021; Raij, Uutela, & Hari, 2000). It has been further shown that this region is involved in the learning and retrieval of grapheme-phoneme mappings (Romanovska & Bonte, 2021; Xu, Kolozsvari, Oostenveld, & Hamalainen, 2020; Younger & Booth, 2018) and plays a critical role in reading development across languages (Liebig et al., 2017; Tan, Laird, Li, & Fox, 2005).

Moreover, we found that the cortical tracking of spoken and written word structures converged in the anterior scalp regions, suggesting a relatively supra-modal mechanism for supra-syllabic (word) processing. As proposed in **Chapter 5**, two non-mutually exclusive models could explain such supra-modal effects of word tracking, namely an "early integration" model and a "late co-activation model". The early integration model suggests that the internal parsing of written words is built upon the existing mechanisms for spoken word processing. As revealed by widespread syllable-tracking responses in both modalities, letter strings can readily activate the corresponding speech sounds (and vice versa) (Blomert & Froyen, 2010; Froyen, Bonte, van Atteveldt, & Blomert, 2009). Therefore, the product of written word parsing might be essentially the same as that of spoken word parsing, and thus manifest itself as overlapped cortical responses in the auditory-sensitive anterior scalp region. However, this model cannot explain the significant word-tracking effect observed in a separate set of posterior channels that specifically responded to the written words. This implies that written syllables can first be spontaneously grouped into meaningful chunks, as reported in studies on the hierarchical tracking of non-linguistic visual stimuli (Henin et al., 2021), and then directly access the amodal representation of word identities and semantic information stored in the anterior part of the brain (Booth

et al., 2002; Deniz et al., 2019; Lau et al., 2008; Ralph, Jefferies, Patterson, & Rogers, 2017; Voss & Federmeier, 2011). It has been found that the anteriorly located higher associative and heteromodal cortices, e.g., the inferior frontal gyrus, contribute to the decoding of semantic/conceptual information, irrespective of stimulus type (e.g., words, pictures) and input modality (Kaplan, Man, & Greening, 2015; Keitel, Gross, & Kayser, 2020). Accordingly, we termed this alternative interpretation of the supra-modal word tracking effect as the "late co-activation" model. Just like the dual routes for reading, the two models proposed here may both be at work during the hierarchical tracking of spoken and written language structures, whereas their relative contribution may vary across individuals depending on the participants' reading skills (Kast, Elmer, Jancke, & Meyer, 2010; Ziegler & Goswami, 2005). It thus fuels our interest to investigate the cortical tracking of written language structures in beginning and struggling readers in future studies.

## 2.3 Altered slow cortical oscillations for supra-syllabic parsing in dyslexia

Another important vein of this dissertation was to investigate how slow cortical tracking of supra-syllabic structures is associated with atypical development of reading and phonological skills in dyslexia. With a focus on spoken language, we found that although the pseudoword tracking of adult dyslexic readers gradually builds up with increasing exposure to the statistical structures, it occurs at a significantly slower pace compared to typical readers (**Chapter 3**). Moreover, the cortical tracking of word structures elicited a stronger shift toward a more integrated topology (relative to syllable tracking) in the theta-band network in dyslexic readers, characterized by an increased engagement of right frontal cortex (**Chapter 4**). Pooled across typical and dyslexic readers, correlational analyses further indicated that individuals with lower reading and/or phonological skills tended to (1) demonstrate less efficient cortical tracking of word-like structures during statistical learning (**Chapter 3**); (2) rely more strongly on larger and familiar units (i.e., the real words in our study) in the hierarchy for speech processing (**Chapter 3**); and (3) employ a more integrated theta-band network for word tracking (**Chapter 4**). These findings are generally in line with the temporal sampling framework (TSF) of dyslexia and may extend this theory to include the influence of slow oscillations on speech processing in a supra-syllabic time window.

According to TSF, the dyslexic brain entrains less precisely to slow temporal information in the speech signal, e.g., at prosodic (delta) and syllabic (theta) rates (Goswami, 2011; Goswami & Leong, 2013; Hämäläinen, Salminen, & Leppänen, 2013; Lallier et al., 2017). Such deficits may disrupt the development of fine-grained phonological representations even before a child starts to learn to read, and may affect the acquisition of grapheme-phoneme mappings later on (Goswami, 2011; Peelle & Davis, 2012). Our results showed that the capacity of dyslexic readers to track meaningless word-like higher-order structures was also reduced. This was associated with less consistent phase-locking of slow cortical oscillations to the fluctuations in transitional probabilities, which may lead to unstable representation of speech sounds at different levels (Hornickel & Kraus, 2013), such as inaccurate extraction of auditory word forms (Zhang, Riecke, & Bonte, 2021), impaired sampling of constituting phoneme (clusters) and phonemic features (Bonte, Poelmans, & Blomert, 2007; Di Liberto et al., 2018; Noordenbos, Segers, Mitterer, Serniclaes, & Verhoeven, 2013), as well the long-term development of phonemic categories (Vandermosten, Wouters, Ghesquiere, & Golestani, 2019). Such less specialized temporal sampling/parsing functions may render speech tracking a rather demanding process for dyslexic readers and thus requires a more integrated network organization. As stated in Section 2.2.2, when engaging in tasks that provoke active efforts, the brain network topology is likely to show enhanced global interconnectivity and an increased number of hub nodes connecting functionally specialized modules (Finc et al., 2017; Shine et al., 2016; Vourkas et al., 2014). Therefore, our observation of a more integrated theta-network topology in dyslexic readers may reflect a costly, sub-optimal functional organization of brain networks, responding to increased cognitive demands induced by syllable-to-word integration. In contrast, two recent studies reported a reduced integration in the theta (and delta) network topology in dyslexic readers when they listened to stories (Mandke et al., 2022; child study) or learned to bind speech sounds with artificial letters (Fraga-González et al., 2021). It is suggested that the functional organization of brain networks dynamically changes across rest and various task states (Bullmore & Sporns, 2012; Hutchison et al., 2013; Shine et al., 2016), and that network integration continues to increase with brain maturation until early adulthood (Cao, Huang, Peng, Dong, & He, 2016; Smit, de Geus, Boersma, Boomsma, & Stam, 2016; Uddin, Supekar, Ryali, & Menon, 2011). Hence, although our study extended the TSF to consider not only slow oscillatory activities but also their large-scale topology during hierarchical speech processing,

further research is required to achieve a more systematic and state/task-dependent view of altered network organization associated with dyslexia. It is also of interest to investigate how local and large-scale oscillatory activities interact to modulate the temporal sampling/parsing of hierarchical language structures, and disentangle the relatively short-term effects (e.g., learning) from longer-term changes (e.g., brain maturation, accumulating experience) over the developmental course of learning to read.

In addition to atypical temporal evolution and spatial organization of slow cortical oscillations, we also observed peculiar strategies for speech-structure tracking associated with inferior reading/phonological skills. First, participants who were less efficient in rapid symbol naming showed stronger real word tracking (**Chapter 3**). This suggests a greater reliance on larger and familiar units in the language hierarchy during speech processing, potentially due to a bias toward internal (lexical) knowledge over their quickly decaying representations of sensory input (Hancock, Pugh, & Hoeft, 2017; Jaffe-Dax, Kimel, & Ahissar, 2018; Perrachione et al., 2016). Second, deficient readers relied on more bilaterally and more anteriorly distributed brain circuits during speech-structure tracking (**Chapter 3 and 4**), in accord with previous neuroimaging research in dyslexia (Cao et al., 2016; Finn et al., 2014; Mao, Liu, Perkins, & Cao, 2021; Qi et al., 2016). The bilateral frontal cortices that dyslexic readers additionally employ for speech processing have been identified as part of a multi-demand system supporting a range of domain-general cognitive functions, such as working memory, executive control and mental programming (Diachek, Blank, Siegelman, Affourtit, & Fedorenko, 2020; Duncan, 2010; Fedorenko, Duncan, & Kanwisher, 2013). As such, both strategies of our adult dyslexic readers, could be interpreted as a compensatory mechanism (Hoeft et al., 2011; Shaywitz & Shaywitz, 2005). These mechanisms could counterbalance their language (and sensory) processing deficits (Ligges, Ungureanu, Ligges, Blanz, & Witte, 2010), by e.g., facilitating the representation and maintenance of phonological and lexical information (Margolis et al., 2020; Vasic, Lohr, Steinbrink, Martin, & Wolf, 2008; Xu, Yang, Siok, & Tan, 2015). It should be investigated in future developmental (and longitudinal) studies whether the alterations observed here indeed emerge as compensatory mechanisms after the onset of reading difficulties, or manifest themselves early on and lead to specific speech/reading impairments.

## 3 Paradigm shift and outlook

The research reported in this dissertation concentrated on the cortical tracking of hierarchical structure in spoken and written language, and related such mechanisms to (a)typical reading development. As discussed above, our findings add empirical support to the multi-time resolution model of cortical speech processing (Giraud & Poeppel, 2012; Poeppel, Idsardi, & van Wassenhove, 2008) and (an extended version of) the temporal sampling framework for dyslexia (Goswami, 2011; Lallier et al., 2017). In addition, our studies invite paradigm shifts toward focusing on temporally more incremental (learning course), spatially more large-scale, methodologically more causal and translational, and more ecologically valid aspects to further our understanding of the neurocognitive processes of spoken and written language processing. Each of these aspects are explained in the following paragraphs.

First, we zoomed into the incremental temporal trajectory of pseudoword learning and found slower establishment of cortical tracking along with poor explicit recognition in dyslexic readers (**Chapter 3**). This aligns with prior work indicating a domain-general statistical learning difficulty in dyslexia (Schmalz et al., 2017; Singh & Conway, 2021), characterized by reduced sensitivity to various statistical regularities embedded in the language hierarchy, such as phonotactic probabilities (Bonte et al., 2007; Noordenbos et al., 2013) and artificial grammar (Pothos & Kirk, 2004; Van Witteloostuijn, Boersma, Wijnen, & Rispens, 2017), and also those in non-linguistic temporal sequences (Howard, Howard, Japikse, & Eden, 2006; Lum, Ullman, & Conti-Ramsden, 2013). However, research thus far rarely addressed the incremental learning gains and the associated changes in the neural activity while this implicit learning process took place. Combining learning tasks with simultaneous neuroimaging provides objective measures to index how brain circuits dynamically fine-tune their activities and interconnectivities in response to the incoming stimuli, which is otherwise difficult to be assessed merely based on the learning outcome. This approach can also be used to investigate other reading-related learning processes whose neural mechanisms are not well understood, for instance, the statistical learning of orthographic regularities (Tong, Zhang, & He, 2020; Tong, Wang, & Tong, 2020) and the associative learning of print-speech sound mappings (Hämäläinen, Parviainen, Hsu, & Salmelin, 2019; Romanovska & Bonte, 2021; Xu et al., 2020). Furthermore, applying such an approach over a

developmental course may provide learning-based precursors that predict the long-term plasticity related to the acquisition of specific reading/phonological skills.

Second, exploiting recent developments in graph theoretical analysis that characterizes spatially more large-scale aspects, we observed a reorganization of functional brain networks associated with changes in the internal (and external) state (i.e., syllable versus word tracking; **Chapter 4**). Only recently, has there been an increase in studies starting to explore whether and how the large-scale network topology of dyslexic readers may deviate from the typically reading controls during reading-related tasks. This includes speech tracking (Mandke et al., 2022; Zhang, Riecke, Fraga-González, & Bonte, 2022), phonological judgment (Mao et al., 2021; Vourkas et al., 2011; Yang & Tan, 2020; J. Zhang et al., 2021), visual/orthographic processing (Dushanova & Tsokov, 2021; Taskov & Dushanova, 2020; Yang & Tan, 2020) and letter-speech sound binding (Fraga-González et al., 2021). Together, these studies shifted the focus from *where* in the brain a dyslexia-related deficit resides to *how* dyslexia is associated with the deficient coordination of segregated neural circuits facing the challenges imposed by complex behavioral tasks. Even though not conclusive, it has been suggested that changes in interconnectivity among brain regions might be a more sensitive indicator of complex cognitive processes such as reading than changes in the magnitude of local brain activation (Kim et al., 2021; Lee, Yoon, & Lee, 2020; Sevel, Craggs, Price, Staud, & Robinson, 2015). Therefore, in future work, it is interesting to increase our scope about how local and large-scale brain activities are modulated in more diverse and dynamic contexts, e.g., during the statistical learning of pseudoword structures as in **Chapter 3**, and how these mechanisms are altered in dyslexia.

Third, we utilized non-invasive brain stimulation (NIBS) to investigate the causal contribution of slow cortical oscillations to acoustic processing (**Chapter 2**). NIBS techniques, which are considerably easy and inexpensive to apply and well tolerated by human subjects, open up new avenues in cognitive neuroscience to validate theories about brain-behavioral relationships generated from prior correlational evidence, by directly manipulating brain functioning (Polanía, Nitsche, & Ruff, 2018; Vosskuhl, Strüber, & Herrmann, 2018). Meanwhile, the NIBS approach is uniquely valuable in translational research due to its potential to identify causal targets for clinical intervention (Begemann, Brand, Ćurčić-Blake, Aleman, & Sommer, 2020; Siddiqi, Kording, Parvizi, & Fox, 2022), for review on the

implications in neurodevelopmental disorders, see Finisguerra, Borgatti, and Urgesi (2019) and Santos et al. (2021). Despite the null results in our study, Turker and Hartwigsen (2021) systematically reviewed 15 NIBS studies to date in children and adults with dyslexia and reported generally positive effects of reading improvement (e.g., better (pseudo)word and text reading) after behavioral interventions combined with NIBS. This stirs our interest to involve NIBS in future studies, especially learning-related research. For instance, by applying word-rate tACS during the statistical learning of pseudowords, we may be able to test whether the cortical oscillations induced by external force would facilitate the extraction of implicit word structures. Alternatively, as revealed in a recent study, we may apply inhibitory theta-burst stimulation to the left dorsolateral prefrontal cortex to unlock the "bottleneck" imposed by the cognitive control system in the adult brain (which prioritizes access to explicit over implicit memories) and boost the participants' implicit word-segmentation performances (Smalle, Daikoku, Szmalec, Duyck, & Möttönen, 2022). More importantly, it is useful to investigate whether dyslexic readers would benefit from NIBS targeting either the oscillatory mechanisms tracking the perceptual input and internally constructed concepts, or other domain-general mechanisms such as working memory and cognitive control, during a variety of learning processes.

Finally, we provided an important first extension to the study of oscillatory mechanisms associated with the hierarchical processing of written language, using lab-controlled, simplified stimuli (**Chapter 5**). It is a useful first step towards identifying the temporal component of written language structure parsing, as natural reading processes additionally involve a spatial(-temporal) component associated with fast eye movements (and shifts of attention) to voluntarily sample the orthographic information in a serial manner (Archer et al., 2020; Vidyasagar, 2013). Thus, during natural reading, theta oscillations may guide eye movements to shift the focus of attention, while low gamma oscillations may control the serial sampling of text that falls under the attentional spotlight (Archer et al., 2020). Therefore, an interesting but challenging question to investigate in future research is how fast and slow cortical oscillations interact in iterative cycles of sampling and parsing (via e.g., CFC) (Lallier et al., 2017) to achieve fluent comprehension during natural reading. On the other hand, it is also noteworthy that the word-tracking responses observed in our studies, irrespective of the input modality, may not be entirely driven by existing word knowledge. This is because our stimuli were

created by repeating four tri-syllabic words, resulting in constant transitional probabilities within each word (i.e., 1.0) and across word boundaries (i.e., 0.33). Meanwhile, all stimuli were presented in an isochronous fashion, which is not the case with natural language. In other words, our results are also likely to be related to the extraction of statistical regularities and adaptations to rhythmic sensory input in specially constructed sequences (Batterink & Paller, 2017; Buiatti et al., 2009; Frost et al., 2015). Thus, the current findings on hierarchical language tracking need to be tested in more ecologically valid situations, such as natural narrative speech and text comprehension.

## 4 Conclusion

This dissertation investigated the cortical tracking mechanisms of spoken and written language structures, and their associations with (a)typical reading development. Specifically, our studies focused on the contribution of slow cortical oscillations to low-level sensory sampling in a sub-syllabic time window, and to higher-level cognitive parsing at the supra-syllabic scale. Although we observed null effects of 4-Hz tACS on sound onset perception (**Chapter 2**), we call on future investigations on an indirect role of slow cortical oscillations, presumably via a cross-frequency modulation of higher frequency oscillations, on the development of (categorical) representation of phonemes and syllables. In the subsequent chapters, taking advantage of (frequency-tagged) EEG responses, we demonstrated (1) a gradual establishment of slow-rate phase synchronization tracking novel pseudoword structures acquired via implicit statistical learning of available regularities in speech (**Chapter 3**); (2) that the cortical tracking of familiar words triggers a shift of network topology into a more integrated theta-band network, compared to syllable tracking (**Chapter 4**); and (3) that hierarchically organized cortical tracking also applies to written language, with a modality-specific processing of physically presented syllables, in addition to a relatively supra-modal tracking of internally constructed word structures (**Chapter 5**). Together, these results suggest that hierarchical language tracking, especially at the supra-syllabic level, is a dynamic, functionally coordinated and relatively amodal process modulated by slow cortical oscillations.

We also investigated whether and how the slow cortical tracking of speech structures is altered in individuals with dyslexia, who showed (1) a significantly slower build-up of pseudoword tracking (**Chapter 3**) and (2) a stronger shift toward a more integrated theta-network topology accompanied by an increased engagement of the right frontal site during syllable-to-word integration (**Chapter 4**), compared to the typically reading controls. These findings may extend the temporal sampling framework of dyslexia to include the influence of slow oscillations on speech processing in a supra-syllabic time window, taking into account aspects such as the temporal evolution and large-scale network organization. Moreover, we observed a set of potentially compensatory mechanisms in adults with dyslexia, including a greater reliance on larger and familiar linguistic units, along with more bilaterally and anteriorly distributed brain substrates for speech processing. Developmental studies in children are needed to probe into the long-term changes in the functional organization of (slow) oscillatory activities, and their association with the trajectory of reading acquisition. This may in turn inspire the development of tailored intervention programs for individuals with developmental dyslexia.

