Atypical brain-to-brain synchronization during listening to continuous natural speech in dyslexia

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Research Highlights

- Brain-to-brain synchronization of dyslexics was atypical while listening to speech.
- Compared to typical readers, both stronger and weaker synchronization was found.
- Reading-related measures correlated with the strength of synchronization.

Abstract

Listening to speech elicits brain activity time-locked to the speech sounds. This so-called neural entrainment to speech was found to be atypical in dyslexia, a reading impairment associated with neural speech processing deficits. We hypothesized that the neural responses of dyslexic readers to real-life speech would be atypically synchronized compared to typical readers, and that the strength of brain-to-brain synchronization would be reflected in reading-related measures.

We recorded magnetoencephalograms (MEG) of 23 dyslexic and 21 typically reading adults during listening to ~10 min of natural Finnish speech consisting of excerpts from radio news, a podcast, a self-recorded audiobook chapter and small talk. The amplitude envelopes of band-pass-filtered MEG source signals were correlated between subjects in the cortically-constrained source space in six frequency bands. The resulting inter-subject correlations (ISCs) of dyslexic and typical readers were compared with a permutation-based *t*-test. Neuropsychological measures of phonological processing, technical reading, and working memory were correlated with the ISCs utilizing the Mantel test.

During listening to speech, ISCs were reduced in dyslexic compared to typical readers in delta (0.5–4 Hz), alpha (8–12 Hz), and high gamma (55–90 Hz) frequency bands. In theta (4–8 Hz), beta (12–25 Hz), and low gamma (25–45 Hz) frequency bands, dyslexics had mainly enhanced ISC to speech compared to controls. Furthermore, we found that ISCs across both groups were associated with phonological processing, technical reading, and working memory.

The atypical brain-to-brain synchronization to natural speech in dyslexics supports the temporal sampling deficit theory of dyslexia. It also suggests over-synchronization to phoneme-rate information in speech, which could be the reason for less accurate sampling of phonemes from speech in dyslexia. These irregularities in parsing speech are likely part of the complex neural factors contributing to dyslexia. The associations between neural coupling and reading-related skills further support this notion.

Keywords: natural speech, dyslexia, brain-to-brain synchronization, inter-subject correlation, magnetoencephalography, reading skills

Declarations of Interest

None.

1 Introduction

Language processing and comprehension are essential for human communication and interaction. Neural speech processing deficiencies are typical for individuals with developmental dyslexia, a learning disorder further characterized by reading and writing difficulties affecting up to 17% of the population (Elliott and Grigorenko, 2014). The speech processing deficit in dyslexia has been investigated widely (for reviews, see Ramus et al., 2003; Schulte-Körne and Bruder, 2010), however, mostly utilizing unnatural, repetitive stimuli that barely resemble real-life speech. It has been argued that to truly understand the mechanisms of language processing in real-life situations, naturalistic stimuli should be used (Hasson et al., 2018). The core question of this study is whether the neural dynamics of processing natural speech are atypical in dyslexia.

This question has been illuminated from different angles previously. For example, acoustic and rhythmic properties of the speech stimulus *per se* are reflected by neural oscillations in the brain which has been suggested to enhance speech intelligibility (Doelling et al., 2014; Luo and Poeppel, 2007; Obleser and Weisz, 2012; Peelle and Davis, 2012), differently so in dyslexics than typical readers (De Vos et al., 2017a; Power et al., 2016). The natural brain rhythms (i.e., oscillations) thereby seem to interplay with the speech stimulus that is processed (for a review, see Meyer, 2018). One interesting aspect, however, has not gained much attention in the field of speech processing in dyslexia: Brain synchronization. Incoming information, such as speech, is processed in a similar manner when neural activity is synchronized between individuals, which leads to a common understanding and goal-directed behaviour (Hasson et al., 2012). The extent of synchronization can be estimated with inter-subject correlation (ISC), a model-free analysis approach that has been proven viable to extract shared brain activations across participants during natural stimulation due to the time-varying dynamics of the stimulus (Abrams et al., 2013; Hasson et al., 2004; Lankinen et al., 2014; Thiede et al., in prep.). ISC extracts cortical areas that respond to those dynamics, which in speech are manifold: For example, acoustic, phonological, syntactic, and semantic features likely activate lower- and higher-level brain functions related to processing and comprehension of speech. In a functional magnetic resonance imaging (fMRI) study, Wilson and colleagues (2008) have found ISCs in healthy adult participants

listening to natural speech in bilateral temporal areas, the default mode network, bilateral inferior frontal gyrus, and areas close to premotor regions. The first objective of the current study was to confirm and extend our knowledge of the brain areas that couple between healthy adult participants during listening to natural speech using magnetoencephalography (MEG) which allows for a more thorough investigation of temporal aspects of the neural signal compared to fMRI.

Certain brain dynamics have been repeatedly shown to be abnormal in dyslexia, specifically during speech processing. For example, temporal sampling deficits have been proposed to play a role in dyslexia, especially in the low delta- and theta frequency bands which are involved in syllable encoding (Goswami, 2011; Hämäläinen et al., 2012; Molinaro et al., 2016). Moreover, Giraud and Poeppel (2012) have proposed that speech parsing at rates comparable to low-gamma frequencies is altered in dyslexia. Indeed, brain measures during processing of speech correlate with reading-related tests. For example, an abnormal right rather than left-lateralized auditory steady-state response in dyslexics was associated with behavioural tests of phonology, and further, a phonemic oversampling, i.e., faster than normal oscillatory rate, has been associated with memory deficits in dyslexia (Lehongre et al., 2011). The second objective of the present study was to investigate whether brain activity of dyslexics during listening to speech is atypically synchronized compared to typical readers. We hypothesized that especially lower frequency bands (Goswami, 2011; Hämäläinen et al., 2012; Molinaro et al., 2016) show weaker brain-to-brain synchronization between dyslexic than typical readers, whereas higher frequency bands could show enhanced synchronization between dyslexic compared to typical readers (Lehongre et al., 2011). Thirdly, we examined the association between brain-to-brain synchronization and neurophysiological measures across both groups. We hypothesized that the strength of synchronization is associated with reading-related test performances.

These hypotheses were assessed by comparing the ISCs of MEG amplitude envelopes during listening to natural speech in dyslexic and typical readers. The MEG amplitude envelopes were extracted in the cortically-constrained source space of each individual in six frequency bands of interest (delta, theta, alpha, beta, low gamma, high gamma). Then, pairwise correlations were computed and averaged to obtain group correlations that were compared between groups.

2 Methods

This study has been preregistered at ClinicalTrials.gov (NCT02622360) as part of a research project on speech- and short-term memory functions in dyslexia.

2.1 Participants

Forty-nine Finnish-speaking right-handed adult participants aged between 18 and 45 years and without a history of neurological diseases volunteered in the study, 26 with confirmed dyslexia and 23 typical readers. Participants were recruited from an organization for learning impairments (HERO Ry, Helsinki, Finland) as well as from university and adult education email lists, a related project website, and by an advertisement in social media. To be included in the dyslexic group, participants had to have 1) a diagnosis from a psychologist, special education teacher, or similar, 2) evident reading-related problems in childhood indicated by the adult reading history questionnaire (ARHQ; Lefly and Pennington, 2000) and confirmed in an interview, and 3) below-norm performance (less than one standard deviation from the age-matched average) in at least two reading subtests in either speed or accuracy (see Section 2.2). To be included in the control group, 1) participants or their relatives had to have no language-related disorders, 2) the ARHQ indicated no reading-related problems in childhood, and 3) participants had to perform within norm in at least two reading subtests. Exclusion criteria for the study were attention deficits (ADD) as tested by the Adult ADHD Self-Report Scale ASRS-v1.1 questionnaire (Kessler et al., 2005), other language impairments, such as developmental language disorder (DLD; formerly specific language impairment, SLI), other neurological or psychiatric diseases, medication severely affecting the central nervous system, a special education track in school indicative of wider cognitive impairments, non-compensated hearing or sight deficits, and a performance intelligence quotient (IQ) below 80. Data of four participants were excluded as anatomical MRIs could not be obtained due to metal in the body or pregnancy (three dyslexics, one control), and data from one participant had to be excluded due to technical reasons during the MEG measurement which resulted in missing trigger markers (control). The final sample consisted of 44 participants, of which 23 were in the dyslexic and 21 in the control group. Background information are summarized in Table 1; statistics were performed with SPSS version

24.0 (IBM Corp, 2016, Armonk, NY, USA). Participants gave their written consent after they had been informed about the study. All procedures were carried out according to the Declaration of Helsinki, and the Coordinating Ethics Committee (Hospital District of Helsinki and Uusimaa) approved the study protocol.

