

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

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Summary

Human language is a complex, hierarchically organized structure that unfolds over time (Greenfield, 1991; Kotz & Schwartz, 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.