# References

Abla, D., Katahira, K., & Okanoya, K. (2009). On-line assessment of statistical learning by event-related potentials. *Journal of Cognitive Neuroscience, 20*(6), 952-964. https://doi.org/10.1162/jocn.2008.20058

Abrams, D. A., Nicol, T., Zecker, S., & Kraus, N. (2009). Abnormal cortical processing of the syllable rate of speech in poor readers. *Journal of Neuroscience, 29*(24), 7686-7693. https://doi.org/10.1523/jneurosci.5242-08.2009

Ackermann, H., Mathiak, K., & Ivry, R. B. (2004). Temporal organization of "internal speech" as a basis for cerebellar modulation of cognitive functions. *Behavioral and Cognitive Neuroscience Reviews, 3*(1), 14-22. https://doi.org/10.1177/1534582304263251

Ahissar, E., Nagarajan, S., Ahissar, M., Protopapas, A., Mahncke, H., & Merzenich, M. M. (2001). Speech comprehension is correlated with temporal response patterns recorded from auditory cortex. *Proceedings of the National Academy of Sciences, 98*(23), 13367-13372. https://doi.org/10.1073/pnas.201400998

Ahissar, M., Lubin, Y., Putter-Katz, H., & Banai, K. (2006). Dyslexia and the failure to form a perceptual anchor. *Nature Neuroscience, 9*(12), 1558-1564. https://doi.org/10.1038/nn1800

Ahveninen, J., Hämäläinen, M., Jääskeläinen, I. P., Ahlfors, S. P., Huang, S., Lin, F.-H., Raij, T., Sams, M., Vasios, C. E., & Belliveau, J. W. (2011). Attention-driven auditory cortex short-term plasticity helps segregate relevant sounds from noise. *Proceedings of the National Academy of Sciences, 108*(10), 4182-4187. https://doi.org/10.1073/pnas.1016134108

Alekseichuk, I., Turi, Z., Amador de Lara, G., Antal, A., & Paulus, W. (2016). Spatial working memory in humans depends on theta and high gamma synchronization in the prefrontal cortex. *Current Biology, 26*(12), 1513-1521. https://doi.org/10.1016/j.cub.2016.04.035

Alexandrou, A. M., Saarinen, T., Kujala, J., & Salmelin, R. (2018). Cortical tracking of global and local variations of speech rhythm during connected natural speech perception. *Journal of Cognitive Neuroscience, 30*(11), 1704-1719. https://doi.org/10.1162/jocn_a_01295

Alizadeh, S., Jamalabadi, H., Schonauer, M., Leibold, C., & Gais, S. (2017). Decoding cognitive concepts from neuroimaging data using multivariate pattern analysis. *NeuroImage, 159*, 449-458. https://doi.org/10.1016/j.neuroimage.2017.07.058

Anderson, M. J., & Robinson, J. (2001). Permutation tests for linear models. *Australian & New Zealand Journal of Statistics, 43*(1), 75-88. https://doi.org/10.1111/1467-842X.00156

Araújo, S., & Faísca, L. (2019). A meta-analytic review of naming-speed deficits in developmental dyslexia. *Scientific Studies of Reading, 23*(5), 349-368. https://doi.org/10.1080/10888438.2019.1572758

Aravena, S., Snellings, P., Tijms, J., & Van der Molen, M. W. (2013). A lab-controlled simulation of a letter-speech sound binding deficit in dyslexia. *Journal of Experimental Child Psychology, 115*(4), 691-707. https://doi.org/10.1016/j.jecp.2013.03.009

Arciuli, J., & Simpson, I. C. (2012). Statistical learning is related to reading ability in children and adults. *Cognitive Science, 36*(2), 286-304. https://doi.org/10.1111/j.1551-6709.2011.01200.x

Archer, K., Pammer, K., & Vidyasagar, T. R. (2020). A temporal sampling basis for visual processing in developmental dyslexia. *Frontiers in Human Neuroscience, 14*, 213. https://doi.org/10.3389/fnhum.2020.00213

Asamoah, B., Khatoun, A., & Mc Laughlin, M. (2019). Analytical bias accounts for some of the reported effects of tACS on auditory perception. *Brain Stimulation, 12*(4), 1001-1009. https://doi.org/10.1016/j.brs.2019.03.011

Aslin, R. N. (2017). Statistical learning: A powerful mechanism that operates by mere exposure. *Wiley Interdisciplinary Reviews in Cognitive Science, 8*, e1373. https://doi.org/10.1002/wcs.1373

Atiani, S., Elhilali, M., David, S. V., Fritz, J. B., & Shamma, S. A. (2009). Task difficulty and performance induce diverse adaptive patterns in gain and shape of primary auditory cortical receptive fields. *Neuron, 61*(3), 467-480. https://doi.org/10.1016/j.neuron.2008.12.027

Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences, 6*(1), 47-52. https://doi.org/10.1016/s1364-6613(00)01819-2

Bailey, S. K., Aboud, K. S., Nguyen, T. Q., & Cutting, L. E. (2018). Applying a network framework to the neurobiology of reading and dyslexia. *Journal of Neurodevelopmental Disorders, 10*, 37. https://doi.org/10.1186/s11689-018-9251-z

Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering event structure in continuous narrative perception and memory. *Neuron, 95*(3), 709-721. https://doi.org/10.1016/j.neuron.2017.06.041

Baltus, A., & Herrmann, C. S. (2015). Auditory temporal resolution is linked to resonance frequency of the auditory cortex. *International Journal of Psychophysiology, 98*(1), 1-7. https://doi.org/10.1016/j.ijpsycho.2015.08.003

Banai, K., & Ahissar, M. (2010). On the importance of anchoring and the consequences of its impairment in dyslexia. *Dyslexia, 16*(3), 240-257. https://doi.org/10.1002/dys.407

Banai, K., & Ahissar, M. (2018). Poor sensitivity to sound statistics impairs the acquisition of speech categories in dyslexia. *Language, Cognition and Neuroscience, 33*(3), 321-332. https://doi.org/10.1080/23273798.2017.1408851

Bassett, D. S., & Sporns, O. (2017). Network neuroscience. *Nature Neuroscience, 20*(3), 353-364. https://doi.org/10.1038/nn.4502

Bastiaansen, M. C. M., Linden, M. V. D., Keurs, M. T., Dijkstra, T., & Hagoort, P. (2005). Theta responses are involved in lexical — Semantic retrieval during language processing. *Journal of Cognitive Neuroscience, 17*(3), 530-541. https://doi.org/10.1162/0898929053279469

Bastiaansen, M. C. M., Magyari, L., & Hagoort, P. (2010). Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. *Journal of Cognitive Neuroscience, 22*(7), 1333-1347. https://doi.org/10.1162/jocn.2009.21283

Bastiaansen, M. C. M., Oostenveld, R., Jensen, O., & Hagoort, P. (2008). I see what you mean: Theta power increases are involved in the retrieval of lexical semantic information. *Brain and Language, 106*(1), 15-28. https://doi.org/10.1016/j.bandl.2007.10.006

Bastiaansen, M. C. M., van Berkum, J. J. A., & Hagoort, P. (2002). Syntactic processing modulates the θ rhythm of the human EEG. *NeuroImage, 17*(3), 1479-1492. https://doi.org/10.1006/nimg.2002.1275

Bastiaansen, M. C. M., van der Linden, M., ter Keurs, M., Dijkstra, T., & Hagoort, P. (2005). Theta responses are involved in lexical-semantic retrieval during language processing. *Journal of Cognitive Neuroscience, 17*(3), 530-541. https://doi.org/10.1162/0898929053279469

Batterink, L. J., & Paller, K. A. (2017). Online neural monitoring of statistical learning. *Cortex, 90*, 31-45. https://doi.org/10.1016/j.cortex.2017.02.004

Batterink, L. J., & Paller, K. A. (2019). Statistical learning of speech regularities can occur outside the focus of attention. *Cortex, 115*, 56-71. https://doi.org/10.1016/j.cortex.2019.01.013

Batterink, L. J., Reber, P. J., Neville, H. J., & Paller, K. A. (2015). Implicit and explicit contributions to statistical learning. *Journal of Memory and Language, 83*, 62-78. https://doi.org/10.1016/j.jml.2015.04.004

Begemann, M. J., Brand, B. A., Ćurčić-Blake, B., Aleman, A., & Sommer, I. E. (2020). Efficacy of non-invasive brain stimulation on cognitive functioning in brain disorders: A meta-analysis. *Psychological Medicine, 50*(15), 2465-2486. https://doi.org/10.1017/s0033291720003670

Beneventi, H., Tønnessen, F. E., Ersland, L., & Hugdahl, K. (2010). Working memory deficit in dyslexia: Behavioral and fMRI evidence. *International Journal of Neuroscience, 120*(1), 51-59. https://doi.org/10.3109/00207450903275129

Benitez-Burraco, A. (2010). Neurobiology and neurogenetics of dyslexia. *Neurologia, 25*(9), 563-581. https://doi.org/10.1016/S2173-5808(20)70105-7

Benjamin, L., Dehaene-Lambertz, G., & Fló, A. (2021). Remarks on the analysis of steady-state responses: Spurious artifacts introduced by overlapping epochs. *Cortex*. https://doi.org/10.1016/j.cortex.2021.05.023

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological), 57*(1), 289-300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bertels, J., San Anton, E., Boursain, E., Bulf, H., & Destrebecqz, A. (2021). Visual statistical learning in infancy: Discrimination of fine-grained regularities depends on early test trials. *Infancy*. https://doi.org/10.1111/infa.12445

Berwick, R. C., Friederici, A. D., Chomsky, N., & Bolhuis, J. J. (2013). Evolution, brain, and the nature of language. *Trends in Cognitive Sciences, 17*(2), 89-98. https://doi.org/10.1016/j.tics.2012.12.002

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19*(12), 2767-2796. https://doi.org/10.1093/cercor/bhp055

Bindman, L. J., Lippold, O. C. J., & Redfearn, J. W. T. (1962). Long-lasting changes in the level of the electrical activity of the cerebral cortex produced by polarizing currents. *Nature, 196*(4854), 584-585. https://doi.org/10.1038/196584a0

Bishop, D. V. M., Hardiman, M. J., & Barry, J. G. (2012). Auditory deficit as a consequence rather than endophenotype of specific language impairment: Electrophysiological evidence. *Plos One, 7*(5), e35851. https://doi.org/10.1371/journal.pone.0035851

Bishop, G. H. (1932). Cyclic changes in excitability of the optic pathway of the rabbit. *American Journal of Physiology-Legacy Content, 103*(1), 213-224. https://doi.org/10.1152/ajplegacy.1932.103.1.213

Black, J. M., Xia, Z. C., & Hoeft, F. (2017). Neurobiological bases of reading disorder part II: The importance of developmental considerations in typical and atypical reading. *Language and Linguistics Compass, 11*(10), e12252. https://doi.org/10.1111/lnc3.12252

Blau, V., Reithler, J., van Atteveldt, N., Seitz, J., Gerretsen, P., Goebel, R., & Blomert, L. (2010). Deviant processing of letters and speech sounds as proximate cause of reading failure: A functional

magnetic resonance imaging study of dyslexic children. *Brain, 133*(3), 868-879. https://doi.org/10.1093/brain/awp308

Blau, V., van Atteveldt, N., Ekkebus, M., Goebel, R., & Blomert, L. (2009). Reduced neural integration of letters and speech sounds links phonological and reading deficits in adult dyslexia. *Current Biology, 19*(6), 503-508. https://doi.org/10.1016/j.cub.2009.01.065

Blau, V., van Atteveldt, N., Formisano, E., Goebel, R., & Blomert, L. (2008). Task-irrelevant visual letters interact with the processing of speech sounds in heteromodal and unimodal cortex. *European Journal of Neuroscience, 28*(3), 500-509. https://doi.org/10.1111/j.1460-9568.2008.06350.x

Blomert, L. (2011). The neural signature of orthographic-phonological binding in successful and failing reading development. *NeuroImage, 57*(3), 695-703. https://doi.org/10.1016/j.neuroimage.2010.11.003

Blomert, L., & Froyen, D. (2010). Multi-sensory learning and learning to read. *International Journal of Psychophysiology, 77*(3), 195-204. https://doi.org/10.1016/j.ijpsycho.2010.06.025

Boemio, A., Fromm, S., Braun, A., & Poeppel, D. (2005). Hierarchical and asymmetric temporal sensitivity in human auditory cortices. *Nature Neuroscience, 8*(3), 389-395. https://doi.org/10.1038/nn1409

Boersma, M., Smit, D. J. A., Boomsma, D. I., De Geus, E. J. C., Delemarre-Van De Waal, H. A., & Stam, C. J. (2013). Growing trees in child brains: Graph theoretical analysis of electroencephalography-derived minimum spanning tree in 5- and 7-year-old children reflects brain maturation. *Brain Connectivity, 3*(1), 50-60. https://doi.org/10.1089/brain.2012.0106

Boersma, P. & Weenink, D. (2018). Praat: doing phonetics by computer. *Version 6.0.37*, retrieved 5 February 2018 from http://www.praat.org/

Boets, B., Op de Beeck, H. P., Vandermosten, M., Scott, S. K., Gillebert, C. R., Mantini, D., Bulthé, J., Sunaert, S., Wouters, J., & Ghesquière, P. (2013). Intact but less accessible phonetic representations in adults with dyslexia. *Science, 342*(6163), 1251-1254. https://doi.org/10.1126/science.1244333

Bonner, M. F., Peelle, J. E., Cook, P. A., & Grossman, M. (2013). Heteromodal conceptual processing in the angular gyrus. *NeuroImage, 71*, 175-186. https://doi.org/10.1016/j.neuroimage.2013.01.006

Bonte, M., Correia, J. M., Keetels, M., Vroomen, J., & Formisano, E. (2017). Reading-induced shifts of perceptual speech representations in auditory cortex. *Scientific Reports, 7*, 5143. https://doi.org/10.1038/s41598-017-05356-3

Bonte, M., Poelmans, H., & Blomert, L. (2007). Deviant neurophysiological responses to phonological regularities in speech in dyslexic children. *Neuropsychologia, 45*(7), 1427-1437. https://doi.org/10.1016/j.neuropsychologia.2006.11.009

Booth, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2002). Modality independence of word comprehension. *Human Brain Mapping, 16*(4), 251-261. https://doi.org/10.1002/hbm.10054

Booth, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2004). Development of brain mechanisms for processing orthographic and phonologic representations. *Journal of Cognitive Neuroscience, 16*(7), 1234-1249. https://doi.org/10.1162/0898929041920496

Bosseler, A., Taulu, S., Pihko, E., Mäkelä, J., Imada, T., Ahonen, A., & Kuhl, P. (2013). Theta brain rhythms index perceptual narrowing in infant speech perception. *Frontiers in Psychology, 4*, 690. https://doi.org/10.3389/fpsyg.2013.00690

Braddick, O., Birtles, D., Wattam-Bell, J., & Atkinson, J. (2005). Motion- and orientation-specific cortical responses in infancy. *Vision Research, 45*(25-26), 3169-3179. https://doi.org/10.1016/j.visres.2005.07.021

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*(4), 433-436. https://doi.org/10.1163/156856897x00357

Bressler, S. L., & Menon, V. (2010). Large-scale brain networks in cognition: Emerging methods and principles. *Trends in Cognitive Sciences, 14*(6), 277-290. https://doi.org/10.1016/j.tics.2010.04.004

Brus, B. T., & Voeten, M. J. M. (1973). *Een-minuut-test: vorm A en B; schoolvorderingentest voor de technische leesvaardigheid, bestemd voor het tweede tot en met het zesde leerjaar van het basisonderwijs; verantwoording en handleiding*: Berkhout.

Buiatti, M., Peña, M., & Dehaene-Lambertz, G. (2009). Investigating the neural correlates of continuous speech computation with frequency-tagged neuroelectric responses. *NeuroImage, 44*(2), 509-519. https://doi.org/10.1016/j.neuroimage.2008.09.015

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience, 13*(2), 400-404. https://doi.org/10.1111/j.1460-9568.2001.01385.x

Bullmore, E., & Sporns, O. (2009). Complex brain networks: Graph theoretical analysis of structural and functional systems. *Nature Reviews Neuroscience, 10*(3), 186-198. https://doi.org/10.1038/nrn2575

Bullmore, E., & Sporns, O. (2012). The economy of brain network organization. *Nature Reviews Neuroscience, 13*(5), 336-349. https://doi.org/10.1038/nrn3214

Burle, B., Spieser, L., Roger, C., Casini, L., Hasbroucq, T., & Vidal, F. (2015). Spatial and temporal resolutions of EEG: Is it really black and white? A scalp current density view. *International Journal of Psychophysiology, 97*(3), 210-220. https://doi.org/10.1016/j.ijpsycho.2015.05.004

Busch, N. A., & VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proceedings of the National Academy of Sciences, 107*(37), 16048-16053. https://doi.org/10.1073/pnas.1004801107

Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science, 304*(5679), 1926-1929. https://doi.org/10.1126/science.1099745

Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2006). High gamma power is phase-locked to theta oscillations in human neocortex. *Science, 313*(5793), 1626-1628. https://doi.org/10.1126/science.1128115

Canolty, R. T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. *Trends in Cognitive Sciences, 14*(11), 506-515. https://doi.org/10.1016/j.tics.2010.09.001

Cao, F., Yan, X., Wang, Z., Liu, Y. N., Wang, J., Spray, G. J., & Deng, Y. (2017). Neural signatures of phonological deficits in Chinese developmental dyslexia. *NeuroImage, 146*, 301-311. https://doi.org/10.1016/j.neuroimage.2016.11.051

Cao, M., Huang, H., Peng, Y., Dong, Q., & He, Y. (2016). Toward developmental connectomics of the human brain. *Frontiers in Neuroanatomy, 10*, 25. https://doi.org/10.3389/fnana.2016.00025

Carreiras, M., Riba, J., Vergara, M., Heldmann, M., & Münte, T. F. (2009). Syllable congruency and word frequency effects on brain activation. *Human Brain Mapping, 30*(9), 3079-3088. https://doi.org/10.1002/hbm.20730

Casini, L., Pech-Georgel, C., & Ziegler, J. C. (2018). It's about time: Revisiting temporal processing deficits in dyslexia. *Developmental Science, 21*(2), e12530. https://doi.org/10.1111/desc.12530

Castellanos, N.P., & Makarov, V.A. (2006). Recovering EEG brain signals: Artifact suppression with wavelet enhanced independent component analysis. *Journal of Neuroscience Methods, 158*, 300–312. https://doi.org/10.1016/j.jneumeth.2006.05.033

Chen, Y., Jin, P., & Ding, N. (2020). The influence of linguistic information on cortical tracking of words. *Neuropsychologia, 148*, 107640. https://doi.org/10.1016/j.neuropsychologia.2020.107640

Choi, D., Batterink, L. J., Black, A. K., Paller, K. A., & Werker, J. F. (2020). Preverbal infants discover statistical word patterns at similar rates as adults: Evidence from neural entrainment. *Psychological Science, 31*(9), 1161-1173. https://doi.org/10.1177/0956797620933237

Christiansen, M. H., Conway, C. M., & Onnis, L. (2012). Similar neural correlates for language and sequential learning: Evidence from event-related brain potentials. *Language and Cognitive Processes, 27*(2), 231-256. https://doi.org/10.1080/01690965.2011.606666

Chung, K. K. H., McBride-Chang, C., Wong, S. W. L., Cheung, H., Penney, T. B., & Ho, C. S. H. (2008). The role of visual and auditory temporal processing for Chinese children with developmental dyslexia. *Annals of Dyslexia, 58*(1), 15-35. https://doi.org/10.1007/s11881-008-0015-4

Chyl, K., Kossowski, B., Debska, A., Luniewska, M., Banaszkiewicz, A., Zelechowska, A., Frost, S. J., Mencl, W. E., Marchewka, A., Pugh, K. R., & Jednorog, K. (2018). Prereader to beginning reader: Changes induced by reading acquisition in print and speech brain networks. *Journal of Child Psychology and Psychiatry, 59*(1), 76-87. https://doi.org/10.1111/jcpp.12774

Clerget, E., Poncin, W., Fadiga, L., & Olivier, E. (2012). Role of Broca's area in implicit motor skill learning: Evidence from continuous theta-burst magnetic stimulation. *Journal of Cognitive Neuroscience, 24*(1), 80-92. https://doi.org/10.1162/jocn_a_00108

Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain, 125*(5), 1054-1069. https://doi.org/10.1093/brain/awf094

Coltheart, M., Curtis, B., Atkins, P., & Haller, M. (2013). *Models of reading aloud: Dual-route and parallel-distributed-processing approaches*: Psychology Press.