2.2 Neuropsychological tests

Neuropsychological tests were conducted by Master students of psychology under the supervision of a licensed clinical psychologist in a session of ca. 2 h at the Cognitive Brain Research Unit, University of Helsinki. Domains of phonological processing, reading, IQ, and memory functions were assessed. Phonological processing was evaluated with the 'Pig Latin' test (Nevala et al., 2006), non-word span length (Laasonen et al., 2002), digit span length (Wechsler, 2008), and rapid alternating stimulus naming (Wolf, 1986). Reading skills were evaluated by word and pseudoword list reading (technical reading) and text reading (reading comprehension; Nevala et al., 2006). The verbal IQ was assessed with similarities and vocabulary subtests, and performance IQ with block design and matrix reasoning subtests (Wechsler, 2005). Memory function was evaluated with the subtests on letter-number series and visual series (Wechsler, 2008). A summary of the neuropsychological test outcomes is presented in Table 2; statistics were performed with SPSS, effect sizes were calculated with Psychometrica Freeware (Lenhard, 2017, Dettelbach, Germany, https://www.psychometrica.de/effect_size.html#cohenb, https://www.psychometrica.de/effect_size.html#nonparametric), and bootstrapped confidence intervals were calculated with the measures-of-effect-size toolbox (Hentschke and Stüttgen, 2011, https://github.com/hhentschke/measures-of-effect-size-toolbox).

2.3 Stimuli and data acquisition

Natural Finnish speech of ≈10 min was used as the auditory stimulus. The stimulus consisted of several shorter excerpts that were merged into one audio file with Audacity® 2.0 software (Audacity Team, 2012, http://audacityteam.org/). All excerpts were spoken by native Finnish speakers and either extracted from online sources (Finnish national broadcast 'Yle' radio news and podcast) or self-recorded (reading a book and small talk, such as asking for directions and exchanging of travel experiences) in a

sound-proof laboratory at the Cognitive Brain Research Unit, University of Helsinki. Consecutive excerpts were joined with a 1-s silent break with 0.5-s fade-out and 0.5-s fade-in.

The neuronal activity of the brain was recorded with an Elekta Neuromag Triux MEG system (MEGIN Oy, Helsinki, Finland) comprising 204 planar gradiometers and 102 magnetometers. The signals were filtered to 0.03–330 Hz and sampled at 1 kHz. Recordings were performed in a magnetically shielded room (Euroshield/ETS Lindgren Oy, Eura, Finland) at BioMag Laboratory in Helsinki University Hospital. Participants listened to the continuous auditory stream binaurally at a comfortable level (≈70–80 dB SPL). The stimulus was presented with Presentation Software (Neurobehavioural Systems Ltd., Berkeley, CA, USA) and conveyed from earphones to the ears via plastic tubes. Resting state MEG data (eyes open) were recorded for each participant for ≈10 min. Other auditory and visual stimuli had been presented before these recordings for ≈80 min in six recording blocks. Data from these recordings will be presented in separate publications. In all MEG recordings, participants were instructed to be seated in an upright position, relax, and listen to the continuous speech stimulus while keeping the head still. In addition, scalp EEG and horizontal and vertical electrooculograms (EOG) were recorded with a 60-channel cap (EasyCap, Herrsching, Germany) with reference and ground electrodes located at the nose and left cheek, respectively. Five head position indicator coils (HPI), the EEG electrodes, and fiducial markers of nasion and both preauricular points were digitized with a Polhemus Isotrak 3D-digitizer (Polhemus Inc., Colchester, VT, USA) in order to establish a transformation between the MEG and MRI coordinate systems. The HPI coils were continuously energized to enable tracking and compensation of head movements throughout the MEG measurement.

Structural T1-weighted magnetic resonance images (MPRAGE sequence) were obtained with a 3T MAGNETOM Skyra whole-body MRI scanner (Siemens Healthcare, Erlangen, Germany) with a standard 32-channel head coil at AMI centre, Aalto University. Each structural MRI consisted of 176 slices with a slice thickness of 1 mm, voxel size of (1 x 1 x 1) mm^3, and field of view of (256 x 256) mm^2. All structural MRIs were checked by a physician who reported no incidental findings.

2.4 Data analysis

For an overview of the most relevant data analysis steps, see Figure 1. The code used for the analysis of this dataset is available at https://github.com/athiede13/free_speech.

MEG data preprocessing

The continuous MEG data were preprocessed by first visually examining all recordings and marking noisy, flat, or otherwise artifact-containing channels as bad (on average 6.2 channels in one recording). External magnetic interference was suppressed with Maxfilter software version 2.2 (MEGIN Oy, Helsinki, Finland) applying temporal signal-space separation (tSSS; Taulu and Simola, 2006) with a buffer length of 10 s and correlation limit of 0.98. The algorithm also corrected for head movements measured with the HPI coils and interpolated the channels manually marked or automatically detected as bad. Physiological artifacts, specifically those resulting from eye blinks, eye movements, and heartbeats, were removed with signal-space projection (SSP; Tesche et al., 1995; Uusitalo and Ilmoniemi, 1997) implemented in MNE-Python (Gramfort et al., 2014; 2013) software package (version 0.17.dev0) using the channels showing the most prominent artifacts (EOG channels for eye-movements and channel 'MEG1541' for heartbeats) to average the artifact events and create the projectors. The noise covariance was estimated with MNE-Python from 'empty-room' data of ≈10 min that were preprocessed similarly to the data from the participants.

MRI data preprocessing

Structural MRI images were preprocessed using the Freesurfer software package (versions 5.3 and 6.0, Martinos Center for Biomedical Imaging, http://freesurfer.net/; Dale et al., 1999; Fischl et al., 1999a, 1999b). The steps applied included segmentation of brain volume with the watershed algorithm (Ségonne et al., 2004), intensity normalization (Sled et al., 1998), segmentation of grey and white matter (Fischl et al., 2004, 2002), and inflation of the cortical surfaces (Fischl et al., 1999a). Manual editing of surfaces was required in 66% of the cases to ensure a correct segmentation of the brain volume, and manual addition of white matter points in 18% to ensure a correct segmentation of grey and white matter.

Coregistration

Coregistration of MRI and MEG was performed with the function *mne coreg* in the MNE-Python software package. First, the digitized fiducials and head-shape points (EEG electrode positions) were manually aligned with the reconstructed head surface from the individual anatomical MRI. Then, the iterative closest point algorithm was applied to minimize the distances of the head-shape points from the head surface.

Source modeling

The segmented cortical surface was decimated (recursively subdivided octahedron) to yield 4098 source points per hemisphere. A single-compartment BEM was applied to compute the forward solution; source points closer than 5 mm to the BEM surface were omitted. A dSPM MNE inverse operator was then computed with a loose orientation constraint of 0.2, depth weighting exponent of 0.8, and the noise covariance estimated from the 'empty-room' data.

Inter-subject correlation (ISC)

For ISC computation, custom scripts were utilized in MATLAB (release 2017a; The MathWorks, Inc., Natick, Massachusetts, USA) as well as the MNE Matlab toolbox (Gramfort et al., 2014) and MEG ISC custom functions (Suppanen, 2014; Thiede, 2014). First, in the listening-to-speech condition, the stimulus durations and temporal alignments with respect to the recordings were determined with the help of the stimulus start and end triggers from Presentation (due to technical reasons, the stimulus was in two parts; 4.77 and 5.45 min). For the determined stimulus durations, the preprocessed MEG signals were band-pass filtered (third-order Butterworth filter, applied in the forward direction only) into six frequency bands of interest (cut-off frequencies; delta: 0.5–4 Hz, theta: 4–8 Hz, alpha: 8–12 Hz, beta: 12–25 Hz, low gamma: 25–45 Hz, high gamma: 55–90 Hz). The analytical signals were computed by applying Hilbert transformation to the band-pass-filtered signal, the resulting signals were low-pass filtered (similar filter as above) at 0.3 Hz, and downsampled to 10 Hz. The previously computed inverse operator was then applied to these complex-valued signals. The absolute value of each source time series was taken, resulting in cortical amplitude envelopes per each participant and frequency band (delta, theta, alpha, beta, low gamma, high gamma). Pairwise correlations of the cortical amplitude

envelopes at corresponding source points were computed across all subject pairs within each experiment group and for each frequency band. The pairwise correlations were averaged for each group, i.e., dyslexic and control group. A duration-weighted averaging was applied for the two speech parts.

The ISC contrast between the groups was then tested in MNE-Python with a spatial permutation-based *t*-test with 5000 permutations. Cluster correction was applied to correct for multiple comparisons.

Correlation between ISC strengths and neuropsychological tests

We tested for correlations between the brain-to-brain coupling strength during listening to speech (ISCs) and neuropsychological test scores using the Mantel test (Mantel, 1967). The neuropsychological test scores were combined into four composite measures: phonological processing, technical reading, working memory, and IQ (see Section 2.2).

Computations were carried out with custom scripts in MATLAB and MNE Python. Similarity matrices were computed as models for the Mantel test by averaging the test scores between each subject pair for all four neuropsychological composites (Figure 4). Surrogate models were computed by random permutation of the model data for 5000 times. The Mantel test was performed as a Spearman rank correlation between the top triangle of the ISC matrix (all pairwise combinations) and the top triangle of the similarity matrix reflecting the neuropsychological composite (four composites of interest: phonological processing, technical reading, working memory, IQ). The ISC matrix contained values for each subject pair (946 pairs) and source location (20484 locations), and an uncorrected *p*-value was estimated for each source with the Mantel test.