Cone, N. E., Burman, D. D., Bitan, T., Bolger, D. J., & Booth, J. R. (2008). Developmental changes in brain regions involved in phonological and orthographic processing during spoken language processing. *NeuroImage, 41*(2), 623-635. https://doi.org/10.1016/j.neuroimage.2008.02.055

Cui, Z. X., Xia, Z. C., Su, M. M., Shu, H., & Gong, G. L. (2016). Disrupted white matter connectivity underlying developmental dyslexia: A machine learning approach. *Human Brain Mapping, 37*(4), 1443-1458. https://doi.org/10.1002/hbm.23112

Cunillera, T., Càmara, E., Toro, J. M., Marco-Pallares, J., Sebastián-Galles, N., Ortiz, H., Pujol, J., & Rodríguez-Fornells, A. (2009). Time course and functional neuroanatomy of speech segmentation in adults. *NeuroImage, 48*(3), 541-553. https://doi.org/10.1016/j.neuroimage.2009.06.069

Cutini, S., Szucs, D., Mead, N., Huss, M., & Goswami, U. (2016). Atypical right hemisphere response to slow temporal modulations in children with developmental dyslexia. *NeuroImage, 143*, 40-49. https://doi.org/10.1016/j.neuroimage.2016.08.012

Daikoku, T. (2018). Neurophysiological markers of statistical learning in music and language: Hierarchy, entropy, and uncertainty. *Brain Sciences, 8*(6). https://doi.org/10.3390/brainsci8060114

De Jong, R., Toffanin, P., & Harbers, M. (2010). Dynamic crossmodal links revealed by steady-state responses in auditory–visual divided attention. *International Journal of Psychophysiology, 75*(1), 3-15. https://doi.org/10.1016/j.ijpsycho.2009.09.013

De Vos, A., Vanvooren, S., Vanderauwera, J., Ghesquière, P., & Wouters, J. (2017). Atypical neural synchronization to speech envelope modulations in dyslexia. *Brain and Language, 164*, 106-117. https://doi.org/10.1016/j.bandl.2016.10.002

Deco, G., Tononi, G., Boly, M., & Kringelbach, M. L. (2015). Rethinking segregation and integration: Contributions of whole-brain modelling. *Nature Reviews Neuroscience, 16*(7), 430-439. https://doi.org/10.1038/nrn3963

Dehaene-Lambertz, G., Monzalvo, K., & Dehaene, S. (2018). The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. *PLOS Biology, 16*(3), e2004103. https://doi.org/10.1371/journal.pbio.2004103

Dehaene, S. (2010). *Reading in the brain: The new science of how we read*. London, United Kingdom: Penguin Books.

Dehaene, S., & Changeux, J.-P. (1997). A hierarchical neuronal network for planning behavior. *Proceedings of the National Academy of Sciences, 94*(24), 13293-13298. https://doi.org/10.1073/pnas.94.24.13293

Dehaene, S., Cohen, L., Morais, J., & Kolinsky, R. (2015). Illiterate to literate: Behavioural and cerebral changes induced by reading acquisition. *Nature Reviews Neuroscience, 16*, 234-244. https://doi.org/10.1038/nrn3924

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition, 79*(1-2), 1-37. https://doi.org/10.1016/s0010-0277(00)00123-2

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9-21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Deniz, F., Nunez-Elizalde, A. O., Huth, A. G., & Gallant, J. L. (2019). The representation of semantic information across human cerebral cortex during listening versus reading is invariant to stimulus modality. *The Journal of Neuroscience, 39*(39), 7722-7736. https://doi.org/10.1523/jneurosci.0675-19.2019

Depessemier, P., & Andries, C. (2009). *GL&SCHR: dyslexie bij+ 16-jarigen: test voor Gevorderd Lezen & SCHRijven*: Garant.

Di Liberto, G. M., O'Sullivan, J. A., & Lalor, E. C. (2015). Low-frequency cortical entrainment to speech reflects phoneme-level processing. *Current Biology, 25*(19), 2457-2465. https://doi.org/10.1016/j.cub.2015.08.030

Di Liberto, G. M., Peter, V., Kalashnikova, M., Goswami, U., Burnham, D., & Lalor, E. C. (2018). Atypical cortical entrainment to speech in the right hemisphere underpins phonemic deficits in dyslexia. *NeuroImage, 175*, 70-79. https://doi.org/10.1016/j.neuroimage.2018.03.072

Diachek, E., Blank, I., Siegelman, M., Affourtit, J., & Fedorenko, E. (2020). The domain-general multiple demand (MD) network does not support core aspects of language comprehension: A large-scale fMRI investigation. *The Journal of Neuroscience, 40*(23), 4536-4550. https://doi.org/10.1523/jneurosci.2036-19.2020

Dimitriadis, S. I., Laskaris, N. A., Simos, P. G., Micheloyannis, S., Fletcher, J. M., Rezaie, R., & Papanicolaou, A. C. (2013). Altered temporal correlations in resting-state connectivity fluctuations in children with reading difficulties detected via MEG. *NeuroImage, 83*, 307-317. https://doi.org/10.1016/j.neuroimage.2013.06.036

Dimitriadis, S. I., Simos, P. G., Fletcher, J. M., & Papanicolaou, A. C. (2019). Typical and aberrant functional brain flexibility: Lifespan development and aberrant organization in traumatic brain injury and dyslexia. *Brain Sciences, 9*(12), 380. https://doi.org/10.3390/brainsci9120380

Ding, N., Melloni, L., Yang, A., Wang, Y., Zhang, W., & Poeppel, D. (2017). Characterizing neural entrainment to hierarchical linguistic units using electroencephalography (EEG). *Frontiers in Human Neuroscience, 11*, 481. https://doi.org/10.3389/fnhum.2017.00481

Ding, N., Melloni, L., Zhang, H., Tian, X., & Poeppel, D. (2016). Cortical tracking of hierarchical linguistic structures in connected speech. *Nature Neuroscience, 19*(1), 158-164. https://doi.org/10.1038/nn.4186

Ding, N., Pan, X. Y., Luo, C., Su, N. F., Zhang, W., & Zhang, J. F. (2018). Attention is required for knowledge-based sequential grouping: Insights from the integration of syllables into words. *Journal of Neuroscience, 38*(5), 1178-1188. https://doi.org/10.1523/Jneurosci.2606-17.2017

Ding, N., Patel, A. D., Chen, L., Butler, H., Luo, C., & Poeppel, D. (2017). Temporal modulations in speech and music. *Neuroscience and Biobehavioral Reviews, 81*(Pt B), 181-187. http://doi.org/10.1016/j.neubiorev.2017.02.011

Ding, N., & Simon, J. Z. (2014). Cortical entrainment to continuous speech: Functional roles and interpretations. *Frontiers in Human Neuroscience, 8*, 311. https://doi.org/10.3389/fnhum.2014.00311

Doelling, K. B., Arnal, L. H., Ghitza, O., & Poeppel, D. (2014). Acoustic landmarks drive delta-theta oscillations to enable speech comprehension by facilitating perceptual parsing. *NeuroImage, 85*, 761-768. https://doi.org/10.1016/j.neuroimage.2013.06.035

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: Mental programs for intelligent behaviour. *Trends in Cognitive Sciences, 14*(4), 172-179. https://doi.org/10.1016/j.tics.2010.01.004

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences, 23*(10), 475-483. https://doi.org/10.1016/s0166-2236(00)01633-7

Dushanova, J. A., & Tsokov, S. A. (2021). Altered electroencephalographic networks in developmental dyslexia after remedial training: A prospective case-control study. *Neural Regeneration Research, 16*(4), 734-743. https://doi.org/10.4103/1673-5374.295334

Edwards, E. S., Burke, K., Booth, J. R., & McNorgan, C. (2018). Dyslexia on a continuum: A complex network approach. *Plos One, 13*(12), e0208923. https://doi.org/10.1371/journal.pone.0208923

Elmer, S., Valizadeh, S. A., Cunillera, T., & Rodriguez-Fornells, A. (2021). Statistical learning and prosodic bootstrapping differentially affect neural synchronization during speech segmentation. *NeuroImage, 235*, 118051. https://doi.org/10.1016/j.neuroimage.2021.118051

Emmendorfer, A. K. (2022). *Electrophysiological correlates of phonological and temporal regularities in speech processing* [Doctoral dissertation, Maastricht University]. WorldCat. https://doi.org/10.26481/dis.20220222ae

Farthouat, J., Atas, A., Wens, V., De Tiège, X., & Peigneux, P. (2018). Lack of frequency-tagged magnetic responses suggests statistical regularities remain undetected during NREM sleep. *Scientific Reports, 8*, 11719. https://doi.org/10.1038/s41598-018-30105-5

Farthouat, J., Franco, A., Mary, A., Delpouve, J., Wens, V., Op de Beeck, M., De Tiège, X., & Peigneux, P. (2017). Auditory magnetoencephalographic frequency-tagged responses mirror the ongoing segmentation processes underlying statistical learning. *Brain Topography, 30*, 220-232. https://doi.org/10.1007/s10548-016-0518-y

Fedorenko, E., Duncan, J., & Kanwisher, N. (2012). Language-selective and domain-general regions lie side by side within Broca's area. *Current Biology, 22*(21), 2059-2062. https://doi.org/10.1016/j.cub.2012.09.011

Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences, 110*(41), 16616-16621. https://doi.org/10.1073/pnas.1315235110

Fedorenko, E., & Thompson-Schill, S. L. (2014). Reworking the language network. *Trends in Cognitive Sciences, 18*(3), 120-126. https://doi.org/10.1016/j.tics.2013.12.006

Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. *Nature Reviews Neuroscience, 12*(2), 105-118. https://doi.org/10.1038/nrn2979

Finc, K., Bonna, K., Lewandowska, M., Wolak, T., Nikadon, J., Dreszer, J., Duch, W., & Kühn, S. (2017). Transition of the functional brain network related to increasing cognitive demands. *Human Brain Mapping, 38*(7), 3659-3674. https://doi.org/10.1002/hbm.23621

Finisguerra, A., Borgatti, R., & Urgesi, C. (2019). Non-invasive brain stimulation for the rehabilitation of children and adolescents with neurodevelopmental disorders: A systematic review. *Frontiers in Psychology, 10*, 135. https://doi.org/10.3389/fpsyg.2019.00135

Finn, E. S., Shen, X., Holahan, J. M., Scheinost, D., Lacadie, C., Papademetris, X., Shaywitz, S. E., Shaywitz, B. A., & Constable, R. T. (2014). Disruption of functional networks in dyslexia: A whole-brain, data-driven analysis of connectivity. *Biological Psychiatry, 76*(5), 397-404. https://doi.org/10.1016/j.biopsych.2013.08.031

Fitch, W. T., & Martins, M. D. (2014). Hierarchical processing in music, language, and action: Lashley revisited. *Annals of the New York Academy of Sciences, 1316*(1), 87-104. https://doi.org/10.1111/nyas.12406

Forkstam, C., Hagoort, P., Fernandez, G., Ingvar, M., & Petersson, K. M. (2006). Neural correlates of artificial syntactic structure classification. *NeuroImage, 32*(2), 956-967. https://doi.org/10.1016/j.neuroimage.2006.03.057

Fornito, A., Zalesky, A., & Breakspear, M. (2015). The connectomics of brain disorders. *Nature Reviews Neuroscience, 16*(3), 159-172. https://doi.org/10.1038/nrn3901

Forster, K. I., & Chambers, S. M. (1973). Lexical access and naming time. *Journal of verbal learning and verbal behavior, 12*(6), 627-635. https://doi.org/10.1016/S0022-5371(73)80042-8

Fraga-González, G., Pleisch, G., Di Pietro, S. V., Neuenschwander, J., Walitza, S., Brandeis, D., Karipidis, I. I., & Brem, S. (2021). The rise and fall of rapid occipito-temporal sensitivity to letters: Transient specialization through elementary school. *Developmental Cognitive Neuroscience, 49*, 100958. https://doi.org/10.1016/j.dcn.2021.100958

Fraga-González, G., Smit, D. J. A., Van der Molen, M. J. W., Tijms, J., Stam, C. J., de Geus, E. J. C., & Van der Molen, M. W. (2018). EEG resting state functional connectivity in adult dyslexics using phase lag index and graph analysis. *Frontiers in Human Neuroscience, 12,* 341. https://doi.org/10.3389/fnhum.2018.00341

Fraga-González, G., Smit, D. J. A., Van der Molen, M. J. W., Tijms, J., Stam, C. J., de Geus, E. J. C., & Van der Molen, M. W. (2021). Graph analysis of EEG functional connectivity networks during a letter-speech sound binding task in adult dyslexics. *Frontiers in Psychology, 12*, 767839. https://doi.org/10.3389/fpsyg.2021.767839

Fraga-González, G., Van der Molen, M. J. W., Zaric, G., Bonte, M., Tijms, J., Blomert, L., Stam, C. J., & Van der Molen, M. W. (2016). Graph analysis of EEG resting state functional networks in dyslexic readers. *Clinical Neurophysiology, 127*(9), 3165-3175. https://doi.org/10.1016/j.clinph.2016.06.023

Fraga-González, G., Žarić, G., Tijms, J., Bonte, M., & Van Der Molen, M. (2017). Contributions of letter-speech sound learning and visual print tuning to reading improvement: Evidence from brain potential and dyslexia training studies. *Brain Sciences, 7*(1), 10. https://doi.org/10.3390/brainsci7010010

Fransson, P., Åden, U., Blennow, M., & Lagercrantz, H. (2011). The functional architecture of the infant brain as revealed by resting-state fMRI. *Cerebral Cortex, 21*(1), 145-154. https://doi.org/10.1093/cercor/bhq071

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences, 6*(2), 78-84. https://doi.org/10.1016/s1364-6613(00)01839-8

Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews, 91*(4), 1357-1392. https://doi.org/10.1152/physrev.00006.2011

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences, 16*(5), 262-268. https://doi.org/10.1016/j.tics.2012.04.001

Friederici, A. D. (2020). Hierarchy processing in human neurobiology: How specific is it? *Philosophical Transactions of the Royal Society B: Biological Sciences, 375*(1789), 20180391. https://doi.org/10.1098/rstb.2018.0391

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences, 103*(7), 2458-2463. https://doi.org/10.1073/pnas.0509389103

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences, 9*(10), 474-480. https://doi.org/10.1016/j.tics.2005.08.011

Frost, R., Armstrong, B. C., Siegelman, N., & Christiansen, M. H. (2015). Domain generality versus modality specificity: The paradox of statistical learning. *Trends in Cognitive Science, 19*(3), 117-125. https://doi.org/10.1016/j.tics.2014.12.010

Froyen, D. J. W., Bonte, M. L., van Atteveldt, N., & Blomert, L. (2009). The long road to automation: Neurocognitive development of letter-speech sound processing. *Journal of Cognitive Neuroscience, 21*(3), 567-580. https://doi.org/10.1162/jocn.2009.21061

Froyen, D., van Atteveldt, N., Bonte, M., & Blomert, L. (2008). Cross-modal enhancement of the MMN to speech-sounds indicates early and automatic integration of letters and speech-sounds. *Neuroscience Letters, 430*(1), 23-28. https://doi.org/10.1016/j.neulet.2007.10.014

Gabay, Y., Thiessen, E. D., & Holt, L. L. (2015). Impaired statistical learning in developmental dyslexia. *Journal of Speech, Language, and Hearing Research, 58*(3), 934-945. https://doi.org/10.1044/2015_JSLHR-L-14-0324

Geiser, E., Zaehle, T., Jancke, L., & Meyer, M. (2008). The neural correlate of speech rhythm as evidenced by metrical speech processing. *Journal of Cognitive Neuroscience, 20*(3), 541-552. https://doi.org/10.1162/jocn.2008.20029

Gerton, B. K., Brown, T. T., Meyer-Lindenberg, A., Kohn, P., Holt, J. L., Olsen, R. K., & Berman, K. F. (2004). Shared and distinct neurophysiological components of the digits forward and backward tasks as revealed by functional neuroimaging. *Neuropsychologia, 42*(13), 1781-1787. https://doi.org/10.1016/j.neuropsychologia.2004.04.023

Getz, H., Ding, N., Newport, E. L., & Poeppel, D. (2018). Cortical tracking of constituent structure in language acquisition. *Cognition, 181*, 135-140. https://doi.org/10.1016/j.cognition.2018.08.019

Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: Emerging computational principles and operations. *Nature Neuroscience, 15*(4), 511-517. https://doi.org/10.1038/nn.3063

Giraud, A.-L., & Ramus, F. (2013). Neurogenetics and auditory processing in developmental dyslexia. *Current Opinion in Neurobiology, 23*(1), 37-42. https://doi.org/10.1016/j.conb.2012.09.003

Goldstein, M. H., Waterfall, H. R., Lotem, A., Halpern, J. Y., Schwade, J. A., Onnis, L., & Edelman, S. (2010). General cognitive principles for learning structure in time and space. *Trends in Cognitive Sciences, 14*(6), 249-258. https://doi.org/10.1016/j.tics.2010.02.004

Google Text-To-Speech. (2018). *Version 3.14.9*. Mountain View, California: Google Inc.

Goswami, U. (2011). A temporal sampling framework for developmental dyslexia. *Trends in Cognitive Sciences, 15*(1), 3-10. https://doi.org/10.1016/j.tics.2010.10.001

Goswami, U. (2018). A neural basis for phonological awareness? An oscillatory temporal-sampling perspective. *Current Directions in Psychological Science, 27*(1), 56-63. https://doi.org/10.1177/0963721417727520

Goswami, U. (2019). Speech rhythm and language acquisition: An amplitude modulation phase hierarchy perspective. *Annals of the New York Academy of Sciences, 1453*(1), 67-78. https://doi.org/10.1111/nyas.14137

Goswami, U., Fosker, T., Huss, M., Mead, N., & Szucs, D. (2011). Rise time and formant transition duration in the discrimination of speech sounds: The Ba-Wa distinction in developmental dyslexia. *Developmental Science, 14*(1), 34-43. https://doi.org/10.1111/j.1467-7687.2010.00955.x

Goswami, U., & Leong, V. (2013). Speech rhythm and temporal structure: Converging perspectives? *Laboratory Phonology, 4*(1), 67-92. https://doi.org/10.1515/lp-2013-0004

Goswami, U., Power, A. J., Lallier, M., & Facoetti, A. (2014). Oscillatory "temporal sampling" and developmental dyslexia: Toward an over-arching theoretical framework. *Frontiers in Human Neuroscience, 8*, 904. https://doi.org/10.3389/fnhum.2014.00904

Goswami, U., Thomson, J., Richardson, U., Stainthorp, R., Hughes, D., Rosen, S., & Scott, S. K. (2002). Amplitude envelope onsets and developmental dyslexia: A new hypothesis. *Proceedings of the National Academy of Sciences, 99*(16), 10911-10916. https://doi.org/10.1073/pnas.122368599

Goswami, U., Wang, H. L. S., Cruz, A., Fosker, T., Mead, N., & Huss, M. (2011). Language-universal sensory deficits in developmental dyslexia: English, Spanish, and Chinese. *Journal of Cognitive Neuroscience, 23*(2), 325-337. https://doi.org/10.1162/jocn.2010.21453

Gow Jr., D. W. (2012). The cortical organization of lexical knowledge: A dual lexicon model of spoken language processing. *Brain and Language, 121*(3), 273-288. https://doi.org/10.1016/j.bandl.2012.03.005

Gray, M. J., Frey, H.-P., Wilson, T. J., & Foxe, J. J. (2015). Oscillatory recruitment of bilateral visual cortex during spatial attention to competing rhythmic inputs. *Journal of Neuroscience, 35*(14), 5489-5503. https://doi.org/10.1523/jneurosci.2891-14.2015

Greenfield, P. M. (1991). Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences, 14*(4), 531-551. https://doi.org//10.1017/S0140525X00071235

Gross, J., Hoogenboom, N., Thut, G., Schyns, P., Panzeri, S., Belin, P., & Garrod, S. (2013). Speech rhythms and multiplexed oscillatory sensory coding in the human brain. *PLOS Biology, 11*(12), e1001752. https://doi.org/10.1371/journal.pbio.1001752

Gupta, N., Singh, S. S., & Stopfer, M. (2016). Oscillatory integration windows in neurons. *Nature Communications, 7*(1), 13808. https://doi.org/10.1038/ncomms13808

Habib, M. (2000). The neurological basis of developmental dyslexia - An overview and working hypothesis. *Brain, 123*, 2373-2399. https://doi.org/10.1093/brain/123.12.2373

Hage, S. R., & Nieder, A. (2016). Dual neural network model for the evolution of speech and language. *Trends in Neurosciences, 39*(12), 813-829. https://doi.org/10.1016/j.tins.2016.10.006

Hagoort, P., & Indefrey, P. (2014). The neurobiology of language beyond single words. *Annual Review of Neuroscience, 37*(1), 347-362. https://doi.org/10.1146/annurev-neuro-071013-013847

Hämäläinen, J., Leppänen, P. H. T., Torppa, M., Müller, K., & Lyytinen, H. (2005). Detection of sound rise time by adults with dyslexia. *Brain and Language, 94*(1), 32-42. https://doi.org/10.1016/j.bandl.2004.11.005

Hämäläinen, J. A., Parviainen, T., Hsu, Y. F., & Salmelin, R. (2019). Dynamics of brain activation during learning of syllable-symbol paired associations. *Neuropsychologia, 129*, 93-103. https://doi.org/10.1016/j.neuropsychologia.2019.03.016

Hämäläinen, J. A., Rupp, A., Soltész, F., Szücs, D., & Goswami, U. (2012). Reduced phase locking to slow amplitude modulation in adults with dyslexia: An MEG study. *NeuroImage, 59*(3), 2952-2961. https://doi.org/10.1016/j.neuroimage.2011.09.075

Hämäläinen, J. A., Salminen, H. K., & Leppänen, P. H. T. (2013). Basic auditory processing deficits in dyslexia. *Journal of Learning Disabilities, 46*(5), 413-427. https://doi.org/10.1177/0022219411436213

Hancock, R., Pugh, K. R., & Hoeft, F. (2017). Neural noise hypothesis of developmental dyslexia. *Trends in Cognitive Sciences, 21*(6), 434-448. http://dx.doi.org/10.1016/j.tics.2017.03.008

Heerebout, B. T., & Phaf, R. H. (2010). Emergent oscillations in evolutionary simulations: Oscillating networks increase switching efficacy. *Journal of Cognitive Neuroscience, 22*(5), 807-823. https://doi.org/10.1162/jocn.2009.21205

Heiervang, E., Stevenson, J., & Hugdahl, K. (2002). Auditory processing in children with dyslexia. *Journal of Child Psychology and Psychiatry, 43*(7), 931-938. https://doi.org/10.1111/1469-7610.00097

Henin, S., Turk-Browne, N. B., Friedman, D., Liu, A., Dugan, P., Flinker, A., Doyle, W., Devinsky, O., & Melloni, L. (2019). Statistical learning shapes neural sequence representations. *bioRxiv*, 583856. https://doi.org/10.1101/583856

Henin, S., Turk-Browne, N. B., Friedman, D., Liu, A., Dugan, P., Flinker, A., Doyle, W., Devinsky, O., & Melloni, L. (2021). Learning hierarchical sequence representations across human cortex and hippocampus. *Science Advances, 7*(8), eabc4530. https://doi.org/10.1126/sciadv.abc4530

Henry, M. J., & Obleser, J. (2012). Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proceedings of the National Academy of Sciences, 109*(49), 20095-20100. https://doi.org/10.1073/pnas.1213390109

Heo, M., & Leon, A. C. (2010). Sample sizes required to detect two-way and three-way interactions involving slope differences in mixed-effects linear models. *Journal of Biopharmaceutical Statistics, 20*(4), 787-802. https://doi.org/10.1080/10543401003618819

Herrmann, C. S., Rach, S., Neuling, T., & Struber, D. (2013). Transcranial alternating current stimulation: A review of the underlying mechanisms and modulation of cognitive processes. *Frontiers in Human Neuroscience, 7*, 279. https://doi.org/10.3389/fnhum.2013.00279

Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences, 4*(4), 131-138. https://doi.org/10.1016/s1364-6613(00)01463-7

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8*(5), 393-402. https://doi.org/10.1038/nrn2113

Hoeft, F., McCandliss, B. D., Black, J. M., Gantman, A., Zakerani, N., Hulme, C., Lyytinen, H., Whitfield-Gabrieli, S., Glover, G. H., Reiss, A. L., & Gabrieli, J. D. E. (2011). Neural systems predicting long-term outcome in dyslexia. *Proceedings of the National Academy of Sciences, 108*(1), 361-366. https://doi.org/10.1073/pnas.1008950108

Hoff, G. E. A.-J., van den Heuvel, M., Benders, M. J. N. L., Kersbergen, K. J., & de Vries, L. S. (2013). On development of functional brain connectivity in the young brain. *Frontiers in Human Neuroscience, 7*, 650. https://doi.org/10.3389/fnhum.2013.00650

Hornickel, J., & Kraus, N. (2013). Unstable representation of sound: A biological marker of dyslexia. *Journal of Neuroscience, 33*(8), 3500-3504. https://doi.org/10.1523/JNEUROSCI.4205-12.2013

Hosseini, S. M. H., Black, J. M., Soriano, T., Bugescu, N., Martinez, R., Raman, M. M., Kesler, S. R., & Hoeft, F. (2013). Topological properties of large-scale structural brain networks in children with familial risk for reading difficulties. *NeuroImage, 71*, 260-274. https://doi.org/10.1016/j.neuroimage.2013.01.013

Howard, J. H., Howard, D. V., Japikse, K. C., & Eden, G. F. (2006). Dyslexics are impaired on implicit higher-order sequence learning, but not on implicit spatial context learning. *Neuropsychologia, 44*(7), 1131-1144. https://doi.org/10.1016/j.neuropsychologia.2005.10.015

Huettig, F., Lachmann, T., Reis, A., & Petersson, K. M. (2018). Distinguishing cause from effect - many deficits associated with developmental dyslexia may be a consequence of reduced and suboptimal reading experience. *Language, Cognition and Neuroscience, 33*(3), 333-350. https://doi.org/10.1080/23273798.2017.1348528

Hulme, C., & Snowling, M. J. (2014). The interface between spoken and written language: Developmental disorders. *Philosophical Transactions of the Royal Society B: Biological Sciences, 369*(1634), 20120395. https://doi.org/10.1098/rstb.2012.0395

Hulsemann, M. J., Naumann, E., & Rasch, B. (2019). Quantification of phase-amplitude coupling in neuronal oscillations: Comparison of phase-locking value, mean vector length, modulation index, and generalized-linear-modeling-cross-frequency-coupling. *Frontiers in Neuroscience, 13*, 573. https://doi.org/10.3389/fnins.2019.00573

Hutchison, R. M., Womelsdorf, T., Allen, E. A., Bandettini, P. A., Calhoun, V. D., Corbetta, M., Penna, S. D., Duyn, J. H., Glover, G. H., Gonzalez-Castillo, J., Handwerker, D. A., Keilholz, S., Kiviniemi, V., Leopold, D. A., de Pasquale, F., Sporns, O., Walter, M., & Chang, C. (2013). Dynamic functional connectivity: Promise, issues, and interpretations. *NeuroImage, 80*, 360-378. https://doi.org/10.1016/j.neuroimage.2013.05.079

Hwang, K., Hallquist, M. N., & Luna, B. (2013). The development of hub architecture in the human functional brain network. *Cerebral Cortex, 23*(10), 2380-2393. https://doi.org/10.1093/cercor/bhs227

Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience, 2*(3), 194-203. https://doi.org/10.1038/35058500

Jaffe-Dax, S., Frenkel, O., & Ahissar, M. (2017). Dyslexics' faster decay of implicit memory for sounds and words is manifested in their shorter neural adaptation. *Elife, 6*, e20557. https://doi.org/10.7554/eLife.20557

Jensen, O. (2006). Maintenance of multiple working memory items by temporal segmentation. *Neuroscience, 139*(1), 237-249. https://doi.org/10.1016/j.neuroscience.2005.06.004

Jensen, O., & Colgin, L. L. (2007). Cross-frequency coupling between neuronal oscillations. *Trends in Cognitive Sciences, 11*(7), 267-269. https://doi.org/10.1016/j.tics.2007.05.003

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience, 15*(8), 1395-1399. https://doi.org/10.1046/j.1460-9568.2002.01975.x

Jin, P. Q., Zou, J. J., Zhou, T., & Ding, N. (2018). Eye activity tracks task-relevant structures during speech and auditory sequence perception. *Nature Communications, 9*, 5374. https://doi.org/10.1038/s41467-018-07773-y

Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: A metanalysis of 35 neuroimaging studies. *NeuroImage, 20*(2), 693-712. https://doi.org/10.1016/s1053-8119(03)00343-4

Joon Kim, Y., Grabowecky, M., Paller, K. A., Muthu, K., & Suzuki, S. (2007). Attention induces synchronization-based response gain in steady-state visual evoked potentials. *Nature Neuroscience, 10*(1), 117-125. https://doi.org/10.1038/nn1821

Kabdebon, C., Peña, M., Buiatti, M., & Dehaene-Lambertz, G. (2015). Electrophysiological evidence of statistical learning of long-distance dependencies in 8-month-old preterm and full-term infants. *Brain and Language, 148*, 25-36. https://doi.org/10.1016/j.bandl.2015.03.005

Kaplan, J. T., Man, K., & Greening, S. G. (2015). Multivariate cross-classification: Applying machine learning techniques to characterize abstraction in neural representations. *Frontiers in Human Neuroscience, 9*, 151. https://doi.org/10.3389/fnhum.2015.00151

Karipidis, I. I., Pleisch, G., Rothlisberger, M., Hofstetter, C., Dornbierer, D., Stampfli, P., & Brem, S. (2017). Neural initialization of audiovisual integration in prereaders at varying risk for developmental dyslexia. *Human Brain Mapping, 38*(2), 1038-1055. https://doi.org/10.1002/hbm.23437

Kast, M., Elmer, S., Jancke, L., & Meyer, M. (2010). ERP differences of pre-lexical processing between dyslexic and non-dyslexic children. *International Journal of Psychophysiology, 77*(1), 59-69. https://doi.org/10.1016/j.ijpsycho.2010.04.003

Keetels, M., Bonte, M., & Vroomen, J. (2018). A selective deficit in phonetic recalibration by text in developmental dyslexia. *Frontiers in Psychology, 9*, 710. https://doi.org/10.3389/fpsyg.2018.00710

Keitel, A., Gross, J., & Kayser, C. (2020). Shared and modality-specific brain regions that mediate auditory and visual word comprehension. *eLife, 9*, e56972. https://doi.org/10.7554/elife.56972

Keitel, C., Maess, B., Schröger, E., & Müller, M. M. (2013). Early visual and auditory processing rely on modality-specific attentional resources. *NeuroImage, 70*, 240-249. https://doi.org/10.1016/j.neuroimage.2012.12.046

Keitel, C., Thut, G., & Gross, J. (2017). Visual cortex responses reflect temporal structure of continuous quasi-rhythmic sensory stimulation. *NeuroImage, 146*, 58-70. https://doi.org/10.1016/j.neuroimage.2016.11.043

Kershner, J. R. (2016). Network dynamics in dyslexia: Review and implications for remediation. *Research in Developmental Disabilities, 59*, 24-34. https://doi.org/10.1016/j.ridd.2016.07.014

Kershner, J. R. (2020). Neuroscience and education: Cerebral lateralization of networks and oscillations in dyslexia. *Laterality, 25*(1), 109-125. https://doi.org/10.1080/1357650x.2019.1606820

Keuleers, E., Brysbaert, M., & New, B. (2010). SUBTLEX-NL: A new measure for Dutch word frequency based on film subtitles. *Behavior Research Methods, 42*(3), 643-650. https://doi.org/10.3758/brm.42.3.643

Kim, H., Kang, S. H., Kim, S. H., Kim, S. H., Hwang, J., Kim, J.-G., Han, K., & Kim, J. B. (2021). Drinking coffee enhances neurocognitive function by reorganizing brain functional connectivity. *Scientific Reports, 11*(1). https://doi.org/10.1038/s41598-021-93849-7

Kim, R., Seitz, A., Feenstra, H., & Shams, L. (2009). Testing assumptions of statistical learning: Is it long-term and implicit? *Neuroscience Letters, 461*(2), 145-149. https://doi.org/10.1016/j.neulet.2009.06.030

Kinsbourne, M., Rufo, D. T., Gamzu, E., Palmer, R. L., & Berliner, A. K. (1991). Neuropsychological deficits in adults with dyslexia. *Developmental Medicine & Child Neurology, 33*(9), 763-775. https://doi.org/10.1111/j.1469-8749.1991.tb14960.x

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3?

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews, 29*(2-3), 169-195. https://doi.org/10.1016/S0165-0173(98)00056-3

Klingberg, T., Hedehus, M., Temple, E., Salz, T., Gabrieli, J. D. E., Moseley, M. E., & Poldrack, R. A. (2000). Microstructure of temporo-parietal white matter as a basis for reading ability. *Neuron, 25*(2), 493-500. https://doi.org/10.1016/s0896-6273(00)80911-3

Klink, K., Paßmann, S., Kasten, F. H., & Peter, J. (2020). The modulation of cognitive performance with transcranial alternating current stimulation: A systematic review of frequency-specific effects. *Brain Sciences, 10*(12), 932. https://doi.org/10.3390/brainsci10120932

Koechlin, E., & Jubault, T. (2006). Broca's area and the hierarchical organization of human behavior. *Neuron, 50*(6), 963-974. https://doi.org/10.1016/j.neuron.2006.05.017

Kolozsvári, O. B., Xu, W., Gerike, G., Parviainen, T., Nieminen, L., Noiray, A., & Hämäläinen, J. A. (2021). Coherence between brain activation and speech envelope at word and sentence levels showed age-related differences in low frequency bands. *Neurobiology of Language, 2*(2), 226-253. https://doi.org/10.1162/nol_a_00033

Kösem, A., Bosker, H. R., Jensen, O., Hagoort, P., & Riecke, L. (2020). Biasing the perception of spoken words with transcranial alternating current stimulation. *Journal of Cognitive Neuroscience, 32*(8), 1428-1437. https://doi.org/10.1162/jocn_a_01579

Kösem, A., Bosker, H. R., Takashima, A., Meyer, A., Jensen, O., & Hagoort, P. (2018). Neural entrainment determines the words we hear. *Current Biology, 28*(18), 2867-2875. https://doi.org/10.1016/j.cub.2018.07.023

Kösem, A., Gramfort, A., & van Wassenhove, V. (2014). Encoding of event timing in the phase of neural oscillations. *NeuroImage, 92*, 274-284. https://doi.org/10.1016/j.neuroimage.2014.02.010

Kotz, S. A., & Schwartze, M. (2010). Cortical speech processing unplugged: A timely subcortico-cortical framework. *Trends in Cognitive Sciences, 14*(9), 392-399. https://doi.org/10.1016/j.tics.2010.06.005

Krishnamurthy, L. C., Krishnamurthy, V., Crosson, B., Rothman, D. L., Schwam, D. M., Greenberg, D., Pugh, K. R., & Morris, R. D. (2019). Strength of resting state functional connectivity and local GABA concentrations predict oral reading of real and pseudo-words. *Scientific Reports, 9*, 11385. https://doi.org/10.1038/s41598-019-47889-9

Kruskal, J. B. (1956). On the shortest spanning subtree of a graph and the traveling salesman problem. *Proceedings of the American Mathematical Society, 7*(1), 48-50. https://doi.org/10.2307/2033241

Kuhl, P. K. (2004). Early language acquisition: Cracking the speech code. *Nature Reviews Neuroscience, 5*(11), 831-843. https://doi.org/10.1038/nrn1533

Kuntzelman, K., & Miskovic, V. (2017). Reliability of graph metrics derived from resting-state human EEG. *Psychophysiology, 54*(1), 51-61. https://doi.org/10.1111/psyp.12600

Kuperberg, G. R., Holcomb, P. J., Sitnikova, T., Greve, D., Dale, A. M., & Caplan, D. (2003). Distinct patterns of neural modulation during the processing of conceptual and syntactic anomalies. *Journal of Cognitive Neuroscience, 15*(2), 272-293. https://doi.org/10.1162/089892903321208204

Laasonen, M., Service, E., & Virsu, V. (2001). Temporal order and processing acuity of visual, auditory, and tactile perception in developmentally dyslexic young adults. *Cognitive, Affective, & Behavioral Neuroscience, 1*(4), 394-410. https://doi.org/10.3758/cabn.1.4.394

Lai, M., Demuru, M., Hillebrand, A., & Fraschini, M. (2018). A comparison between scalp- and source-reconstructed EEG networks. *Scientific Reports, 8*, 12269. https://doi.org/10.1038/s41598-018-30869-w

Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science, 320*(5872), 110-113. https://doi.org/10.1126/science.1154735

Lakatos, P., Shah, A. S., Knuth, K. H., Ulbert, I., Karmos, G., & Schroeder, C. E. (2005). An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *Journal of Neurophysiology, 94*(3), 1904-1911. https://doi.org/10.1152/jn.00263.2005

Lallier, M., Molinaro, N., Lizarazu, M., Bourguignon, M., & Carreiras, M. (2017). Amodal atypical neural oscillatory activity in dyslexia: A cross-linguistic perspective. *Clinical Psychological Science, 5*(2), 379-401. https://doi.org/10.1177/2167702616670119

Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jeffress (Ed.), *Cerebral mechanisms in behavior: The Hixon Symposium* (pp. 112–146). Oxford, United Kingdom: Bobbs-Merrill.