Spatial cluster correction was applied based on proximity of the source locations in the source space with a cluster forming threshold set at $p < .05$ from the Mantel tests.. The proximity of the source locations or connectivity matrix was computed in MNE-Python based on the source space. A customized MNE-Python -based function determined the cluster sizes for each of the 5000 surrogate models to build a null distribution of the cluster sizes, from which the cutoff size for a 'significant cluster' was calculated. The 'significant clusters' were visualized on the *fsaverage* brain provided by Freesurfer.

This procedure was repeated for each neuropsychological composite in each frequency band, in total 24 times.

3 Results

3.1 Interbrain synchronization during listening to speech

ISCs were significantly larger than zero in all frequency bands and in both groups and exhibited different correlation strengths across frequency bands (Figure 2, Table 3). In the delta frequency band, the control participants had significant ISC in temporal, parietal, and central areas; the maximum was in the right mid-cingulate cortex. Dyslexics exhibited ISC in right central and parietal areas, peaking at right postcentral areas. In the theta band, controls had synchronized activity in a defined area depicting the left anterior cingulate cortex, whereas in dyslexics the synchronization pattern was more distributed towards left focal fronto–parietal and temporal areas, and right frontal and temporal areas, peaking at a location roughly corresponding to the left supplementary motor area. In the alpha band, ISC was found in bilateral inferior frontal gyrus, inferior temporal, and frontal areas with peaks in frontal areas in both groups. In the beta band, we observed bilateral frontal and temporal ISCs in both groups and the maxima were in left middle temporal cortex. The low gamma band showed frontal and parietal ISCs in both hemispheres in both groups, and additional strong bilateral occipital ISCs in the dyslexic group only. The high gamma band synchronized in both groups in bilateral superior parietal and postcentral areas that extended into occipital areas in the dyslexic group.

3.2 Synchronization differences between dyslexics and controls

Clusters depicting the brain areas that synchronized significantly differently (corrected for $p < .05$) between the control and dyslexic group are shown in Figure 3, and the maximal differences of these areas are summarized in Table 3. The results show that the ISC contrast between the groups manifested in distinct brain areas that differed between frequency bands. Whereas in the delta, alpha, and high gamma bands, controls synchronized stronger than dyslexics, in the theta, beta, and low gamma bands, we predominantly found stronger ISC in dyslexics (Figure 3).

In the delta band, typical readers had significantly stronger ISCs than dyslexics in bilateral auditory cortices, bilateral mid-cingulate cortices, and left central as well as frontal areas.

In the theta band, a large cluster of stronger synchronization in the dyslexic than control group was found in the right middle and superior temporal, inferior and superior parietal, and central areas, peaking in the superior parietal cortex. In the left hemisphere, stronger ISCs in dyslexics compared to controls were found in superior temporal and fronto–parietal areas. Stronger ISCs in the control than dyslexic group was found in small left-hemispheric clusters located at the temporal pole and orbitofrontal cortex.

In the alpha band, frontal and mid-cingulate areas showed higher ISCs in controls than in dyslexics.

In the beta band, stronger ISC was found in the dyslexic than control group in a left-hemispheric cluster including superior and middle temporal areas which also contained the maximal difference between the groups, as well as in more focal left-hemispheric occipital pole, superior parietal, and frontal areas. In the right hemisphere, dyslexics synchronized stronger than controls in focal superior and middle frontal areas including the frontal pole, as well as occipito–parietal areas. Small clusters of enhanced synchronization in controls were found in right central areas.

In the low gamma band, dyslexics showed stronger ISC in a large left-hemispheric cluster comprising occipital and temporal areas with a peak in the fusiform area as well as in a smaller cluster comprising occipital areas of the right hemisphere. Small clusters of enhanced synchronization in controls were found in right occipital and bilateral frontal areas.

In the high gamma band, controls had higher ISC than dyslexics in bilateral frontal, and right temporal areas, peaking in right anterior cingulate cortex.

3.3 Correlation of neuropsychological tests and ISC strengths

All significant correlations of neuropsychological measures and brain synchronization during listening to speech are visualized as clusters on the *fsaverage* brain in Figures 5 and 6. Significant correlations were found in all frequency bands, being stronger and comprising larger brain areas in low frequency bands up to 25 Hz. The brain areas of the peak correlations between neuropsychological composites and brain synchronization are summarized in Table 3.

Phonological processing correlated with brain synchronization during listening to speech in all six frequency bands (Figure 5). The locations of significant correlations differed between the bands. The largest clusters were found in delta, theta and beta bands. In the delta band, significant correlations were found in left-hemispheric postcentral/superior parietal, precentral, supramarginal, frontal, transverse, middle and superior temporal areas as well as right-hemispheric central, frontal, inferior and middle temporal areas. The largest correlation between ISC strength and phonological processing scores was $r = 0.24$ in the left supramarginal gyrus (Table 3). In the theta band, significant clusters were found in left-hemispheric temporal pole, orbitofrontal, rostral middle frontal, central, and occipital areas, with the largest correlation in the orbitofrontal cortex. In the right hemisphere, a large occipital-pole cluster showed significant correlation, as well as smaller central, inferior temporal, and frontal-pole clusters. In the alpha band, bilateral superior parietal, orbitofrontal, and cingulate areas were correlated with phonological processing, showing a maximum correlation at the right precuneus. In the beta band, left-hemispheric insula, and right-hemispheric middle and superior temporal, pre- and postcentral, pars opercularis, pars triangularis, caudal middle and rostral middle frontal areas showed significant correlations between phonological processing and brain synchronization during listening to speech. The maximum correlation was $r = 0.29$ in the right postcentral area. In the low gamma band, a small cluster in the right middle temporal cortex showed significant correlations. In the high gamma band, small clusters in left superior frontal, right superior parietal/postcentral, inferior parietal and occipital areas were significantly correlated to phonological processing skills. The maximum correlation of $r = 0.29$ was located in the right postcentral cluster.

Technical reading correlated with brain synchronization during listening to speech in the delta, theta, alpha, beta, and low gamma band (Figure 6). In the delta band, significant regressions between technical reading and brain synchronization during listening to speech were found in the left superior and inferior parietal cortex, central, superior, middle and temporal areas, and insula. Right-hemispheric correlations were located in inferior and middle temporal cortex, supramarginal, inferior parietal, and postcentral areas with a maximum correlation in the right inferior temporal cortex. In the theta band, significant regressions were found in the left insula only. In the alpha band, bilateral anterior

cingulate cortices showed significant correlations with technical reading. In the beta band, regressions were significant in small clusters in postcentral areas bilaterally, and in a small cluster in the right supramarginal area. In the low gamma band, a medium-sized cluster in the occipital right hemisphere was correlated with technical reading. No significant regressions were found for the high gamma band.

Working memory function correlated significantly with brain synchronization in the delta band in a right superior medial frontal brain area (Figure 6). In the other frequency bands, no significant regressions were found.

IQ correlated significantly with brain synchronization in delta and high gamma bands (Supplementary Figure 1). In the delta band, left supramarginal, pre- and postcentral, insula, and medial temporal areas showed significant correlations, with the maximum in the left supramarginal area. In the right hemisphere, ISCs in medial and inferior temporal areas, rostral middle and lateral orbitofrontal areas, as well as insula, were correlated with IQ. In the high gamma band, a small cluster in the right inferior temporal cortex was correlated with IQ. In the other frequency bands, no significant correlations emerged.

4 Discussion

The aim of the present study was to examine the neural dynamics of dyslexic and typical readers during listening to natural speech. To this end, typical readers and participants with confirmed dyslexia listened to several short excerpts of native Finnish speech while their neural activity was recorded with MEG, which – compared to fMRI – enabled us to analyze the temporal aspect of the neural signal in more detail. We found significant ISC in six commonly investigated frequency bands and could thus delineate neural dynamics at different paces, i.e., slow and fast rhythms in the brain. These rhythms are postulated to have neurophysiologically meaningful functions in speech processing (Meyer, 2018).

Firstly, our results confirm and extend the knowledge on between-subjects coupling of brain areas during listening to continuous speech. Secondly, our results suggest atypical synchronization patterns during speech processing between dyslexic participants. We found lower brain-to-brain synchronization between dyslexic compared to typical readers in the low delta, alpha and high gamma frequency bands, and mostly enhanced coupling between dyslexics in theta, beta, and low gamma frequency bands. Thirdly, reading-related measures were correlated with the strength of brain-to-brain coupling during listening to speech. The strongest correlations, observed in most of the frequency bands, were found for phonological processing, followed by technical reading, and working memory function.

The ISC patterns we observed in typical readers were consistent with those previously found with fMRI during listening to natural speech (Wilson et al., 2008); both studies showed significant ISC in bilateral temporal, inferior frontal, midline, and parietal areas. Bilateral temporal areas are known to be involved in speech processing and comprehension (see e.g., Hickok and Poeppel, 2007), and therefore were expected to show ISC in our study. Inferior frontal, midline and parietal areas, specifically premotor areas, belong to the default mode network, the synchronization of which has been suggested to reflect varying semantic complexity of the incoming speech and/or systematic downregulation with increasing difficulty or level of engagement to the content of the speech (cf. Wilson et al., 2008). We found additional ISC in postcentral and occipital areas that did not appear in the earlier fMRI study, although occipital ISC was only found in the dyslexic group. The postcentral area showing ISC comprises

somatosensory cortex, whose activity likely reflects the sound-to-articulation mapping process that has been suggested to subserve the speech processing network (Giraud and Poeppel, 2012). Stimulus-dependent processing demands could have synchronized the activation of the postcentral areas in our study.