Lau, E., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience, 9*(12), 920-933. https://doi.org/10.1038/nrn2532

Lau, E., Stroud, C., Plesch, S., & Phillips, C. (2006). The role of structural prediction in rapid syntactic analysis. *Brain and Language, 98*(1), 74-88. https://doi.org/10.1016/j.bandl.2006.02.003

Lee, M., Yoon, J.-G., & Lee, S.-W. (2020). Predicting motor imagery performance from resting-state EEG using dynamic causal modeling. *Frontiers in Human Neuroscience, 14*, 321. https://doi.org/10.3389/fnhum.2020.00321

Lee, S. M.-K., Cui, Y., & Tong, S. X. (2022). Toward a model of statistical learning and reading: Evidence from a meta-analysis. *Review of Educational Research*, 003465432110731. https://doi.org/10.3102/00346543211073188

Lehongre, K., Morillon, B., Giraud, A.-L., & Ramus, F. (2013). Impaired auditory sampling in dyslexia: Further evidence from combined fMRI and EEG. *Frontiers in Human Neuroscience, 7*, 454. https://doi.org/10.3389/fnhum.2013.00454

Lehongre, K., Ramus, F., Villiermet, N., Schwartz, D., & Giraud, A.-L. (2011). Altered low-gamma sampling in auditory cortex accounts for the three main facets of dyslexia. *Neuron, 72*(6), 1080-1090. https://doi.org/10.1016/j.neuron.2011.11.002

Leong, V., & Goswami, U. (2014). Assessment of rhythmic entrainment at multiple timescales in dyslexia: Evidence for disruption to syllable timing. *Hearing Research, 308*, 141-161. https://doi.org/10.1016/j.heares.2013.07.015

Leong, V., & Goswami, U. (2014). Impaired extraction of speech rhythm from temporal modulation patterns in speech in developmental dyslexia. *Frontiers in Humam Neuroscience, 8*, 96. https://doi.org/10.3389/fnhum.2014.00096

Leong, V., Hämäläinen, J., Soltesz, F., & Goswami, U. (2011). Rise time perception and detection of syllable stress in adults with developmental dyslexia. *Journal of Memory and Language, 64*(1), 59-73. https://doi.org/10.1016/j.jml.2010.09.003

Li, Y., & Bi, H.-Y. (2022). Comparative research on neural dysfunction in children with dyslexia under different writing systems: A meta-analysis study. *Neuroscience & Biobehavioral Reviews*, 104650. https://doi.org/10.1016/j.neubiorev.2022.104650

Liberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revised. *Cognition, 21*(1), 1-36. https://doi.org/10.1016/0010-0277(85)90021-6

Liebig, J., Froehlich, E., Morawetz, C., Braun, M., Jacobs, A. M., Heekeren, H. R., & Ziegler, J. C. (2017). Neurofunctionally dissecting the reading system in children. *Developmental Cognitive Neuroscience, 27*, 45-57. https://doi.org/10.1016/j.dcn.2017.07.002

Lieder, I., Adam, V., Frenkel, O., Jaffe-Dax, S., Sahani, M., & Ahissar, M. (2019). Perceptual bias reveals slow-updating in autism and fast-forgetting in dyslexia. *Nature Neuroscience, 22*, 256–264. https://doi.org/10.1038/s41593-018-0308-9

Ligges, C., Ungureanu, M., Ligges, M., Blanz, B., & Witte, H. (2010). Understanding the time variant connectivity of the language network in developmental dyslexia: New insights using Granger causality. *Journal of Neural Transmission, 117*(4), 529-543. https://doi.org/10.1007/s00702-010-0367-x

Lisman, J. E., & Idiart, M. A. (1995). Storage of 7+/-2 short-term memories in oscillatory subcycles. *Science, 267*(5203), 1512-1515. https://doi.org/10.1126/science.7878473

Litt, R. A., & Nation, K. (2014). The nature and specificity of paired associate learning deficits in children with dyslexia. *Journal of Memory and Language, 71*(1), 71-88. https://doi.org/10.1016/j.jml.2013.10.005

Livingstone, M.S., Rosen, G.D., Drislane, F.W., Galaburda, A.M. (1991). Physiological and anatomical evidence for a magnocellular defect in developmental dyslexia. *Proceedings of the National Academy of Sciences, 88*(18), 7943–7947. https://doi.org/10.1073/pnas.88.18.7943

Lizarazu, M., Lallier, M., Bourguignon, M., Carreiras, M., & Molinaro, N. (2021). Impaired neural response to speech edges in dyslexia. *Cortex, 135*, 207-218. https://doi.org/10.1016/j.cortex.2020.09.033

Lizarazu, M., Lallier, M., Molinaro, N., Bourguignon, M., Paz-Alonso, P. M., Lerma-Usabiaga, G., & Carreiras, M. (2015). Developmental evaluation of atypical auditory sampling in dyslexia: Functional and structural evidence. *Human Brain Mapping, 36*(12), 4986-5002. https://doi.org/10.1002/hbm.22986

Lochy, A., Jacques, C., Maillard, L., Colnat-Coulbois, S., Rossion, B., & Jonas, J. (2018). Selective visual representation of letters and words in the left ventral occipito-temporal cortex with intracerebral recordings. *Proceedings of the National Academy of Sciences, 115*(32), E7595-E7604. https://doi.org/10.1073/pnas.1718987115

Lochy, A., Van Belle, G., & Rossion, B. (2015). A robust index of lexical representation in the left occipito-temporal cortex as evidenced by EEG responses to fast periodic visual stimulation. *Neuropsychologia, 66*, 18-31. https://doi.org/10.1016/j.neuropsychologia.2014.11.007

Lochy, A., Van Reybroeck, M., & Rossion, B. (2016). Left cortical specialization for visual letter strings predicts rudimentary knowledge of letter-sound association in preschoolers. *Proceedings of the National Academy of Sciences, 113*(30), 8544-8549. https://doi.org/10.1073/pnas.1520366113

Lövdén, M., Garzón, B., & Lindenberger, U. (2020). Human skill learning: Expansion, exploration, selection, and refinement. *Current Opinion in Behavioral Sciences, 36*, 163-168. https://doi.org/10.1016/j.cobeha.2020.11.002

Lu, L., Sheng, J., Liu, Z., & Gao, J.-H. (2021). Neural representations of imagined speech revealed by frequency-tagged magnetoencephalography responses. *NeuroImage, 229*, 117724. https://doi.org/10.1016/j.neuroimage.2021.117724

Lum, J. A. G., Ullman, M. T., & Conti-Ramsden, G. (2013). Procedural learning is impaired in dyslexia: Evidence from a meta-analysis of serial reaction time studies. *Research in Developmental Disabilities, 34*(10), 3460-3476. https://doi.org/10.1016/j.ridd.2013.07.017

Luo, H., & Poeppel, D. (2007). Phase patterns of neuronal responses reliably discriminate speech in human auditory cortex. *Neuron, 54*(6), 1001-1010. https://doi.org/10.1016/j.neuron.2007.06.004

Lyon, G. R., Shaywitz, S. E., & Shaywitz, B. A. (2003). A definition of dyslexia. *Annals of Dyslexia, 53*, 1-14. https://doi.org/10.1007/s11881-003-0001-9

Mainela-Arnold, E., & Evans, J. L. (2014). Do statistical segmentation abilities predict lexical-phonological and lexical-semantic abilities in children with and without SLI? *Journal of Child Language, 41*(2), 327-351. https://doi.org/10.1017/S0305000912000736327

Maisog, J. M., Einbinder, E. R., Flowers, D. L., Turkeltaub, P. E., & Eden, G. F. (2008). A meta-analysis of functional neuroimaging studies of dyslexia. *Annals of the New York Academy of Sciences, 1145*(1), 237-259. https://doi.org/10.1196/annals.1416.024

Mandke, K., Flanagan, S., Macfarlane, A., Gabrielczyk, F., Wilson, A., Gross, J., & Goswami, U. (2022). Neural sampling of the speech signal at different timescales by children with dyslexia. *NeuroImage*, *253*, 119077. https://doi.org/10.1016/j.neuroimage.2022.119077

Mao, J., Liu, L., Perkins, K., & Cao, F. (2021). Poor reading is characterized by a more connected network with wrong hubs. *Brain and Language, 220*, 104983. https://doi.org/10.1016/j.bandl.2021.104983

Marchesotti, S., Nicolle, J., Merlet, I., Arnal, L. H., Donoghue, J. P., & Giraud, A.-L. (2020). Selective enhancement of low-gamma activity by tACS improves phonemic processing and reading accuracy in dyslexia. *PLOS Biology, 18*(9). https://doi.org/10.1371/journal.pbio.3000833

Margolis, A. E., Pagliaccio, D., Davis, K. S., Thomas, L., Banker, S. M., Cyr, M., & Marsh, R. (2020). Neural correlates of cognitive control deficits in children with reading disorder. *Brain Imaging and Behavior, 14*(5), 1531-1542. https://doi.org/10.1007/s11682-019-00083-x

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods, 164*(1), 177-190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Martin, A., Schurz, M., Kronbichler, M., & Richlan, F. (2015). Reading in the brain of children and adults: A meta-analysis of 40 functional magnetic resonance imaging studies. *Human Brain Mapping, 36*(5), 1963-1981. https://doi.org/10.1002/hbm.22749

MATLAB. (2017). *Version 9.2.0 (R2017a)*. Natick, Massachusetts: The MathWorks Inc.

Mattingly, I. G. (1972) Reading, the linguistic process and linguistic awareness. In J. F. Kavanagh & I. G. Mattingly (Ed.) *Language by ear and by eyes: The relationships between speech and reading*, (pp. 133–147). Cambridge, MA: MIT Press.

Maurer, U., Brem, S., Kranz, F., Bucher, K., Benz, R., Halder, P., Steinhausen, H.-C., & Brandeis, D. (2006). Coarse neural tuning for print peaks when children learn to read. *NeuroImage, 33*(2), 749-758. https://doi.org/10.1016/j.neuroimage.2006.06.025

McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences, 7*(7), 293-299. https://doi.org/10.1016/S1364-6613(03)00134-7

McNealy, K., Mazziotta, J. C., & Dapretto, M. (2006). Cracking the language code: Neural mechanisms underlying speech parsing. *Journal of Neuroscience, 26*(29), 7629-7639. https://doi.org/10.1523/JNEUROSCI.5501-05.2006

Menghini, D., Hagberg, G. E., Caltagirone, C., Petrosini, L., & Vicari, S. (2006). Implicit learning deficits in dyslexic adults: An fMRI study. *NeuroImage, 33*(4), 1218–1226. https://doi.org/10.1016/j.neuroimage.2006.08.024

Menon, V. (2011). Large-scale brain networks and psychopathology: A unifying triple network model. *Trends in Cognitive Sciences, 15*(10), 483-506. https://doi.org/10.1016/j.tics.2011.08.003

Meulemans, T., & Van Der Linden, M. (2003). Implicit learning of complex information in amnesia. *Brain and Cognition, 52*(2), 250-257. https://doi.org/10.1016/s0278-2626(03)00081-2

Meyer, L. (2018). The neural oscillations of speech processing and language comprehension: State of the art and emerging mechanisms. *European Journal of Neuroscience, 48*(7), 2609-2621. https://doi.org/10.1111/ejn.13748

Meyer, L., Grigutsch, M., Schmuck, N., Gaston, P., & Friederici, A. D. (2015). Frontal–posterior theta oscillations reflect memory retrieval during sentence comprehension. *Cortex, 71*, 205-218. https://doi.org/10.1016/j.cortex.2015.06.027

Milne, A. E., Wilson, B., & Christiansen, M. H. (2018). Structured sequence learning across sensory modalities in humans and nonhuman primates. *Current Opinion in Behavioral Sciences, 21*, 39-48. https://doi.org/10.1016/j.cobeha.2017.11.016

Miniussi, C., Harris, J. A., & Ruzzoli, M. (2013). Modelling non-invasive brain stimulation in cognitive neuroscience. *Neuroscience & Biobehavioral Reviews, 37*(8), 1702-1712. https://doi.org/10.1016/j.neubiorev.2013.06.014

Molinaro, N., Lizarazu, M., Lallier, M., Bourguignon, M., & Carreiras, M. (2016). Out-of-synchrony speech entrainment in developmental dyslexia. *Human Brain Mapping, 37*(8), 2767-2783. https://doi.org/10.1002/hbm.23206

Montani, V., Chanoine, V., Grainger, J., & Ziegler, J. C. (2019). Frequency-tagged visual evoked responses track syllable effects in visual word recognition. *Cortex, 121*, 60-77. https://doi.org/10.1016/j.cortex.2019.08.014

Monzalvo, K., & Dehaene-Lambertz, G. (2013). How reading acquisition changes children's spoken language network. *Brain and Language, 127*(3), 356-365. https://doi.org/10.1016/j.bandl.2013.10.009

Morken, F., Helland, T., Hugdahl, K., & Specht, K. (2017). Reading in dyslexia across literacy development: A longitudinal study of effective connectivity. *NeuroImage, 144*, 92-100. https://doi.org/10.1016/j.neuroimage.2016.09.060

Müller, M. M., Teder-Sälejärvi, W., & Hillyard, S. A. (1998). The time course of cortical facilitation during cued shifts of spatial attention. *Nature Neuroscience, 1*(7), 631-634. https://doi.org/10.1038/2865

Neuling, T., Rach, S., Wagner, S., Wolters, C. H., & Herrmann, C. S. (2012). Good vibrations: Oscillatory phase shapes perception. *NeuroImage, 63*(2), 771-778. https://doi.org/10.1016/j.neuroimage.2012.07.024

Neustadter, E., Mathiak, K., & Turetsky, B. I. (2016). Chapter 13 - EEG and MEG Probes of Schizophrenia Pathophysiology. In T. Abel & T. Nickl-Jockschat (Eds.), *The Neurobiology of Schizophrenia* (pp. 213-236). San Diego, CA: Academic Press.

Niesen, M., Vander Ghinst, M., Bourguignon, M., Wens, V., Bertels, J., Goldman, S., Choufani, G., Hassid, S., & De Tiège, X. (2020). Tracking the effects of top–down attention on word discrimination using frequency-tagged neuromagnetic responses. *Journal of Cognitive Neuroscience, 32*(5), 877-888. https://doi.org/10.1162/jocn_a_01522

Noordenbos, M. W., Segers, E., Mitterer, H., Serniclaes, W., & Verhoeven, L. (2013). Deviant neural processing of phonotactic probabilities in adults with dyslexia. *NeuroReport, 24*(13), 746-750. https://doi.org/10.1097/WNR.0b013e328364b67c

Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of Vision, 15*(6), 4. https://doi.org/10.1167/15.6.4

Nordt, M., Hoehl, S., & Weigelt, S. (2016). The use of repetition suppression paradigms in developmental cognitive neuroscience. *Cortex, 80*, 61-75. http://doi.org/10.1016/j.cortex.2016.04.002

Nozaradan, S., Peretz, I., Missal, M., & Mouraux, A. (2011). Tagging the neuronal entrainment to beat and meter. *Journal of Neuroscience, 31*(28), 10234-10240. https://doi.org/10.1523/jneurosci.0411-11.2011

Ordin, M., Polyanskaya, L., Soto, D., & Molinaro, N. (2020). Electrophysiology of statistical learning: Exploring the online learning process and offline learning product. *European Journal of Neuroscience, 51*(9), 2008-2022. https://doi.org/10.1111/ejn.14657

Osterhout, L., Holcomb, P. J., & Swinney, D. A. (1994). Brain potentials elicited by garden-path sentences: Evidence of the application of verb information during parsing. *Journal of Experimental Psychology: Learning Memory and Cognition, 20*(4), 786-803. https://doi.org/10.1037/0278-7393.20.4.786

Otte, W. M., van Diessen, E., Paul, S., Ramaswamy, R., Subramanyam Rallabandi, V. P., Stam, C. J., & Roy, P. K. (2015). Aging alterations in whole-brain networks during adulthood mapped with the minimum spanning tree indices: The interplay of density, connectivity cost and life-time trajectory. *NeuroImage, 109*, 171-189. https://doi.org/10.1016/j.neuroimage.2015.01.011

Overath, T., McDermott, J. H., Zarate, J. M., & Poeppel, D. (2015). The cortical analysis of speech-specific temporal structure revealed by responses to sound quilts. *Nature Neuroscience, 18*(6), 903-911. https://doi.org/10.1038/nn.4021

Pammer, K. (2013). Temporal sampling in vision and the implications for dyslexia. *Frontiers in Human Neuroscience, 7*, 933. https://doi.org/10.3389/fnhum.2013.00933

Parker, G. J. M., Luzzi, S., Alexander, D. C., Wheeler-Kingshott, C. A. M., Ciccarelli, O., & Lambon Ralph, M. A. (2005). Lateralization of ventral and dorsal auditory-language pathways in the human brain. *NeuroImage, 24*(3), 656-666. https://doi.org/10.1016/j.neuroimage.2004.08.047

Paulesu, E., Démonet, J.-F., Fazio, F., McCrory, E., Chanoine, V., Brunswick, N., Cappa, S. F., Cossu, G., Habib, M., Frith, C. D., & Frith, U. (2001). Dyslexia: Cultural diversity and biological unity. *Science, 291*(5511), 2165-2167. https://doi.org/10.1126/science.1057179

Paulus, W. (2011). Transcranial electrical stimulation (tES – tDCS; tRNS, tACS) methods. *Neuropsychological Rehabilitation, 21*(5), 602-617. https://doi.org/10.1080/09602011.2011.557292

Pavlidou, E. P., & Bogaerts, L. (2019). Implicit statistical learning across modalities and its relationship with reading in childhood. *Frontiers in Psychology, 10*, 1834. https://doi.org/10.3389/fpsyg.2019.01834

Peelen, M. V., Atkinson, A. P., & Vuilleumier, P. (2010). Supramodal representations of perceived emotions in the human brain. *Journal of Neuroscience, 30*(30), 10127-10134. https://doi.org/10.1523/jneurosci.2161-10.2010

Peelle, J. E., & Davis, M. H. (2012). Neural oscillations carry speech rhythm through to comprehension. *Frontiers in Psychology, 3*, 320. https://doi.org/10.3389/fpsyg.2012.00320

Peelle, J. E., Gross, J., & Davis, M. H. (2013). Phase-locked responses to speech in human auditory cortex are enhanced during comprehension. *Cerebral Cortex, 23*(6), 1378-1387. https://doi.org/10.1093/cercor/bhs118

Pei, C., Qiu, Y., Li, F., Huang, X., Si, Y., Li, Y., Zhang, X., Chen, C., Liu, Q., Cao, Z., Ding, N., Gao, S., Alho, K., Yao, D., & Xu, P. (2021). The different brain areas occupied for integrating information of hierarchical linguistic units: A study based on EEG and TMS. *bioXriv*, 2021.11.22.469495. https://doi.org/10.1101/2021.11.22.469495

Pellegrino, F., Coupé, C., & Marsico, E. (2011). A cross-language perspective on speech information rate. *Language, 87*(3), 539-558. https://www.jstor.org/stable/23011654

Peña, M., & Melloni, L. (2012). Brain oscillations during spoken sentence processing. *Journal of Cognitive Neuroscience, 24*(5), 1149-1164. https://doi.org/10.1162/jocn_a_00144

Pennington, B.F. (2006). From single to multiple deficit models of developmental disorders. *Cognition*, *101*, 385-413. https://doi.org/10.1016/j.cognition.2006.04.008

Pennington, B. F., & Peterson, R. L. (2015). Neurodevelopmental disorders: Learning disorders. *Psychiatry, 1*, 765-778. https://doi.org/10.1002/9781118753378.ch46

Perfetti, C., & Helder, A. (2021). Incremental comprehension examined in event-related potentials: Word-to-text integration and structure building. *Discourse Processes, 58*(1), 2-21. https://doi.org/10.1080/0163853x.2020.1743806

Perrachione, T. K., Del Tufo, S. N., Winter, R., Murtagh, J., Cyr, A., Chang, P., Halverson, K., Ghosh, S. S., Christodoulou, J. A., & Gabrieli, J. D. E. (2016). Dysfunction of rapid neural adaptation in dyslexia. *Neuron, 92*(6), 1383-1397. https://doi.org/10.1016/j.neuron.2016.11.020

Perruchet, P., & Pacton, S. (2006). Implicit learning and statistical learning: One phenomenon, two approaches. *Trends in Cognitive Sciences, 10*(5), 233-238. https://doi.org/10.1016/j.tics.2006.03.006

Perruchet, P., & Vinter, A. (1998). PARSER: A model for word segmentation. *Journal of Memory and Language, 39*(2), 246-263. https://doi.org/10.1006/jmla.1998.2576

Peter, B., McCollum, H., Daliri, A., & Panagiotides, H. (2019). Auditory gating in adults with dyslexia: An ERP account of diminished rapid neural adaptation. *Clinical Neurophysiology, 130*(11), 2182-2192. https://doi.org/10.1016/j.clinph.2019.07.028

Peterson, R. L., & Pennington, B. F. (2012). Developmental dyslexia. *The Lancet, 379*(9830), 1997-2007. https://doi.org/10.1016/S0140-6736(12)60198-6

Peterson, R. L., & Pennington, B. F. (2015). Developmental dyslexia. *Annual Review of Clinical Psychology, 11*, 283-307. https://doi.org/10.1146/annurev-clinpsy-032814-112842

Poelmans, H., Luts, H., Vandermosten, M., Boets, B., Ghesquière, P., & Wouters, J. (2011). Reduced sensitivity to slow-rate dynamic auditory information in children with dyslexia. *Research in Developmental Disabilities, 32*(6), 2810-2819. https://doi.org/10.1016/j.ridd.2011.05.025

Poeppel, D. (2003). The analysis of speech in different temporal integration windows: Cerebral lateralization as 'asymmetric sampling in time'. *Speech Communication, 41*(1), 245-255. https://doi.org/10.1016/s0167-6393(02)00107-3

Poeppel, D., & Assaneo, M. F. (2020). Speech rhythms and their neural foundations. *Nature Reviews Neuroscience, 21*, 322-334. https://doi.org/10.1038/s41583-020-0304-4

Poeppel, D., Idsardi, W. J., & van Wassenhove, V. (2008). Speech perception at the interface of neurobiology and linguistics. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*(1493), 1071-1086. https://doi.org/10.1098/rstb.2007.2160

Polanía, R., Michael, Korman, C., Batsikadze, G., & Paulus, W. (2012). The importance of timing in segregated theta phase-coupling for cognitive performance. *Current Biology, 22*(14), 1314-1318. https://doi.org/10.1016/j.cub.2012.05.021

Polanía, R., Nitsche, M. A., & Ruff, C. C. (2018). Studying and modifying brain function with non-invasive brain stimulation. *Nature Neuroscience, 21*(2), 174-187. https://doi.org/10.1038/s41593-017-0054-4

Pothos, E. M., & Kirk, J. (2004). Investigating learning deficits associated with dyslexia. *Dyslexia, 10*(1), 61-76. https://doi.org/10.1002/dys.266

Power, A. J., Colling, L. J., Mead, N., Barnes, L., & Goswami, U. (2016). Neural encoding of the speech envelope by children with developmental dyslexia. *Brain and Language, 160*, 1-10. https://doi.org/10.1016/j.bandl.2016.06.006

Power, A. J., Mead, N., Barnes, L., & Goswami, U. (2013). Neural entrainment to rhythmic speech in children with developmental dyslexia. *Frontiers in Hum Neurosci, 7*, 777. https://doi.org/10.3389/fnhum.2013.00777

Presentation Software. *Version 20.0*. Berkeley, California: Neurobehavioral Systems, Inc.

Priori, A., Hallett, M., & Rothwell, J. C. (2009). Repetitive transcranial magnetic stimulation or transcranial direct current stimulation? *Brain Stimulation, 2*(4), 241-245. https://doi.org/10.1016/j.brs.2009.02.004

Qi, T., Gu, B., Ding, G., Gong, G., Lu, C., Peng, D., Malins, J. G., & Liu, L. (2016). More bilateral, more anterior: Alterations of brain organization in the large-scale structural network in Chinese dyslexia. *NeuroImage, 124*, 63-74. https://doi.org/10.1016/j.neuroimage.2015.09.011

Qi, Z. H., Araujo, Y. S., Georgan, W. C., Gabrieli, J. D. E., & Arciuli, J. (2019). Hearing matters more than seeing: A cross-modality study of statistical learning and reading ability. *Scientific Studies of Reading, 23*(1), 101-115. https://doi.org/10.1080/10888438.2018.1485680

Raij, T., Uutela, K., & Hari, R. (2000). Audiovisual integration of letters in the human brain. *Neuron, 28*(2), 617-625. https://doi.org/10.1016/s0896-6273(00)00138-0

Ralph, M. A. L., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience, 18*(1), 42-55. https://doi.org/10.1038/nrn.2016.150

Ramus, F. (2003). Developmental dyslexia: Specific phonological deficit or general sensorimotor dysfunction? *Current Opinion in Neurobiology, 13*(2), 212-218. https://doi.org/10.1016/S0959-4388(03)00035-7

Ramus, F. (2004). Neurobiology of dyslexia: A reinterpretation of the data. *Trends in Neurosciences, 27*(12), 720-726. https://doi.org/10.1016/j.tins.2004.10.004

Reato, D., Rahman, A., Bikson, M., & Parra, L. C. (2010). Low-intensity electrical stimulation affects network dynamics by modulating population rate and spike timing. *Journal of Neuroscience, 30*(45), 15067-15079. https://doi.org/10.1523/jneurosci.2059-10.2010

Reato, D., Rahman, A., Bikson, M., & Parra, L. (2013). Effects of weak transcranial alternating current stimulation on brain activity — A review of known mechanisms from animal studies. *Frontiers in Human Neuroscience, 7*, 687. https://doi.org/10.3389/fnhum.2013.00687

Regan, D. (1989). *Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine*. Amsterdam, Netherlands: Elsevier.

Richards, T. L., & Berninger, V. W. (2008). Abnormal fMRI connectivity in children with dyslexia during a phoneme task: Before but not after treatment. *Journal of Neurolinguistics, 21*(4), 294-304. https://doi.org/10.1016/j.jneuroling.2007.07.002

Richlan, F. (2012). Developmental dyslexia: Dysfunction of a left hemisphere reading network. *Frontiers in Human Neuroscience, 6*, 120. https://doi.org/10.3389/fnhum.2012.00120

Richlan, F. (2020). The functional neuroanatomy of developmental dyslexia across languages and writing systems. *Frontiers in Psychology, 11*, 155. https://doi.org/10.3389/fpsyg.2020.00155

Richlan, F., Kronbichler, M., & Wimmer, H. (2009). Functional abnormalities in the dyslexic brain: A quantitative meta-analysis of neuroimaging studies. *Human Brain Mapping, 30*(10), 3299-3308. https://doi.org/10.1002/hbm.20752

Riecke, L., Formisano, E., Sorger, B., Baskent, D., & Gaudrain, E. (2018). Neural entrainment to speech modulates speech intelligibility. *Current Biology, 28*(2), 161-169, e5. https://doi.org/10.1016/j.cub.2017.11.033

Riecke, L., Sack, A. T., & Schroeder, C. E. (2015). Endogenous delta/theta sound-brain phase entrainment accelerates the buildup of auditory streaming. *Current Biology, 25*(24), 3196-3201. https://doi.org/10.1016/j.cub.2015.10.045

Riecke, L., & Zoefel, B. (2018). Conveying temporal information to the auditory system via transcranial current stimulation. *Acta Acustica United with Acustica, 104*(5), 883-886. https://doi.org/10.3813/Aaa.919235

Roberts, B. M., Hsieh, L.-T., & Ranganath, C. (2013). Oscillatory activity during maintenance of spatial and temporal information in working memory. *Neuropsychologia, 51*(2), 349-357. https://doi.org/10.1016/j.neuropsychologia.2012.10.009

Rodriguez-Fornells, A., Cunillera, T., Mestres-Misse, A., & de Diego-Balaguer, R. (2009). Neurophysiological mechanisms involved in language learning in adults. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1536), 3711-3735. https://doi.org/10.1098/rstb.2009.0130

Rohe, T., Ehlis, A. C., & Noppeney, U. (2019). The neural dynamics of hierarchical Bayesian causal inference in multisensory perception. *Nature Communications, 10*, 1907. https://doi.org/10.1038/s41467-019-09664-2

Romanovska, L., & Bonte, M. (2021). How learning to read changes the listening brain. *Frontiers in Psychology, 12*, 726882. https://doi.org/10.3389/fpsyg.2021.726882

Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha–gamma versus theta–gamma codes for distinct WM information? *Trends in Cognitive Sciences, 18*(1), 16-25. https://doi.org/10.1016/j.tics.2013.10.010

Rueckl, J. G., Paz-Alonso, P. M., Molfese, P. J., Kuo, W.-J., Bick, A., Frost, S. J., Hancock, R., Wu, D. H., Mencl, W. E., Duñabeitia, J. A., Lee, J.-R., Oliver, M., Zevin, J. D., Hoeft, F., Carreiras, M., Tzeng, O. J. L., Pugh, K. R., & Frost, R. (2015). Universal brain signature of proficient reading: Evidence from four contrasting languages. *Proceedings of the National Academy of Sciences, 112*(50), 15510-15515. https://doi.org/10.1073/pnas.1509321112

Rufener, K. S., Krauel, K., Meyer, M., Heinze, H. J., & Zaehle, T. (2019). Transcranial electrical stimulation improves phoneme processing in developmental dyslexia. *Brain Stimulation, 12*(4), 930-937. https://doi.org/10.1016/j.brs.2019.02.007

Rufener, K. S., & Zaehle, T. (2021). Dysfunctional auditory gamma oscillations in developmental dyslexia: A potential target for a tACS-based intervention. *Progress in Brain Research, 264*, 211-232. https://doi.org/10.1016/bs.pbr.2021.01.016

Saffran, J. R. (2018). Statistical learning as a window into developmental disabilities. *Journal of Neurodevelopmental Disorders, 10*, 35. https://doi.org/10.1186/s11689-018-9252-y

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science, 274*(5294), 1926-1928. https://doi.org/10.1126/science.274.5294.1926

Saffran, J. R., Newport, E. L., & Aslin, R. N. (1996). Word segmentation: The role of distributional cues. *Journal of Memory and Language, 35*(4), 606-621. https://doi.org/10.1006/jmla.1996.0032

Saffran, J. R., Newport, E. L., Aslin, R. N., Tunick, R. A., & Barrueco, S. (1997). Incidental language learning: Listening (and learning) out of the corner of your ear. *Psychological Science, 8*(2), 101-105. https://doi.org/10.1111/j.1467-9280.1997.tb00690.x

Saha, N. M., Del Tufo, S. N., & Cutting, L. E. (2019). Learning lexical information depends upon task, learning approach, and reader subtype. *Journal of Learning Disabilities, 52*(6), 442-455. https://doi.org/10.1177/0022219419862266

Salmelin, R., & Kujala, J. (2006). Neural representation of language: Activation versus long-range connectivity. *Trends in Cognitive Sciences, 10*(11), 519-525. https://doi.org/10.1016/j.tics.2006.09.007

Sanders, L. D., Newport, E. L., & Neville, H. J. (2002). Segmenting nonsense: An event-related potential index of perceived onsets in continuous speech. *Nature Neuroscience, 5*(7), 700-703. https://doi.org/10.1038/nn873

Santoro, R., Moerel, M., De Martino, F., Goebel, R., Ugurbil, K., Yacoub, E., & Formisano, E. (2014). Encoding of natural sounds at multiple spectral and temporal resolutions in the human auditory cortex. *Plos Computational Biology, 10*(1), e1003412. https://doi.org/10.1371/journal.pcbi.1003412

Santos, F. H., Mosbacher, J. A., Menghini, D., Rubia, K., Grabner, R. H., & Cohen Kadosh, R. (2021). Effects of transcranial stimulation in developmental neurocognitive disorders: A critical appraisal. *Progress in Brain Research, 264*, 1-40. https://doi.org/10.1016/bs.pbr.2021.01.012

Saur, D., Kreher, B. W., Schnell, S., Kummerer, D., Kellmeyer, P., Vry, M. S., Umarova, R., Musso, M., Glauche, V., Huber, W., Rijntjes, M., Hennig, J., & Weiller, C. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences, 105*(46), 18035-18040. https://doi.org/10.1073/pnas.0805234105

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience and Biobehavioral Reviews, 34*(7), 1015-1022. https://doi.org/10.1016/j.neubiorev.2009.12.006

Schaerlaekens, A. M., Kohnstamm, G. A., & Lejaegere, M. (1999). *Streeflijst woordenschat voor zesjarigen*: Swets & Zeitlinger.

Schmalz, X., Altoè, G., & Mulatti, C. (2017). Statistical learning and dyslexia: A systematic review. *Annals of Dyslexia, 67*, 147-162. https://doi.org/10.1007/s11881-016-0136-0

Schmalz, X., Marinus, E., Coltheart, M., & Castles, A. (2015). Getting to the bottom of orthographic depth. *Psychonomic Bulletin & Review, 22*(6), 1614-1629. https://doi.org/10.3758/s13423-015-0835-2

Schnitzler, A., & Gross, J. (2005). Normal and pathological oscillatory communication in the brain. *Nature Reviews Neuroscience, 6*(4), 285-296. https://doi.org/10.1038/nrn1650

Schurz, M., Wimmer, H., Richlan, F., Ludersdorfer, P., Klackl, J., & Kronbichler, M. (2015). Resting-state and task-based functional brain connectivity in developmental dyslexia. *Cerebral Cortex, 25*(10), 3502-3514. https://doi.org/10.1093/cercor/bhu184

Sejnowski, T. J., & Paulsen, O. (2006). Network oscillations: Emerging computational principles. *Journal of Neuroscience, 26*(6), 1673-1676. https://doi.org/10.1523/jneurosci.3737-05d.2006

Senkowski, D., Schneider, T. R., Foxe, J. J., & Engel, A. K. (2008). Crossmodal binding through neural coherence: Implications for multisensory processing. *Trends in Neurosciences, 31*(8), 401-409. https://doi.org/10.1016/j.tins.2008.05.002

Sevel, L. S., Craggs, J. G., Price, D. D., Staud, R., & Robinson, M. E. (2015). Placebo analgesia enhances descending pain-related effective connectivity: A dynamic causal modeling study of endogenous pain modulation. *The Journal of Pain, 16*(8), 760-768. https://doi.org/10.1016/j.jpain.2015.05.001

Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Fulbright, R. K., Mencl, W. E., Constable, R. T., Skudlarski, P., Fletcher, J. M., Lyon, G. R., & Gore, J. C. (2001). The neurobiology of dyslexia. *Clinical Neuroscience Research, 1*(4), 291-299. https://doi.org/10.1016/S1566-2772(01)00015-9

Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Mencl, W. E., Fulbright, R. K., Skudlarski, P., Constable, R. T., Marchione, K. E., Fletcher, J. M., Lyon, G. R., & Gore, J. C. (2002). Disruption of posterior brain systems for reading in children with developmental dyslexia. *Biological Psychiatry, 52*(2), 101-110. https://doi.org/10.1016/S0006-3223(02)01365-3

Shaywitz, B. A., Skudlarski, P., Holahan, J. M., Marchione, K. E., Constable, R. T., Fulbright, R. K., Zelterman, D., Lacadie, C., & Shaywitz, S. E. (2007). Age-related changes in reading systems of dyslexic children. *Annals of Neurology, 61*(4), 363-370. https://doi.org/10.1002/ana.21093

Shaywitz, S. E., & Shaywitz, B. A. (2005). Dyslexia (specific reading disability). *Biological Psychiatry, 57*(11), 1301-1309. https://doi.org/10.1016/j.biopsych.2005.01.043

Sheng, J., Zheng, L., Lyu, B., Cen, Z., Qin, L., Tan, L. H., Huang, M. X., Ding, N., & Gao, J. H. (2018). The cortical maps of hierarchical linguistic structures during speech perception. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhy191

Shi, F., Yap, P.-T., Gao, W., Lin, W., Gilmore, J. H., & Shen, D. (2012). Altered structural connectivity in neonates at genetic risk for schizophrenia: A combined study using morphological and white matter networks. *NeuroImage, 62*(3), 1622-1633. https://doi.org/10.1016/j.neuroimage.2012.05.026

Shine, J. M., Bissett, P. G., Bell, P. T., Koyejo, O., Balsters, J. H., Gorgolewski, K. J., Moodie, C. A., & Poldrack, R. A. (2016). The dynamics of functional brain networks: Integrated network states during cognitive task performance. *Neuron, 92*(2), 544-554. https://doi.org/10.1016/j.neuron.2016.09.018

Shine, J. M., & Poldrack, R. A. (2018). Principles of dynamic network reconfiguration across diverse brain states. *NeuroImage, 180*(Pt B), 396-405. https://doi.org/10.1016/j.neuroimage.2017.08.010

Shinkareva, S. V., Malave, V. L., Mason, R. A., Mitchell, T. M., & Just, M. A. (2011). Commonality of neural representations of words and pictures. *NeuroImage, 54*(3), 2418-2425. https://doi.org/10.1016/j.neuroimage.2010.10.042

Shrager, J., & Siegler, R. S. (1998). SCADS: A model of children's strategy choices and strategy discoveries. *Psychological Science, 9*(5), 405-410. https://doi.org/10.1111/1467-9280.00076

Siddiqi, S. H., Kording, K. P., Parvizi, J., & Fox, M. D. (2022). Causal mapping of human brain function. *Nature Reviews Neuroscience*. https://doi.org/10.1038/s41583-022-00583-8

Simanova, I., Hagoort, P., Oostenveld, R., & Van Gerven, M. A. J. (2014). Modality-independent decoding of semantic information from the human brain. *Cerebral Cortex, 24*(2), 426-434. https://doi.org/10.1093/cercor/bhs324

Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. *Annual Review of Physiology, 55*(1), 349-374. https://doi.org/10.1146/annurev.ph.55.030193.002025

Singh, S., & Conway, C. M. (2021). Unraveling the interconnections between statistical learning and dyslexia: A review of recent empirical studies. *Frontiers in Human Neuroscience, 15*, 734179. https://doi.org/10.3389/fnhum.2021.734179

Skeide, M. A., & Friederici, A. D. (2016). The ontogeny of the cortical language network. *Nature Reviews Neuroscience, 17*(5), 323-332. https://doi.org/10.1038/nrn.2016.23

Slone, L. K., & Johnson, S. P. (2015). Infants' statistical learning: 2- and 5-month-olds' segmentation of continuous visual sequences. *Journal of Experimental Child Psychology, 133*, 47-56. https://doi.org/10.1016/j.jecp.2015.01.007

Smalle, E. H. M., Daikoku, T., Szmalec, A., Duyck, W., & Möttönen, R. (2022). Unlocking adults' implicit statistical learning by cognitive depletion. *Proceedings of the National Academy of Sciences, 119*(2), e2026011119. https://doi.org/10.1073/pnas.2026011119

Smit, D. J. A., de Geus, E. J. C., Boersma, M., Boomsma, D. I., & Stam, C. J. (2016). Life-span development of brain network integration assessed with phase lag index connectivity and minimum spanning tree graphs. *Brain Connectivity, 6*(4), 312-325. https://doi.org/10.1089/brain.2015.0359

Smith, G. J., Booth, J. R., & McNorgan, C. (2018). Longitudinal task-related functional connectivity changes predict reading development. *Frontiers in Psychology, 9*, 1754. https://doi.org/10.3389/fpsyg.2018.01754

Snowling, M. J. (1980). The development of grapheme-phoneme correspondence in normal and dyslexic readers. *Journal of Experimental Child Psychology, 29*(2), 294-305. https://doi.org/10.1016/0022-0965(80)90021-1

Snowling, M. J., & Stackhouse, J. (2013). *Dyslexia, speech and language: A practitioner's handbook*: John Wiley & Sons.