The areas of the default mode network synchronized in low delta and theta, as well as in low gamma bands. This finding is in line with theories that suggest a functional role for cross-frequency coupling during speech processing and comprehension, specifically delta–theta, and theta–gamma coupling (Doelling et al., 2014; Meyer, 2018). In addition, we found ISC in the beta band with a maximum in the left temporal pole in the control group. The temporal pole has been previously associated to speech processing (Tzourio et al., 1998) as well as to semantic word processing or perception (Crinion et al., 2006; Marinkovic et al., 2003) and memory retrieval (Fink et al., 1996). Also the functional role of the beta band was suggested to be lexical-semantic prediction during speech comprehension (Meyer, 2018). Therefore, our results strongly suggest an important functional role of the beta band in the higher-level process of prediction of words and meaning while listening to speech.

To assess whether the extent of brain-to-brain synchronization differed between the dyslexic and control group, we compared the pairwise correlation maps between the two groups. We found that the brain-to-brain synchronization was different between groups in all frequency bands, however, with different patterns across the frequency bands. In the delta, alpha, and high gamma bands, typical readers showed enhanced brain-to-brain synchronization compared to dyslexic readers. On the other hand, the synchronization was mostly stronger in dyslexic than typical readers in theta, beta, and low gamma bands.

The enhanced ISC in the delta band in typical readers compared to dyslexics is consistent with the temporal sampling deficit theory (Goswami, 2011), which predicts that dyslexics especially in lower frequency bands would show a reduced sampling of information contained in the continuous speech stream. Delta-band synchronization is thought to be involved in the segmentation of intonation phrases (Giraud and Poeppel, 2012; Meyer, 2018). A reduced brain-to-brain coupling in this frequency band could therefore be indicative of deficits in temporally synchronized sampling of phrase

boundaries. Previously shown reduced neural entrainment to the speech envelope in the delta band in dyslexics compared to typical readers (Molinaro et al., 2016) further supports our results. Also phase locking to speech modulations at the delta rate was found to be atypical in dyslexia (Hämäläinen et al., 2012), suggesting additional delta-rate speech processing deficits.

Theta-band synchronization was enhanced in dyslexic compared to typical readers in predominantly right-hemispheric brain areas. Activity in the theta band reflects processing of syllabic information of speech (Luo and Poeppel, 2007; Meyer 2018). According to the temporal sampling deficit theory, theta band activity should show reduced synchronization between dyslexics. Thus, our unexpected finding of enhanced theta coupling in dyslexics is against our hypothesis. It could be that in our study dyslexics show 'over-synchronization' in the theta band that may be related to an increased need of memory retrieval (Rommers et al., 2017; Meyer 2018). Along this line, the largest ISC difference between the groups was in the superior parietal cortex, which has also been associated with memory retrieval (Vilberg and Rugg, 2008). It is noteworthy that previous studies have often looked at phase information in the theta band. We did not extract phase, but amplitude envelopes, which may explain the contrasting findings. However, these possible explanations should be investigated more thoroughly in future studies.

Alpha-band synchronization was diminished in dyslexic compared to typical readers in bilateral frontal and mid-cingulate areas. The syllabic rate in speech has its upper limit in the alpha range (around 10 Hz). A less synchronized brain activity in the alpha band could therefore imply inaccurate parsing of syllables in dyslexia. Syllable tracking has often been suggested to occur mainly in the theta band (see above). However, as discussed above, we did not observe less synchronized theta activity in dyslexics. Similarly, De Vos and colleagues (2017a) did not find atypical brain responses to theta-band speech modulations in dyslexic adolescents, but less synchronized activity to alpha-rate modulations. Alternatively, alpha oscillations have been suggested to aid the storage of syntactic phrases (Meyer 2018). The less synchronized alpha-band activity could suggest that an inefficient storage of syntactic phrases to memory causes the overload in retrieval from memory which could be reflected as over-synchronization in the theta band.

The enhanced beta- and low-gamma-band ISCs in the dyslexics compared to controls support our hypothesis of enhanced coupling in higher frequency bands in dyslexia. Especially activity occurring in the gamma band is thought to track either phoneme-rate information or low-level acoustic features of incoming speech (Meyer, 2018). De Vos and colleagues (2017b) showed that dyslexic children – when beginning to read – exhibited larger auditory steady-state responses to speech-weighted noise amplitude-modulated around 20 Hz (beta band), referred to as phoneme-rate modulations by the authors. This higher neural synchronization to phoneme-rate modulations was correlated with poorer reading and phonological skills in that study. Similarly trending results were obtained for dyslexic adolescents (De Vos et al., 2017a). In that light, our findings support the 'oversampling' hypothesis brought forward by Lehongre and co-workers (2011). According to this hypothesis, phoneme-rate information reflected in the beta and low gamma band could be oversampled, resulting in working-memory overload and therefore slower or less accurate extraction of phonemic information from speech. Alternatively, enhanced synchronization in the beta band has been suggested to be a compensatory mechanism for the processing of phonemic-rate information (De Vos et al., 2017a).

The maximal ISC differences between the groups were localized to the left middle temporal cortex for the beta band and to the left fusiform areas for the low gamma band. In terms of phoneme processing, the left middle temporal cortex would be expected to play a major role, as it is an integral part of speech and word processing (Hickok and Poeppel, 2007). The ISC group differences in the fusiform area in left occipital lobe, in turn, may not have been expected to be involved in phonemic processing. It is possible that visual imagery plays a role here. We speculate that dyslexic participants could try to support the auditory input with visual imagery, i.e., imagining corresponding graphemes while hearing the phonemes. This could represent a previously unknown multimodal compensatory mechanism in dyslexia.

In the high gamma band, we found weaker synchronization in dyslexic readers than in controls. This result was rather unexpected, as we hypothesized that in higher frequency bands dyslexics could show enhanced synchronization than controls (Lehongre et al., 2011). The gamma band as a whole (usually > 30 Hz) has been associated with numerous functions in speech processing, such

as phonemic processing (Giraud and Poeppel, 2012), long-term memory processing (Ward, 2003), lexico-semantic retrieval (Pulvermüller et al., 1996; Mai et al., 2016) as well as tracking of phrase and syllable rhythms in continuous speech (Ding et al., 2015). However, the functional role of high gamma band in speech processing has not been evaluated in detail yet. It is possible that low and high gamma have distinct functions during speech processing (Meyer 2018). High gamma has been suggested to be entrained to the speech envelope (Nourski et al., 2009) and could track phonemic transitions, i.e., the fast changes in the speech envelope (Arnal et al., 2015). The high gamma band could also be important in the interplay with other frequency bands, such as in cross-frequency coupling with the theta band to integrate information from different hierarchical levels of speech processing (Morillon et al., 2012). It may be that the atypical synchronization of the theta band shifts the balance of typical synchronization in and coupling between the bands during speech processing, so that also the possibly integrative high gamma band is less synchronized in dyslexia. However, it remains unclear whether high gamma synchronization plays a crucial role in speech processing and understanding, as mostly lower frequencies have been described to track certain speech features that contribute to fluent processing and understanding.

Most of the above-mentioned studies that investigated oscillations during speech processing have looked at how brain signals in different frequency bands were entrained to the speech signal. However, inter-subject synchronization during processing of speech has been studied to a much smaller extent. Therefore, our interpretations above are limited although our results add valuable new information to the field.

Brain synchronization of both groups was significantly correlated with the neuropsychological composites phonological processing, technical reading, and working memory. The correlations were strongest for the phonological processing composite, followed by technical reading and working memory. The phonological processing composite consisted of the 'Pig Latin' test, non-word span length, digit span length, and rapid alternating stimulus naming, all measures that tap into phonology and its underlying processes. Large brain areas in delta, theta, and beta bands were positively correlated with phonological processing across both groups, meaning the stronger brains synchronized

between participants, the better phonological skills they had. A maximum correlation in the delta band was found in the supramarginal gyrus which incidentally was also the only area consistently correlated with IQ differences. For the theta band, the significant correlations interestingly appeared partly in the brain areas that showed enhanced synchronization in typical readers: higher synchronization was associated with better phonological processing skills. Therefore, it could be that increased synchronization of the left temporal pole and orbitofrontal cortex enhances speech parsing, thus leading to better phonological skills. Also the synchronization of the right occipital area could serve similar functions, even though it did not show significant differences between the groups in the direct comparison. In the beta band, the synchronization in a large cluster around the right postcentral area was associated with phonological processing skills. Again, looking at the direct group comparison, this area was more strongly synchronized in typical than dyslexic readers, although in other areas the opposite contrast was observed. It could be possible that the phoneme information, the parsing of which is reflected in the beta band, was processed inefficiently by dyslexic readers. The over-synchronization in dyslexics found in the direct comparison could mean that those brain areas are not as efficient in processing phoneme information from speech, whereas the postcentral right-hemispheric area that was more synchronized in typical readers and correlated with better phonological processing skills could be more efficient in processing phonemes. Less entrainment to acoustic modulations around 30 Hz in dyslexics has also previously been associated with phonological processing skills (Lehongre et al., 2011), even though the frequency limits slightly differ between their and our study (upper limit for the beta band was 25 Hz in our study).