Song, K., Meng, M., Chen, L., Zhou, K., & Luo, H. (2014). Behavioral oscillations in attention: rhythmic α pulses mediated through θ band. *The Journal of Neuroscience, 34*(14), 4837-4844. https://doi.org/10.1523/jneurosci.4856-13.2014

Spencer, M., Kaschak, M. P., Jones, J. L., & Lonigan, C. J. (2015). Statistical learning is related to early literacy-related skills. *Reading and Writing, 28*, 467-490. https://doi.org/10.1007/s11145-014-9533-0

Spironelli, C., Penolazzi, B., & Angrilli, A. (2008). Dysfunctional hemispheric asymmetry of theta and beta EEG activity during linguistic tasks in developmental dyslexia. *Biological Psychology, 77*(2), 123-131. https://doi.org/10.1016/j.biopsycho.2007.09.009

Sporns, O. (2011). The human connectome: A complex network. *Annals of the New York Academy of Sciences, 1224*, 109-125. https://doi.org/10.1111/j.1749-6632.2010.05888.x

Sporns, O. (2014). Contributions and challenges for network models in cognitive neuroscience. *Nature Neuroscience, 17*(5), 652-660. https://doi.org/10.1038/nn.3690

Sporns, O., Chialvo, D., Kaiser, M., & Hilgetag, C. (2004). Organization, development and function of complex brain networks. *Trends in Cognitive Sciences, 8*(9), 418-425. https://doi.org/10.1016/j.tics.2004.07.008

Stam, C. J. (2014). Modern network science of neurological disorders. *Nature Reviews Neuroscience, 15*(10), 683-695. https://doi.org/10.1038/nrn3801

Stam, C. J., Nolte, G., & Daffertshofer, A. (2007). Phase lag index: Assessment of functional connectivity from multi channel EEG and MEG with diminished bias from common sources. *Human Brain Mapping, 28*(11), 1178-1193. https://doi.org/10.1002/hbm.20346

Stam, C. J., Tewarie, P., van Dellen, E., van Straaten, E. C. W., Hillebrand, A., & Van Mieghem, P. (2014). The trees and the forest: Characterization of complex brain networks with minimum spanning trees. *International Journal of Psychophysiology, 92*(3), 129-138. https://doi.org/10.1016/j.ijpsycho.2014.04.001

Stam, C. J., & van Straaten, E. C. W. (2012). The organization of physiological brain networks. *Clinical Neurophysiology, 123*(6), 1067-1087. https://doi.org/10.1016/j.clinph.2012.01.011

Stanley, W., Mathews, R., Buss, R., & Kotler-Cope, S. (1989). Insight without awareness: On the interaction of verbalization, instruction and practice in a simulated process control task. *The Quarterly Journal of Experimental Psychology, 41*(3), 553–577. https://doi.org/10.1080/14640748908402382

Stein, J., & Walsh, V. (1997). To see but not to read; the magnocellular theory of dyslexia. *Trends in Neurosciences, 20*(4), 147-152. https://doi.org/10.1016/s0166-2236(96)01005-3

Suckling, J., & Bullmore, E. (2004). Permutation tests for factorially designed neuroimaging experiments. *Human Brain Mapping, 22*(3), 193-205. https://doi.org/10.1002/hbm.20027

Symons, A. E., Dick, F., & Tierney, A. T. (2021). Dimension-selective attention and dimensional salience modulate cortical tracking of acoustic dimensions. *NeuroImage, 244*, 118544. https://doi.org/10.1016/j.neuroimage.2021.118544

Tallal, P. (1980). Auditory temporal perception, phonics, and reading disabilities in children. *Brain and Language, 9*(2), 182-198. https://doi.org/10.1016/0093-934x(80)90139-x

Tan, L. H., Laird, A. R., Li, K., & Fox, P. T. (2005). Neuroanatomical correlates of phonological processing of Chinese characters and alphabetic words: A meta-analysis. *Human Brain Mapping, 25*(1), 83-91. https://doi.org/10.1002/hbm.20134

Taskov, T., & Dushanova, J. (2020). Reading-network in developmental dyslexia before and after visual training. *Symmetry, 12*(11), 1842. https://doi.org/10.3390/sym12111842

ten Oever, S., de Graaf, T. A., Bonnemayer, C., Ronner, J., Sack, A. T., & Riecke, L. (2016). Stimulus presentation at specific neuronal oscillatory phases experimentally controlled with tACS: Implementation and applications. *Frontiers in Cellular Neuroscience, 10*, 240. https://doi.org/10.3389/fncel.2016.00240.

ten Oever, S., & Sack, A. T. (2015). Oscillatory phase shapes syllable perception. *Proceedings of the National Academy of Sciences, 112*(52), 15833-15837. https://doi.org/10.1073/pnas.1517519112

Teng, X., Tian, X., Doelling, K., & Poeppel, D. (2018). Theta band oscillations reflect more than entrainment: Behavioral and neural evidence demonstrates an active chunking process. *European Journal of Neuroscience, 48*(8), 2770-2782. https://doi.org/10.1111/ejn.13742

Tewarie, P., van Dellen, E., Hillebrand, A., & Stam, C. J. (2015). The minimum spanning tree: An unbiased method for brain network analysis. *NeuroImage, 104*, 177-188. https://doi.org/10.1016/j.neuroimage.2014.10.015

Thatcher, R. W., North, D. M., & Biver, C. J. (2008). Development of cortical connections as measured by EEG coherence and phase delays. *Human Brain Mapping, 29*(12), 1400-1415. https://doi.org/10.1002/hbm.20474

Theiler, J., Eubank, S., Longtin, A., Galdrikian, B., & Doyne Farmer, J. (1992). Testing for nonlinearity in time series: The method of surrogate data. *Physica D: Nonlinear Phenomena, 58*(1-4), 77-94. https://doi.org/10.1016/0167-2789(92)90102-s

Thiessen, E. D. (2017). What's statistical about learning? Insights from modelling statistical learning as a set of memory processes. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1711). https://doi.org/10.1098/rstb.2016.0056

Thiessen, E. D., Girard, S., & Erickson, L. C. (2016). Statistical learning and the critical period: How a continuous learning mechanism can give rise to discontinuous learning. *Wiley Interdisciplinary Reviews: Cognitive Science, 7*(4), 276-288. https://doi.org/10.1002/wcs.1394

Thompson-Schill, S. L., Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology, 15*(2), 219-224. https://doi.org/10.1016/j.conb.2005.03.006

Thut, G., Schyns, P., & Gross, J. (2011). Entrainment of perceptually relevant brain oscillations by non-invasive rhythmic stimulation of the human brain. *Frontiers in Psychology, 2*, 170. https://doi.org/10.3389/fpsyg.2011.00170

Tong, S. X., Zhang, P., & He, X. (2020). Statistical learning of orthographic regularities in Chinese children with and without dyslexia. *Child Development, 91*(6), 1953-1969. https://doi.org/10.1111/cdev.13384

Tong, X., Wang, Y., & Tong, S. X. (2020). The neural signature of statistical learning of orthography. *Frontiers in Human Neuroscience, 14*, 26. https://doi.org/10.3389/fnhum.2020.00026

Tóth, B., Janacsek, K., Takács, Á., Kóbor, A., Zavecz, Z., & Nemeth, D. (2017). Dynamics of EEG functional connectivity during statistical learning. *Neurobiology of Learning and Memory, 144*, 216-229. https://doi.org/10.1016/j.nlm.2017.07.015

Turk-Browne, N. B., Scholl, B. J., & Chun, M. M. (2008). Babies and brains: Habituation in infant cognition and functional neuroimaging. *Frontiers in Human Neuroscience, 2*, 16. https://doi.org/10.3389/neuro.09.016.2008

Turker, S., & Hartwigsen, G. (2021). The use of noninvasive brain stimulation techniques to improve reading difficulties in dyslexia: A systematic review. *Human Brain Mapping*. https://doi.org/10.1002/hbm.25700

Tyler, L. K., & Marslen-Wilson, W. (2008). Fronto-temporal brain systems supporting spoken language comprehension. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*(1493), 1037-1054. https://doi.org/10.1098/rstb.2007.2158

Uddin, L. Q., Supekar, K. S., Ryali, S., & Menon, V. (2011). Dynamic reconfiguration of structural and functional connectivity across core neurocognitive brain networks with development. *Journal of Neuroscience, 31*(50), 18578-18589. https://doi.org/10.1523/JNEUROSCI.4465-11.2011

van Atteveldt, N., Formisano, E., Goebel, R., & Blomert, L. (2004). Integration of letters and speech sounds in the human brain. *Neuron, 43*(2), 271-282. https://doi.org/10.1016/j.neuron.2004.06.025

van Bergen, E., van der Leij, A., & de Jong, P.F. (2014). The intergenerational multiple deficit model and the case of dyslexia. *Frontiers in Human Neuroscience*, *8*, 346. https://doi.org/10.3389/fnhum.2014.00346

van Dellen, E., Douw, L., Hillebrand, A., de Witt Hamer, P. C., Baayen, J. C., Heimans, J. J., Reijneveld, J. C., & Stam, C. J. (2014). Epilepsy surgery outcome and functional network alterations in longitudinal MEG: a minimum spanning tree analysis. *NeuroImage, 86*, 354-363. https://doi.org/10.1016/j.neuroimage.2013.10.010

van den Bos, K., & Lutje Spelberg, H. (2007). Continu Benoemen & Woorden Lezen (CB&WL)[Continuous naming & word reading]. *Amsterdam, Netherlands: Boom*.

van den Heuvel, M. P., & Sporns, O. (2013). Network hubs in the human brain. *Trends in Cognitive Sciences, 17*(12), 683-696. https://doi.org/10.1016/j.tics.2013.09.012

van den Heuvel, M. P., & Sporns, O. (2019). A cross-disorder connectome landscape of brain dysconnectivity. *Nature Reviews Neuroscience, 20*(7), 435-446. https://doi.org/10.1038/s41583-019-0177-6

van der Mark, S., Klaver, P., Bucher, K., Maurer, U., Schulz, E., Brem, S., Martin, E., & Brandeis, D. (2011). The left occipitotemporal system in reading: Disruption of focal fMRI connectivity to left inferior frontal and inferior parietal language areas in children with dyslexia. *NeuroImage, 54*(3), 2426-2436. https://doi.org/10.1016/j.neuroimage.2010.10.002

Van Ingelghem, M., van Wieringen, A., Wouters, J., Vandenbussche, E., Onghena, P., & Ghesquière, P. (2001). Psychophysical evidence for a general temporal processing deficit in children with dyslexia. *NeuroReport, 12*(16), 3603-3607. https://doi.org/10.1097/00001756-200111160-00046

Van Mieghem, P., & Magdalena, S. M. (2005). Phase transition in the link weight structure of networks. *Physical Review E, 72*(5), 056138. https://doi.org/10.1103/physreve.72.056138

van Witteloostuijn, M., Boersma, P., Wijnen, F., & Rispens, J. (2017). Visual artificial grammar learning in dyslexia: A meta-analysis. *Research in Developmental Disabilities, 70*, 126-137. https://doi.org/10.1016/j.ridd.2017.09.006

Vandermosten, M., Wouters, J., Ghesquière, P., & Golestani, N. (2019). Statistical learning of speech sounds in dyslexic and typical reading children. *Scientific Studies of Reading, 23*(1), 116-127. https://doi.org/10.1080/10888438.2018.1473404

VanRullen, R. (2016). Perceptual cycles. *Trends in Cognitive Sciences, 20*(10), 723-735. https://doi.org/10.1016/j.tics.2016.07.006

Vasic, N., Lohr, C., Steinbrink, C., Martin, C., & Wolf, R. C. (2008). Neural correlates of working memory performance in adolescents and young adults with dyslexia. *Neuropsychologia, 46*(2), 640-648. https://doi.org/10.1016/j.neuropsychologia.2007.09.002

Velde, B., Haartsen, R., & Kemner, C. (2019). Test-retest reliability of EEG network characteristics in infants. *Brain and Behavior, 9*(5), e01269. https://doi.org/10.1002/brb3.1269

Vidyasagar, T. R. (2013). Reading into neuronal oscillations in the visual system: Implications for developmental dyslexia. *Frontiers in Human Neuroscience, 7*, 811. https://doi.org/10.3389/fnhum.2013.00811

Vidyasagar, T. R., & Pammer, K. (2010). Dyslexia: A deficit in visuo-spatial attention, not in phonological processing. *Trends in Cognitive Sciences, 14*(2), 57-63. https://doi.org/10.1016/j.tics.2009.12.003

Vignali, L., Himmelstoss, N. A., Hawelka, S., Richlan, F., & Hutzler, F. (2016). Oscillatory brain dynamics during sentence reading: A fixation-related spectral perturbation analysis. *Frontiers in Human Neuroscience, 10*, 191. https://doi.org/10.3389/fnhum.2016.00191

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., Mazoyer, B., & Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage, 30*(4), 1414-1432. https://doi.org/10.1016/j.neuroimage.2005.11.002

Viswanathan, V., Bharadwaj, H. M., & Shinn-Cunningham, B. G. (2019). Electroencephalographic signatures of the neural representation of speech during selective attention. *eNeuro, 6*(5), 0057-19. https://doi.org/10.1523/Eneuro.0057-19.2019

Volfart, A., Rice, G. E., Lambon Ralph, M. A., & Rossion, B. (2021). Implicit, automatic semantic word categorisation in the left occipito-temporal cortex as revealed by fast periodic visual stimulation. *NeuroImage, 238*, 118228. https://doi.org/10.1016/j.neuroimage.2021.118228

von Stein, A., & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology, 38*(3), 301-313. https://doi.org/10.1016/S0167-8760(00)00172-0

Voss, J. L., & Federmeier, K. D. (2011). FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. *Psychophysiology, 48*(4), 532-546. https://doi.org/10.1111/j.1469-8986.2010.01085.x

Vosskuhl, J., Strüber, D., & Herrmann, C. S. (2018). Non-invasive brain stimulation: A paradigm shift in understanding brain oscillations. *Frontiers in Human Neuroscience, 12*, 211. https://doi.org/10.3389/fnhum.2018.00211

Vourkas, M., Karakonstantaki, E., Simos, P. G., Tsirka, V., Antonakakis, M., Vamvoukas, M., Stam, C. J., Dimitriadis, S., & Micheloyannis, S. (2014). Simple and difficult mathematics in children: A minimum spanning tree EEG network analysis. *Neuroscience Letters, 576*, 28-33. https://doi.org/10.1016/j.neulet.2014.05.048

Vourkas, M., Micheloyannis, S., Simos, P. G., Rezaie, R., Fletcher, J. M., Cirino, P. T., & Papanicolaou, A. C. (2011). Dynamic task-specific brain network connectivity in children with severe reading difficulties. *Neuroscience Letters, 488*(2), 123-128. https://doi.org/10.1016/j.neulet.2010.11.013

Wang, F., Kaneshiro, B., Strauber, C. B., Hasak, L., Nguyen, Q. T. H., Yakovleva, A., Vildavski, V. Y., Norcia, A. M., & Mccandliss, B. D. (2021). Distinct neural sources underlying visual word form processing as

revealed by steady state visual evoked potentials (SSVEP). *Scientific Reports, 11*(1). https://doi.org/10.1038/s41598-021-95627-x

Wang, Z., Cheng-Lai, A., Song, Y., Cutting, L., Jiang, Y., Lin, O., Meng, X., & Zhou, X. (2014). A perceptual learning deficit in Chinese developmental dyslexia as revealed by visual texture discrimination training. *Dyslexia, 20*(3), 280-296. https://doi.org/10.1002/dys.1475

Wenger, E., Brozzoli, C., Lindenberger, U., & Lövdén, M. (2017). Expansion and renormalization of human brain structure during skill acquisition. *Trends in Cognitive Sciences, 21*(12), 930-939. https://doi.org/10.1016/j.tics.2017.09.008

Werker, J. F., & Hensch, T. K. (2015). Critical periods in speech perception: New directions. *Annual Review of Psychology, 66*(1), 173-196. https://doi.org/10.1146/annurev-psych-010814-015104

Widmann, A., Schröger, E., & Maess, B. (2015). Digital filter design for electrophysiological data – a practical approach. *Journal of Neuroscience Methods, 250*, 34-46. https://doi.org/10.1016/j.jneumeth.2014.08.002

Will, U., & Berg, E. (2007). Brain wave synchronization and entrainment to periodic acoustic stimuli. *Neuroscience Letters, 424*(1), 55-60. https://doi.org/10.1016/j.neulet.2007.07.036

Wilson, S. M., Bautista, A., & McCarron, A. (2018). Convergence of spoken and written language processing in the superior temporal sulcus. *NeuroImage, 171*, 62-74. https://doi.org/10.1016/j.neuroimage.2017.12.068

Wimmer, H., & Schurz, M. (2010). Dyslexia in regular orthographies: Manifestation and causation. *Dyslexia, 16*(4), 283-299. https://doi.org/10.1002/dys.411

Wolf, M., & Bowers, P. G. (1999). The double-deficit hypothesis for the developmental dyslexias. *Journal of Educational Psychology, 91*(3), 415-438. https://doi.org/10.1037/0022-0663.91.3.415

Wolf, R. C., Sambataro, F., Lohr, C., Steinbrink, C., Martin, C., & Vasic, N. (2010). Functional brain network abnormalities during verbal working memory performance in adolescents and young adults with dyslexia. *Neuropsychologia, 48*(1), 309-318. https://doi.org/10.1016/j.neuropsychologia.2009.09.020

Xu, M., Yang, J., Siok, W. T., & Tan, L. H. (2015). Atypical lateralization of phonological working memory in developmental dyslexia. *Journal of Neurolinguistics, 33*, 67-77. https://doi.org/10.1016/j.jneuroling.2014.07.004

Xu, W. Y., Kolozsvari, O. B., Oostenveld, R., & Hämäläinen, J. A. (2020). Rapid changes in brain activity during learning of grapheme-phoneme associations in adults. *NeuroImage, 220*, 117058. https://doi.org/10.1016/j.neuroimage.2020.117058

Xue, H., Wang, Z., Tan, Y., Yang, H., Fu, W., Xue, L., & Zhao, J. (2020). Resting-state EEG reveals global network deficiency in dyslexic children. *Neuropsychologia, 138*, 107343. https://doi.org/10.1016/j.neuropsychologia.2020.107343

Yang, C. L., Perfetti, C. A., & Schmalhofer, F. (2007). Event-related potential indicators of text integration across sentence boundaries. *Journal of Experimental Psychology: Learning Memory and Cognition, 33*(1), 55-89. https://doi.org/10.1037/0278-7393.33.1.55

Yang, J., & Tan, L. H. (2020). Whole-brain functional networks for phonological and orthographic processing in Chinese good and poor readers. *Frontiers in Psychology, 10*, 2945. https://doi.org/10.3389/fpsyg.2019.02945

Younger, J. W., & Booth, J. R. (2018). Parietotemporal stimulation affects acquisition of novel grapheme-phoneme mappings in adult readers. *Frontiers in Human Neuroscience, 12*, 109. https://doi.org/10.3389/fnhum.2018.00109

Žarić, G., Correia, J. M., Fraga-González, G., Tijms, J., Van Der Molen, M. W., Blomert, L., & Bonte, M. (2017). Altered patterns of directed connectivity within the reading network of dyslexic children and their relation to reading dysfluency. *Developmental Cognitive Neuroscience, 23*, 1-13. https://doi.org/10.1016/j.dcn.2016.11.003

Zhang, G., Si, Y., & Dang, J. (2019). Revealing the dynamic brain connectivity from perception of speech sound to semantic processing by EEG. *Neuroscience, 415*, 70-76. https://doi.org/10.1016/j.neuroscience.2019.07.023

Zhang, H., Watrous, A. J., Patel, A., & Jacobs, J. (2018). Theta and alpha oscillations are traveling waves in the human neocortex. *Neuron, 98*(6), 1269-1281, e4. https://doi.org/10.1016/j.neuron.2018.05.019

Zhang, J., Liu, L., Li, H., Feng, X., Zhang, M., Liu, L., Meng, X., & Ding, G. (2021). Large-scale network topology reveals brain functional abnormality in Chinese dyslexic children. *Neuropsychologia, 157*, 107886. https://doi.org/10.1016/j.neuropsychologia.2021.107886

Zhang, M., Riecke, L., & Bonte, M. (2021). Neurophysiological tracking of speech-structure learning in typical and dyslexic readers. *Neuropsychologia*, *158*, 107889. https://doi.org/10.1016/j.neuropsychologia.2021.107889

Zhang, M., Riecke, L., Fraga-González, G., & Bonte, M. (2022). Altered brain network topology during speech tracking in developmental dyslexia. *NeuroImage*, *254*, 119142. https://doi.org/10.1016/j.neuroimage.2022.119142

Zhang, M., Xie, W., Xu, Y., & Meng, X. (2018). Auditory temporal perceptual learning and transfer in Chinese-speaking children with developmental dyslexia. *Research in Developmental Disabilities, 74*, 146-159. https://doi.org/10.1016/j.ridd.2018.01.005

Ziegler, J. C., & Goswami, U. (2005). Reading acquisition, developmental dyslexia, and skilled reading across languages: A psycholinguistic grain size theory. *Psychological Bulletin, 131*(1), 3-29. https://doi.org/10.1037/0033-2909.131.1.3

Ziegler, J. C., Perry, C., Ma-Wyatt, A., Ladner, D., & Schulte-Körne, G. (2003). Developmental dyslexia in different languages: Language-specific or universal? *Journal of Experimental Child Psychology, 86*(3), 169-193. https://doi.org/10.1016/s0022-0965(03)00139-5

Zoefel, B., Davis, M. H., Valente, G., & Riecke, L. (2019). How to test for phasic modulation of neural and behavioural responses. *NeuroImage, 202*, 116175. https://doi.org/10.1016/j.neuroimage.2019.116175

# Appendix

Impact Paragraph

How do we learn and understand language? This is probably not only one of the most fascinating and difficult questions for scientists, but also one that each of us will be curious and amazed about at some point in our lives. One way to understand the mystery of language processing is to study its fine-grained brain mechanisms. Research has shown that our brain can align its rhythmic activity, i.e., neural oscillations, to track the hierarchical structure of speech, where smaller units (e.g., syllables) are integrated into larger ones (e.g., words) to convey increasingly complex information. Similar mechanisms seem to apply to reading; however, this topic has been investigated much less so far. Thus, the current research aimed to study how the brain oscillations align to varying units of spoken and written language (here: familiar words, artificial words, random syllables and tones), and whether such mechanism differs in individuals with developmental dyslexia. We took advantage of electroencephalography (EEG) and transcranial alternating current stimulation (tACS), which are non-invasive methods that allow us to measure and modulate brain oscillations during sensory and language processing.