The technical reading composite comprised word and pseudoword list reading scores in speed and accuracy. Thus, this score merely reflects reading skills at the single-word level, but not, e.g., reading comprehension. Technical reading was positively associated to the brain synchronization strength during listening to natural speech in most brain areas in the delta band, with the maximum in the right inferior temporal cortex, a higher synchronization between participants reflecting better technical reading scores. Although some of the brain areas that are correlated with technical reading overlap with those that correlate with IQ, the maxima differ. In line with the group differences in the

delta band, a lower brain synchronization between dyslexic participants is associated with worse technical reading skills. Especially the temporal areas are known to be involved in low-level auditory processing (Hickok and Poeppel, 2007). This low-level auditory processing could be related to the processing of phrase boundaries in the delta band. Worse low-level auditory processing can lead to weaker speech representations in the brain, which can affect reading abilities as in dyslexia (Bailey and Snowling, 2002; Goswami, 2015).

Working-memory capacity correlated with brain synchronization strength only in the delta band. The correlation in such a low frequency band was rather unexpected, as Lehongre and colleagues (2011) previously associated a working-memory deficit with enhanced entrainment to rates above 40 Hz, i.e., in the higher gamma range. The right medial frontal area that was maximally correlated with working-memory capacity in the delta band did not appear to be significantly different between groups, although the direction of correlation suggests that a higher synchronization would be associated with better working-memory skills, and these skills in our two groups are significantly different from each other. Possibly, a within-group correlation analysis could reveal further directions. It could also be that the brain areas associated with working memory are individual, and therefore no synchronized brain activity between participants could be associated to it.

5 Summary and conclusions

With our novel approach of frequency-band-specific inter-subject correlation of MEG acquired during listening to natural speech, we showed that the strength of brain synchronization differs between dyslexic and typical readers, with weaker synchronization in dyslexics in the delta, alpha, and high gamma band, and stronger synchronization in dyslexics in theta, beta, and low gamma bands. Furthermore, the strength of brain synchronization was associated with phonological skills as well as with technical reading and working-memory function. Our findings shed light on how speech processing is reflected in different MEG frequency bands in healthy adults and in those with reading impairments, and suggest how these brain dynamics are associated with behavioural outcomes. Unveiling speech processing in the brain in ecologically valid conditions can help uncover the complex neural basis of dyslexia.

Figures

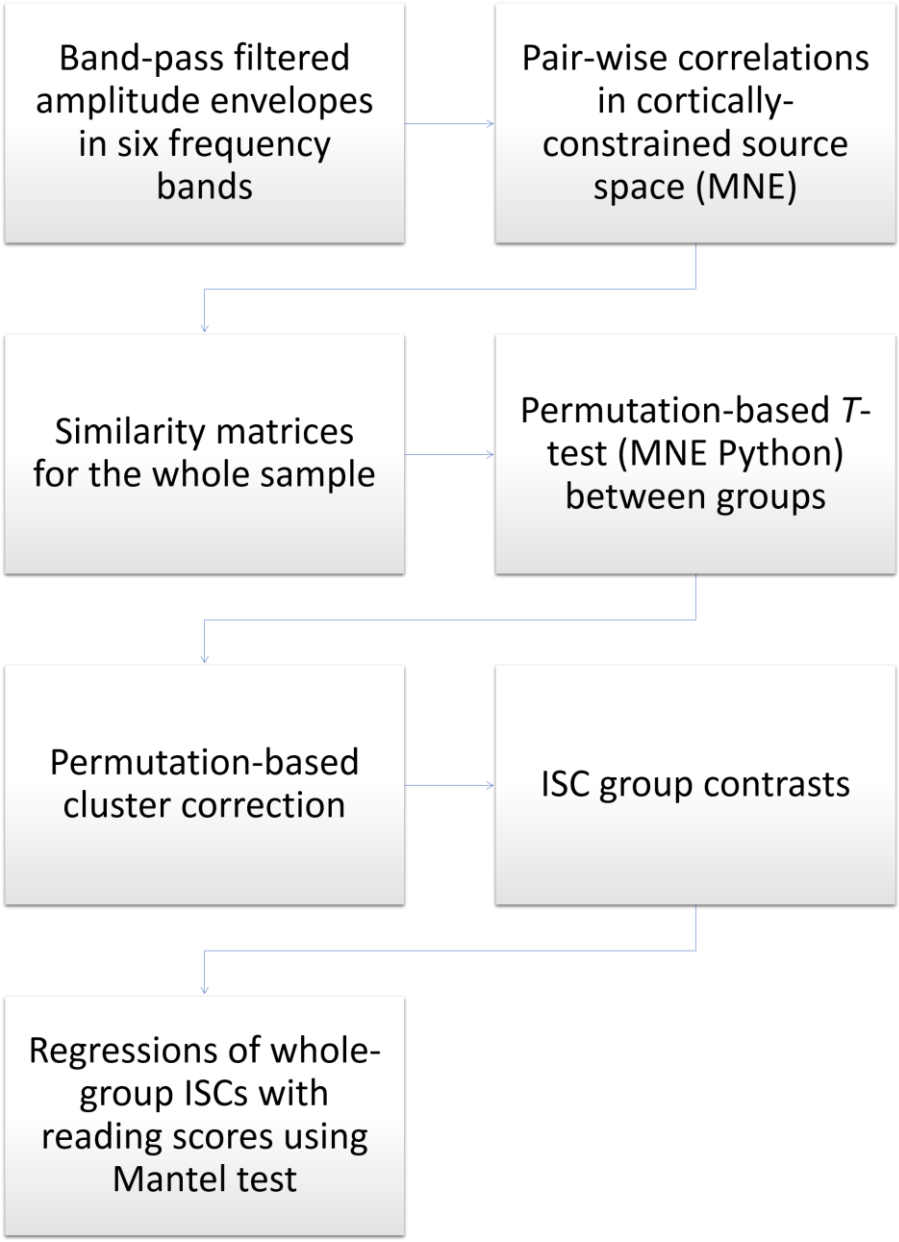

Figure 1. Overview of the data analysis steps.

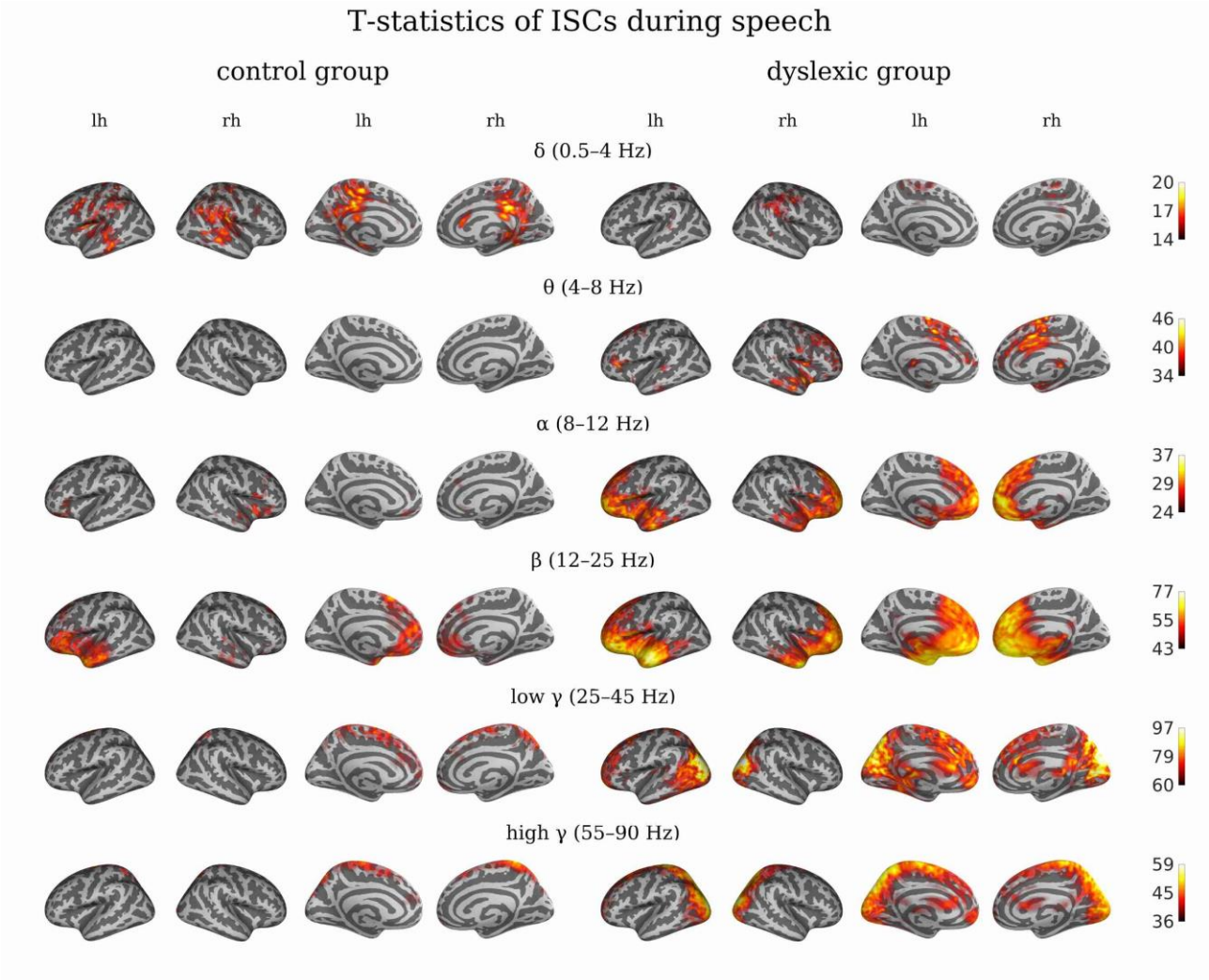

Figure 2. T-statistics of permutation-based one-sample t*-tests for inter-subject correlations (ISCs) during listening to speech in control (left four views) and dyslexic (right four views) group. ISCs are depicted in six MEG frequency bands (delta, theta, alpha, beta, low gamma, high gamma) in lateral (first two views of each group) and medial (last two views of each group) views (lh – left hemisphere, rh – right hemisphere).*

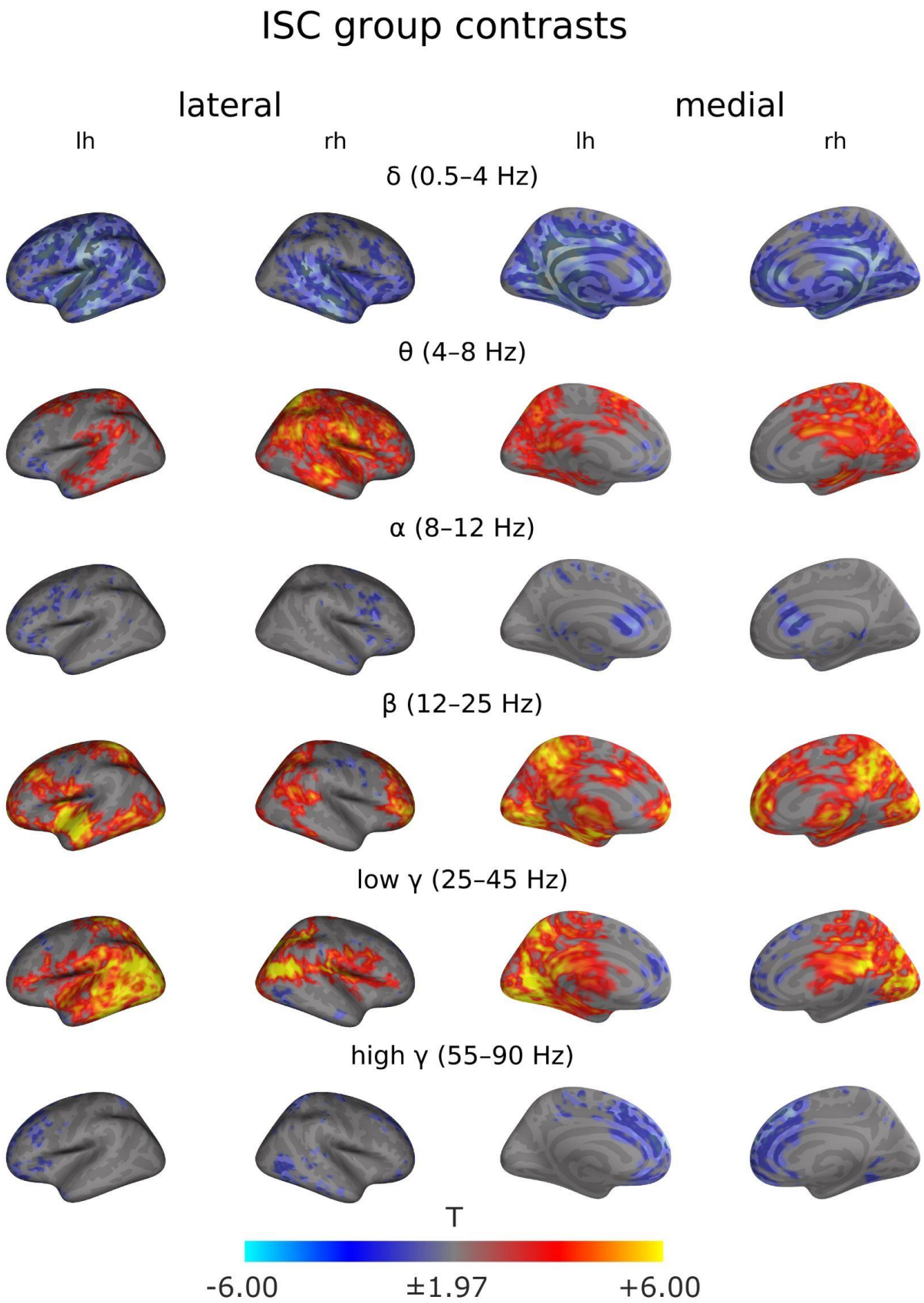

Figure 3. Contrast of inter-subject correlations (ISCs) between the dyslexic and control group for listening to speech. Cold colors indicate stronger ISCs in the control than dyslexic group, and warm colors stronger ISCs in the dyslexic than control group.

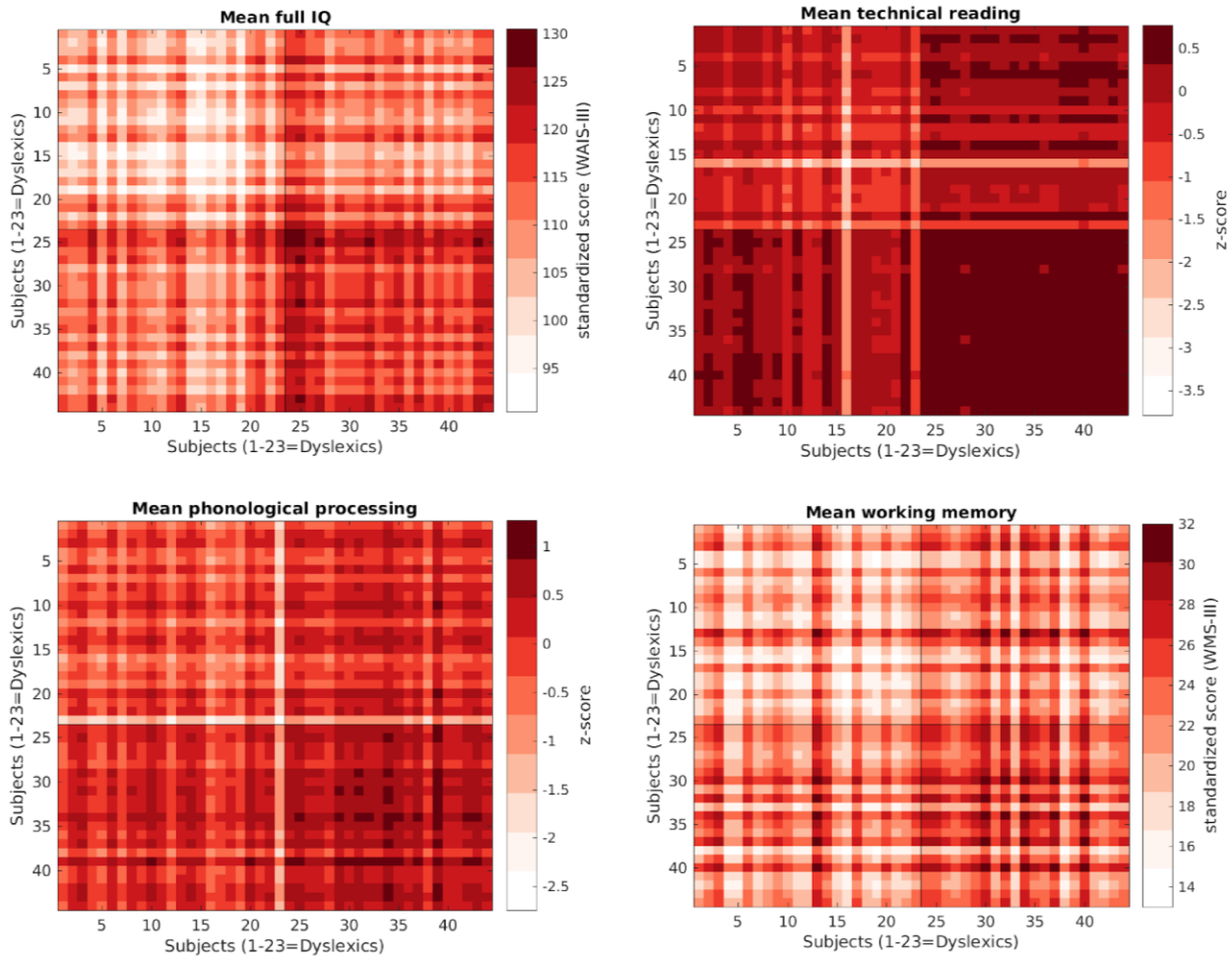

Figure 4. Regression matrices for neuropsychological test composites that were used as models for the Mantel test. Z-scores for phonological processing and technical reading. Standardized test scores for IQ and working memory.