We found that slow cortical oscillations (here: < 8 Hz) did not appear to influence the auditory perception of transient changes (i.e., shorter than syllable length) in simple tones. However, they contributed to the integration of single syllables to familiar and artificial words. In particular, the work presented in this thesis showed that our brain can pick up repeating patterns (here: three-syllable artificial words) in continuous speech by gradually synchronizing its slow cortical oscillations with the implicitly detected word structures. Furthermore, the integration of syllables to words triggers a shift in the network organization of slow cortical oscillations across the brain toward a more globally interconnected pattern, potentially coordinating the higher-level processing of word information. Intriguingly, adults with dyslexia showed a slower build-up of word tracking responses during the learning of artificial words, and a different global brain network organization for syllable-to-word integration compared to typical readers. We also saw that better reading skills were associated with faster learning of artificial words and less long-range connectivity in tracking familiar words. These findings indicate that dyslexic readers tend to rely more heavily on larger, familiar language units and might use additional brain areas to understand language structures. In addition, we observed spatially separated slow cortical oscillations for the processing of spoken and written syllables, whereas the processing of meaningful words exhibited largely common mechanisms independently of input modality. This implies that the existing theoretical framework and research methods on speech perception may lay the foundation for further understanding of reading comprehension.

Together, our findings highlight the plasticity and adaptability of the human brain in language learning and comprehension, and shed light on this topic from more dynamic (concerning the learning course) and more coordinated (concerning the network organization) perspectives. We also call for further research on a longer timescale to explore how local and large-scale oscillatory activities interact to modulate spoken and written language comprehension as children learn to read. Moreover, we made a step forward to bridge the research gap between the processing of spoken and written language, targeting a critical "structure building" process. This may contribute to future studies on the incremental process of natural reading. Importantly, by including dyslexic readers in our research, this dissertation extends our understanding of reading difficulties from deficient auditory (phonological) and/or visual (orthographical) processing to the learning and integration of larger, more complex language structures. This could be especially useful for recognizing and improving the dysfluent reading in individuals with (familial risk of) dyslexia. Future research could apply the learning paradigm used in Chapter 3, in combination with non-invasive brain stimulation tools (such as tACS), to help beginning and dyslexic readers learn new structures in both spoken and written languages. Such investigations may eventually give insights into the development of neuroscience-warranted tools that benefit the early detection and tailored intervention of dyslexia.

The research findings reported in this dissertation have been presented at several (inter)national scientific conferences to contribute to the scientific exchange and progress in the field. All these findings either have been or will be published in open access journals to support accessibility to the scientific community. To promote science communication and collaboration with non-Dutch speaking communities, the research has also been shared with research teams in China and the United States. This may inspire future research into cross-linguistic differences in the development of language, literacy, and bilingualism. Moreover, aspects of the current dissertation concerning dyslexia have been shared with the general public in the Netherlands via local[1] and social[2] media, and on the website of our research group[3].

---

[1] Universiteit van Nederland, https://www.universiteitvannederland.nl/college/hoe-ontstaat-dyslexie

[2] Facebook page "Brain & Language Maastricht", https://www.facebook.com/BrainLanguageMaastricht

[3] M-BIC Brain and Language group, https://mbic-languagelab.nl/en/

# Appendix

Curriculum Vitae

Manli Zhang (张曼莉) was born on September 6<sup>th</sup>, 1991, in Shanghai, China. As one of the first students to enroll in the multi-language (English-Japanese) program, she completed her secondary education at Shanghai Ganquan Foreign Languages Middle School in 2010. Receiving the Freshman Scholarship, Manli went to Beijing and started her bachelor studies in Psychology at Peking University. After exploring her research interests in two internships, where she studied (1) the cross-linguistic differences in early vocabulary acquisition, and (2) the perceptual deficits of developmental dyslexia, she decided to pursue a career in research. She then enrolled in the Research Master program in Developmental and Educational Psychology at Peking University in 2014, with the support of a postgraduate scholarship. Under the supervision of Prof. Xiangzhi Meng, Manli investigated the deficit profiles of (multi-)sensory perception and implemented self-adaptive perceptual training programs in Chinese children with dyslexia. This led her to become fascinated with the "black box" in the brain that governs learning and development, and left four keywords in her mind: *Language*, *Learning*, *Rhythm*, and *Network*. Thus, in her master's thesis, Manli used fMRI to explore the neural substrates of bilingual reading, with a particular focus on interregional connectivity and the balance between "specialization" and "integration" of sub-systems in the brain. She received substantial input on this project from collaborators at the State Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University. In 2017, Manli obtained a Master's degree and the China Scholarship Council (CSC) scholarship to continue her scientific journey as a PhD in Cognitive Neuroscience at Maastricht University. Integrating the four keywords in her EEG and tACS projects, Manli worked closely with Prof. Milene Bonte and Dr. Lars Riecke to investigate the cortical tracking of spoken and written language structures in readers with and without dyslexia. This further motivated her to utilize brain imaging and stimulation tools to assess and facilitate the learning processes of children with special needs. From July, 2022, Manli will start a new chapter in her life as a postdoctoral fellow in Educational Neuroscience at the University of Hong Kong. She will join Prof. Xiuli Shelley Tong's team to study the visual statistical learning of Chinese characters and develop intervention programs for children with dyslexia.

# Appendix

Publications

# Peer-reviewed publications

Li, H., Marks, R. A., Liu, L., Feng, X., **Zhang, M.**, Ai, F., Gao, Y., Tian, M., Yang, X., Zhang, J., Zhong, H., Liu, L., Meng, X., & Ding. G. (2022). The selective contributions of right cerebellar lobules to reading. *Brain Structure and Function, 227*, 963–977.

**Zhang, M.**, Fraga-González, G., Riecke, L., & Bonte, M. (2022). Altered brain network topology during speech tracking in developmental dyslexia. *NeuroImage, 254*, 119142.

**Zhang, M.**, Riecke, L., & Bonte, M. (2021). Neurophysiological tracking of speech-structure learning in typical and dyslexic readers. *Neuropsychologia, 158*, 107889.

Zhang, J., Liu, L., Li, H., Feng, X., **Zhang, M.,** Liu, L., Meng, X., & Ding, G. (2021). Large-scale network topology reveals brain functional abnormality in Chinese dyslexic children. *Neuropsychologia, 157*, 107886.

Yang, X., Zhang, J., Lu, Y., Ding, G., **Zhang, M.,** Meng, X., & Song, Y. (2021). Failure of resting-state frontal-occipital connectivity in linking visual perception with reading fluency in Chinese children with developmental dyslexia. *NeuroImage, 233*, 117911.

**Zhang, M.**, Amon, A., Hanssen, S., Wu, M., Bonte, M., & Riecke, L. (2021). No evidence for modulation of sound rise-time perception by 4-Hz brain oscillations. *Brain Stimulation*, *14*(2), 364-365.

Li, H., Booth, J. R., Feng, X., Wei, N., **Zhang, M.**, Zhang, J., Zhong, H., Lu, C., Liu, L., Meng, X., & Ding. G. (2020). Functional parcellation of the right cerebellar lobule VI in children with normal or impaired reading. *Neuropsychologia, 148*, 107630.

Ang, C., Zhang, J., Chu, M., Li, H., Tian, M., Feng, X., **Zhang, M.**, Liu, L., Meng, X. & Ding, G. (2020). Intrinsic cerebro-cerebellar functional connectivity reveals the function of cerebellum VI in reading-related skills. *Frontiers in Psychology, 11*, 420.

Gao, Y., Zheng, L., Liu, X., Nichols, E. S., **Zhang, M.**, Shang, L., Ding, G., Meng, X. & Liu, L. (2019). First and second language reading difficulty among Chinese-English bilingual children: The prevalence and influences from demographic characteristics. *Frontiers in Psychology, 10*, 2544.

Li, H., Booth, J. R., Belanger, N. N., Feng, X., Tian, M., Xie, W., **Zhang, M.**, Gao, Y., Ang, C., Yang, X., Liu, L., Meng, X. & Ding, G. (2018). Structural correlates of literacy difficulties in the second language: Evidence from Mandarin-speaking children learning English. *NeuroImage, 179*, 288–297.

**Zhang, M.**, Meng, X. & Zheng, X. (2018). The temporal processing deficit in Chinese children with developmental dyslexia: Evidence from perceptual learning studies. *Studies of Psychology and Behavior*, *16*(5), 583–593.

**Zhang, M.**, Xie, W., Xu, Y. & Meng, X. (2018). Auditory temporal perceptual learning and transfer in Chinese-speaking children with developmental dyslexia. *Research in Developmental Disabilities, 74*, 146–159.

Feng, X., Li, L., **Zhang, M.**, Yang, X., Tian, M., Xie, W., Lu, Y., Liu, L., Meng, X. & Ding, G. (2017). Dyslexic children show atypical cerebellar activation and cerebro-cerebellar functional connectivity in orthographic and phonological processing. *Cerebellum, 16*(2), 496–507.

Chen, L., **Zhang, M.**, Ai, F., Xie, W. & Meng, X. (2016). Crossmodal synesthetic congruency improves visual timing in dyslexic children. *Research in Developmental Disabilities, 55*, 14–26.

Liu, L., Li, H., **Zhang, M.**, Wang, Z., Wei, N., Liu, L., Meng, X. & Ding, G. (2016). Aberrant topologies and reconfiguration pattern of functional brain network in children with second language reading impairment. *Developmental Science, 19*(4), 657–672.

# Manuscripts in preparation

**Zhang, M.**, Riecke, L., & Bonte, M. (Under review). Cortical tracking of language structures: Modality-dependent and supra-modal responses.

**Zhang, M.**, Riecke, L., & Bonte, M. (In preparation). The implicit learning of speech-print associations in continuous language streams.

## Conference contributions

**Zhang, M.**, Riecke, L. & Bonte, M. (2019). Poster: Tracking the implicit phonological learning of speech using EEG. In *Eleventh Annual Meeting of the Society for the Neurobiology of Language*, Helsinki, Finland.

**Zhang, M.**, Feng, X., Gao, Y., Yang, X., Xie, W., Ai, F., Li, H., Zhao, X., Zhang, C. Liu, L., Ding, G. & Meng, X. (2017). Poster + Data Blitz: Language-modulated deficits and compensation: Effective and functional connectivity analysis of L1 and L2 reading impairments in Chinese-English bilingual children. In *Cognitvie Neuroscience Society 24th Annual Meeting*, San Francisco, USA.

**Zhang, M.**, Xie, W. & Meng, X. (2015). Presentation: No root no fruit: Auditory temporal processing training enhanced phonological and reading performance in Chinese children with developmental dyslexia. In *The 18th Annual Meeting of the National Academic Congress of Psychology*, China.

# Appendix

## Acknowledgements

Completing this dissertation, a product of nearly five years' work, I feel deeply indebted to a great many people who have supported me along the way. Most of all, I am tremendously fortunate to have Milene and Lars as my supervisors. Thank you both for stirring my wild explorations into scientific thoughts, for pulling me back to earth before I got overwhelmed, and for always believing in me when I had doubts.

My biggest thank you goes to Milene, a passionate scientist, devoted supervisor, and authentic friend. I still remember that we had seven rounds of revision to the research proposal before I got the CSC scholarship. Ever since then, I know that my ideas will be valued and that I will have your support in every attempt I make. Time has proved me right, and told me more. I enjoy the weekly meetings that we exchange thoughts, smoothly and effectively. You are always able to help me get back on track, putting ideas into action. I love the atmosphere you have created in the MBIC language group, fostering thinking, caring and collaboration. I cannot count how many times you have cheered me up when I was feeling down (e.g., paper got rejected), by letting me know that our work worth the (extra) effort. Your insights, confidence and strength have been inspiring me to step forward and conquer the hurdles ahead of me.

I really appreciate Lars's intellectual input, swift feedback, and continuous support during my PhD study. Your immense knowledge and critical thinking have helped me tackle various obstacles and narrow things down. It was your insightful comments that helped me tell the stories more precisely and more concisely. (Sorry though, I decided to spare no words in expressing my gratitude.) And thanks to you, I got acquainted with brain stimulation techniques, which absolutely opened a new path for me in future research. I admire the way you communicate your opinions when you respectfully disagree with someone (e.g., the reviewers). It has energized me to believe in my work, my team and myself.

Thank you both for being with me through every thick in thin. I sincerely hope I continue to have opportunities to interact with you for the rest of my research career.

I would like to express my appreciation to my dissertation committee – not only for their time and patience, but also for their intellectual contributions to my development as a young scientist. Moreover, special thanks to The Netherlands

I had the pleasure of working with the most brilliant and sweetest colleagues at the MBIC language group. Thank you all for giving me such a warm welcome from day one. Bernadette, your warm smile, calm voice, and friendly presence always have a soft, encouraging glow. And your insightful questions at the group meeting have helped me see the bigger picture. Your care for everyone is reflected in every detail, e.g., "It's raining! Manli needs an umbrella because she wears glasses!"[4] I am grateful to have worked by your side. Francesco, you can easily make everyone laugh, so I really enjoyed the meetings and lectures (e.g., Research Practical) when you were present. Also, I got to know about many different projects and ideas through you, so thanks a lot for the great opportunities that you extended to me. Alex, my perfect office mate, it is wonderful to have you around. Many thanks for helping me learn and set up the EEG experiments, and more importantly, always being available when I need someone to talk to. I am more than happy to share the cheerful moment that you earned your PhD. Linda, I knew I was going to fall into your smile when I saw your photo on the group website. It was always fun to have your company when we traveled to conferences/workshops. Your books and notes on statistical modeling were super helpful and I appreciate your generous sharing. Gorka, although technically not a MBIC group member, I would like to thank you for onboarding to my project. If it were not for your help (in both data analysis and paper writing), my vague idea would never have developed into a full study. Alex, Linda and Gorka, I wish you all the best in your amazing new roles!

Meanwhile, I am very grateful to my supervisor, lab-mates, and roommates at PKU. Prof. Meng, your enthusiasm for research opened up my avenue to developmental and educational science. You made an excellent example to think bigger and dive deeper. Words are powerless to express my gratitude to your continuous guidance and support. Xiujie (Amy), you are the most warm-hearted and open-minded person I have ever met. What impresses me the most is your flowing gentleness and serene firmness, to everyone and everything. I am proud to have you as my role model beyond any particular social role. The most joyful moment in 2021 is

---

[4] April 2019, in San Sebastian.

definitely the happy arrival of your little angel, our beloved Jessie! Give her my share of love too!! Weiyi and Yanzhi, one may wonder why you insist on taking the hard road. It is in your shining eyes that I see the answers, and in your footsteps that I follow. "*Ichi-go ichi-e*"[5], I shall cherish every moment we share because I know your pursuit will never end. Wei and Yuan, thank you for visiting me in the Netherlands. It was you who encouraged me to step out of my comfort zone and look for PhD opportunities in Europe. Spot on, roomies! It is the best decision ever.

My sincere gratitude should be extended to those who have inspired me in different aspects. I miss the old days at Ganquan where I became interested in languages. In 2009, I saw an MRI image of the hippocampus on *Mr. Brain*[6], which started a flame of neuroscience in my heart. Prof. Meng (PKU) brought me into the field of language and reading development and provided me with solid training on research skills. Dr. Nai Ding (ZJU) and Dr. Lin Chen (Pitt)'s work motivated my exploration on incremental (and natural) language processing, while Prof. Lucia Melloni (MPI)'s research led me to a scope of learning. I was impressed by the young talents at Prof. Dan Zhang (THU)'s lab and learned about the cutting-edge techniques to study inter-subject interactions in a real classroom setting. Furthermore, Prof. Xiuli Tong (HKU)'s passion resonated with mine for developing training programs and intervention tools for children with special need.

My heartfelt thanks also go to all my friends. Yawen, my first friend here in Maastricht, we had so much fun hanging out and brainstorming. Thank you for always having my back (and I have yours!), I will miss those conversations that made us lose track of time. Hang in there, we almost Ph.inisheD!! Min, my one-month-roomie, you are a surprise "intruder" bringing so many fresh perspectives to my life. Thank you for checking on me from time to time, while respecting an INFJ's odd sense of personal space. What I admire about you is that you have a clear vision of goals and always make your life interesting and fulfilling. Hopefully, our paths will cross again (say, in Hangzhou)! Chen, it is wonderful getting to know you, a super positive, caring, and strong girl. Thanks a lot for always stuffing my cheeks with fine food, and above all, for your wake-up call that pulled me out of the vortex of struggling to include everything in my thesis. You do not need anyone else's definition or approval, so "*be happy with the beautiful things that*

---

[5] Japanese idiom, "one time, one meeting".
[6] A Japanese television series.

*make you, you!*"[7] Yu, we are alike in many ways, so I guess that is why I really enjoyed those long talks and walks with you. As the title of your thesis states, "*Change is the only constant*"[8], we need to embrace the dynamic nature of life. Now that you have embarked on a new adventure, I hope that one day, two free souls can be reunited with smiles and stories. Li, we have shared many moments, both exciting and challenging ones. Thank you for your trust and I apologize if I did not provide you with enough support. But may my blessings accompany you on your path to peace. Peiying, I am not sure if I may call you a "friend", but I am grateful for your company on my journey to find and heal my true self over the past four years (> 150 sessions, and tbc.). Ming, many thanks for letting me stay at your place during my first few weeks at Maastricht. The great time spent with you calm my anxious heart. I look forward to seeing you again along the coast (in Hainan or Hong Kong)! Qian, Jianhua and Luotong, my best wishes for you to dream big, sparkle more and shine bright in your future endeavors. Yuewei, Xueying, Juanzhi, Huidong and Liwen, may passion, purpose, and perseverance lead you wherever your heart desires!

感谢远在 8000 多公里之外的爸爸妈妈！疫情之下，我们已经四年没见，曾经吵着要出去闯一闯的孩子，如今却是归心似箭。离家十多年，岁月让我的眼中装下了更宽广、更丰富的世界，但视频窗口中老爸的白发和老妈的皱纹却变得格外刺眼。说起来，过去你们的看家本领，我不知不觉也练就了好几件。比如电话接通的一声"喂"就泄露了你们心情如何、有没有感冒；要是心情不好，就用我那些不痛不痒的小事让你们转换频道。曾经，每天必须打电话是我羞于启齿的烦恼；而今，在疫情和论文的双重暴击下，每天的通话几乎是救命稻草。虽然有距离、有时差，但知道自己时刻有人牵挂，就像漂泊在外的小船循着灯塔，游得再远也不愁无路回家。还要感谢大伯和舅舅一家的关照，让我家逢年过节不至于孤独寂寥，疫情封控下依旧有所依靠。虽然缺席了家中小宝贝们的成长，但希望当他们长成翩翩少年，我能成为一个让他们敢于去质疑的存在，一起去探索各种多元而非唯一的可能。最后，很抱歉也很遗憾的是没能见上爷爷最后一面。尽管 AD 早已抹去了爷爷的记忆，但相信他若是在天之灵知道最小的孙女一步步登高望远，看到了世界的美轮美奂，思想的波澜万千，一定也会由衷为我高兴的吧！

---

[7] Beyoncé.
[8] Heraclitus.

最後に、自分にも一言。よく頑張った達成感と「あと一歩！」という残念さの中で、四年半余りの留学生活がいよいよ幕を下ろそうとした。何かをやり遂げたことより、新しい発見がいっぱいあったことのほうが微笑ましい。それは、内に秘めた力が「自分の価値を証明する」ことから、「情熱・好奇心・生きがい」などに変わったことの現しだろう。これから出会う様々な人生課題では、「与えることを惜しまず」、「一能一芸に止まらず」、「正解と限界を予め決めず」という三つの点を肝に銘じて、自分探しを続きながら進もう。そして、君のままで、君のそばに。いつも、いつでも、いつまでも。