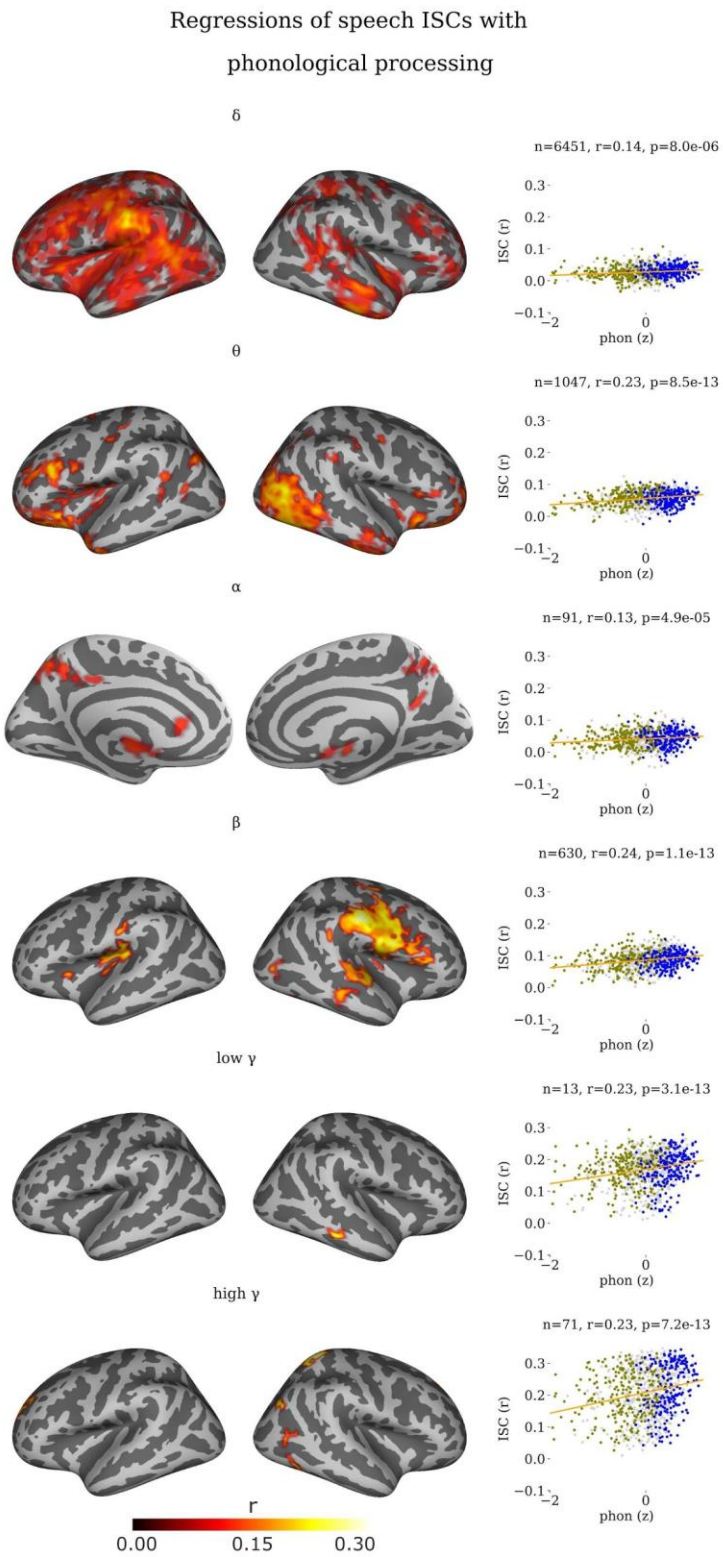

Figure 5. Mantel regressions (r) between phonological processing and brain synchronization adjusted with cluster correction. Left: Significant regressions on left and right brain hemispheres, lateral views, except for alpha band medial view. Right: Mean inter-subject correlations (ISC, r) in largest cluster plotted against phonological processing score (z) for all subject pairs (ocre - dyslexic pairs, blue - control pairs, grey - mixed pairs). Cluster size (n), an estimate of the linear regression (orange line, r), and its significance level (p) are indicated above the scatter plots.

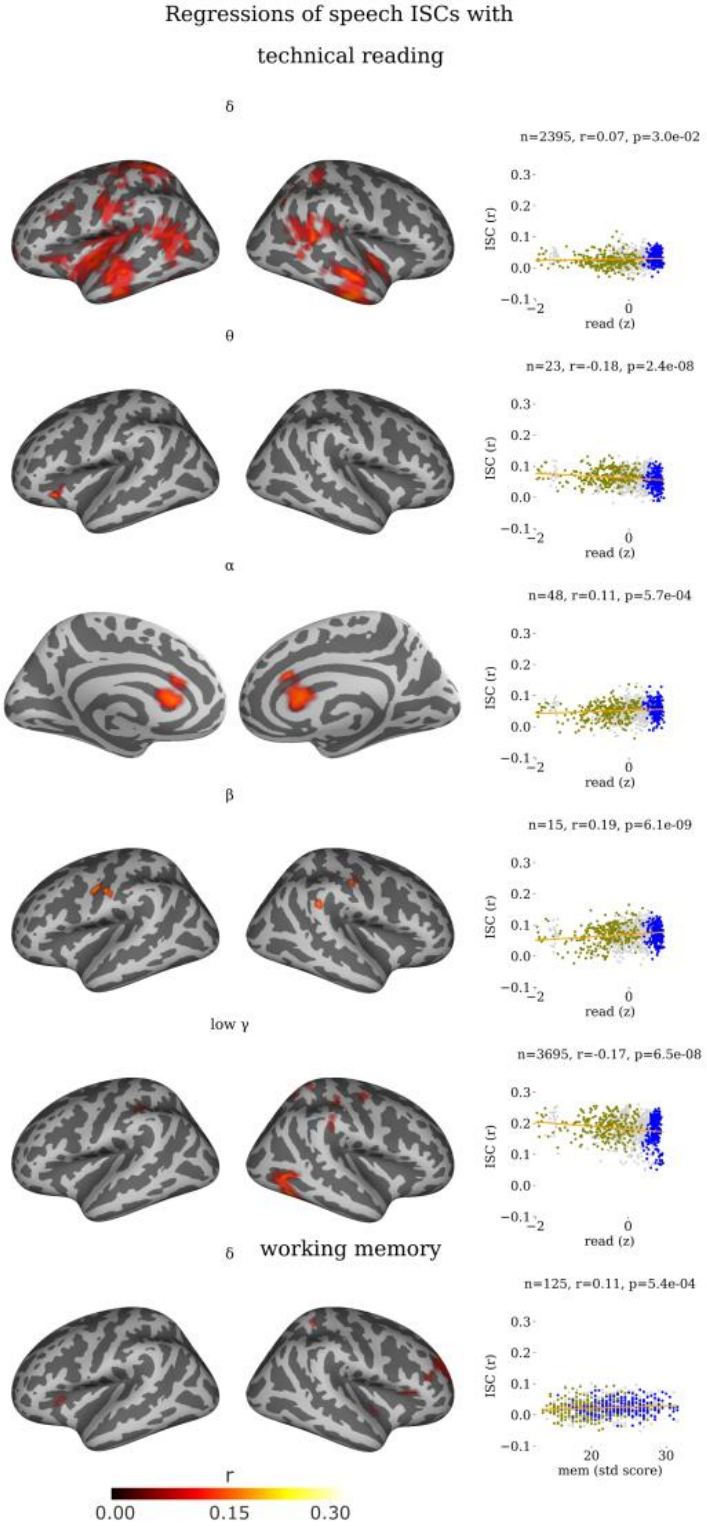

Figure 6. Mantel regressions (r) between technical reading/working memory and brain synchronization adjusted with cluster correction. Left: Significant regressions on left and right brain hemispheres, lateral views, except for alpha band medial view. Right: Mean inter-subject correlations (ISC, r) in largest cluster plotted against phonological processing score (z) for all subject pairs (ocre - dyslexic pairs, blue - control pairs, grey - mixed pairs). Cluster size (n), an estimate of the linear regression (orange line, r), and its significance level (p) are indicated above the scatter plots.

Tables

Table 1. Descriptive statistics about background information regarding both groups (dyslexic, control) and statistics for group differences. For scalar variables (age, education and musical education), means (M, bold) and standard deviations (STD) are reported and independent-sample t*-tests are used for group difference statistics. For the categorical variable (gender), the count for each category (male/female, m/f) is reported and the* X^2*-test is used for group difference statistics.*

VARIABLE	DYSLEXIC GROUP			CONTROL GROUP			STATISTICS		
	N	*M*	*STD*	*N*	*M*	*STD*	t/X^2	*df*	*p*
AGE [YEARS]	23	**31.6**	8.7	21	**30.0**	6.0	0.71	42	.482
GENDER [COUNT]	23	11/12	(m/f)	21	10/11	(m/f)	1.89E-04	1	.989
EDUCATION [YEARS]	23	**15.7**	5.2	20	**17.0**	2.6	-0.95	41	.347
MUSICAL EDUCATION [YEARS]	23	**3.0**	7.8	21	**3.1**	4.8	-0.04	42	.972

*Table 2. Descriptive statistics on neuropsychological test performances for both groups (dyslexic, control). Reported are means, standard deviations (in brackets), mean differences (ΔM) with bootstrapped confidence intervals (CI), t-values with degrees of freedom (df, in brackets) and p-values of group comparisons from independent-sample t-tests, and Cohen's d effect sizes for normally distributed scores in both groups. For non-normally distributed scores in one or both groups(#), median, interquartile range (in brackets), mean differences (ΔM) with bootstrapped confidence intervals (CI), U-values and p-values of group comparisons from Mann-Whitney U-tests, and Cohen's d effect sizes are reported. FDR-corrected significance levels are marked with asterisks (*p < 0.046, **p < 0.01, ***p < 0.001). Composite scores were formed for phonological processing and technical reading by converting the raw scores to z scores and averaging them, and for working memory the composite was formed according to WMS-III (Wechsler, 2008).*

VARIABLE	DYSLEXIC GROUP	CONTROL GROUP	STATISTICS			
			ΔM, CI	*t(df) / U*	*p*	*Cohen's d*
PHONOLOGICAL PROCESSING						
PIG LATIN#	9 (7)	15 (1)	-4.59 [-6.61; -2.70]	77.00	***6.39E-05	1.434
NONWORD SPAN LENGTH	11.26 (2.97)	13.00 (3.02)	-1.74 [-3.41; -0.01]	-1.92(42)	.061	-0.583
RAS TIME#	30 (11.5)	24 (6)	10.62 [6.37; 15.39]	64.00	***3.03E-05	1.617
COMPOSITE#	-0.20 (1.22)	0.49 (0.46)	-0.91 [-1.27; -0.56]	64.00	***3.04E-05	1.617
TECHNICAL READING						
WORD LIST TIME#	31 (13.32)	19.28 (3.27)	15.08 [10.09; 21.14]	22.00	***2.50E-07	2.473
WORD LIST ACCURACY#	30 (1)	30 (0)	-0.78 [-1.34; -0.34]	135.50	**.001	0.810
PSEUDOWORD LIST TIME#	72.94 (37.27)	40.16 (9.33)	41.03 [28.12; 58.26]	5.00	***2.74E-08	3.068
PSEUDOWORD LIST ACCURACY#	21 (9)	28 (4)	-7.63 [-10.13; -5.23]	40.50	***2.16E-06	2.028
COMPOSITE#	-0.34 (1)	0.61 (0.16)	-1.17 [-1.57; -0.84]	2.00	***1.83E-08	3.205
WORKING MEMORY						
COMPOSITE	19.83 (4.80)	24.33 (4.95)	-4.51 [-7.30; -1.65]	-3.06(42)	**.004	-0.924
IQ						
VERBAL IQ	99.57 (13.26)	114.48 (7.43)	-14.91 [-21.37; -8.96]	-4.54(42)	***4.67E-05	-1.370
PERFORMANCE IQ	109.67 (12.50)	121.17 (9.67)	-11.49 [-17.99; -5.21]	-3.39(42)	**.002	-1.023
FULL IQ	104.62 (9.39)	117.82 (6.68)	-13.20 [-17.94; -8.64]	-5.33(42)	***3.68E-06	-1.609

Table 3. Peak MNI coordinates in significant frequency bands, cluster sizes, t/r-statistic, and corresponding automated anatomical labeling (AAL) brain area (Brodmann area, BA, in brackets) for 1) ISC clusters during listening to speech for both groups, 2) ISC brain areas with group differences (con - control group, dys - dyslexic group), and 3) brain areas with significant regression between ISCs during listening to speech and reading-related measures.

frequency band	*cluster size*	*MNI coordinates (x, y, z)*			*t/r*	*AAL brain area (BA)*
1) ISC > 0						
CONTROL GROUP						
delta	10242	4	-31	30	20.57	Cingulum_Mid_R (23)
theta	10242	-11	39	23	36.80	Cingulum_Ant_L (9)
alpha	10242	-22	30	-11	30.83	Frontal_Inf_Orb_L (47)
beta	10242	-34	14	-34	65.48	Temporal_Pole_Mid_L (38)
low gamma	10242	12	-65	58	90.62	Precuneus_R (7)
high gamma	10242	12	-41	71	53.52	Postcentral_R (5)
DYSLEXIC GROUP						
delta	10242	40	-17	32	18.14	Postcentral_R (1)
theta	10242	-10	-7	65	45.78	Supp_Motor_Area_L (6)
alpha	10242	8	57	15	36.72	Frontal_Sup_Medial_R (10)
beta	10242	-50	-11	-21	76.89	Temporal_Mid_L (21)
low gamma	10242	18	-93	18	120.45	Occipital_Sup_R (18)
high gamma	10242	-15	-65	47	63.06	Parietal_Sup_L (7)
2) ISC(CON) VS. ISC(DYS)						
delta	7485	-27	-38	1	-6.97	Hippocampus_L (54)
theta	6544	23	-55	53	7.43	Parietal_Sup_R (7)
alpha	16	14	25	30	-4.64	Cingulum_Mid_R (8)
beta	6195	-50	-14	-18	9.02	Temporal_Mid_L (21)
low gamma	5946	-28	-70	-5	10.16	Fusiform_L (19)

high gamma	834	8	51	20	-5.46	Cingulum_Ant_R (10)
3) CORRELATION OF ISCS WITH READING-RELATED MEASURES						
PHONOLOGICAL PROCESSING						
delta	6451	-57	-24	26	0.24	SupraMarginal_L (40)
theta	921	-10	38	-12	0.28	Frontal_Med_Orb_L (11)
alpha	19	5	-57	22	0.17	Precuneus_R (23)
beta	630	56	-15	40	0.29	Postcentral_R (4)
low gamma	13	65	-26	-13	0.26	Temporal_Mid_R (21)
high gamma	70	25	-45	62	0.29	Postcentral_R (5)
TECHNICAL READING						
delta	810	46	-18	-27	0.21	Temporal_Inf_R (20)
theta	21	-30	28	-6	0.18	Insula_L (47)
alpha	48	5	21	25	0.18	Cingulum_Ant_R (32)
beta	13	-49	-14	29	0.20	Postcentral_L (4)
low gamma	158	31	-58	-5	0.22	Fusiform_R (19)
WORKING MEMORY						
delta	125	14	52	26	0.15	Frontal_Sup_Medial_R (9)
IQ						
delta	1331	-55	-23	28	0.23	SupraMarginal_L (1)
high gamma	10	47	-57	-8	0.26	Temporal_Inf_R (37)

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References

Abrams, D., Ryali, S., Chen, T., Chordia, P., Khouzam, A., Levitin, D.J., Menon, V., 2013. Inter-subject synchronization of brain responses during natural music listening. Eur. J. Neurosci. 37, 1458–69. https://doi.org/10.1111/ejn.12173

Arnal, L.H., Poeppel, D., Giraud, A.-L., 2015. A Neurophysiological Perspective on Speech Processing in "The Neurobiology of Language," Neurobiology of Language. Elsevier Inc. https://doi.org/10.1016/b978-0-12-407794-2.00038-9

Bailey, P.J., Snowling, M.J., 2002. Auditory processing and the development of language and literacy. Br. Med. Bull. 63, 135–146. https://doi.org/10.1093/bmb/63.1.135

Crinion, J.T., Warburton, E.A., Lambon-Ralph, M.A., Howard, D., Wise, R.J.S., 2006. Listening to narrative speech after aphasic stroke: The role of the left anterior temporal lobe. Cereb. Cortex 16, 1116–1125. https://doi.org/10.1093/cercor/bhj053

Dale, A., Fischl, B., Sereno, M.I., 1999. Cortical Surface-Based Analysis: I. Segmentation and Surface Reconstruction. Neuroimage 9, 179–194. https://doi.org/10.1006/nimg.1998.0395

De Vos, A., Vanvooren, S., Vanderauwera, J., Ghesquière, P., Wouters, J., 2017a. Atypical neural synchronization to speech envelope modulations in dyslexia. Brain Lang. 164, 106–117. https://doi.org/10.1016/j.bandl.2016.10.002

De Vos, A., Vanvooren, S., Vanderauwera, J., Ghesquière, P., Wouters, J., 2017b. A longitudinal study investigating neural processing of speech envelope modulation rates in children with (a family risk for) dyslexia. Cortex 93, 206–219. https://doi.org/10.1016/j.cortex.2017.05.007

Ding, N., Melloni, L., Zhang, H., Tian, X., Poeppel, D., 2015. Cortical tracking of hierarchical linguistic structures in connected speech. Nat. Neurosci. 19, 158–164. https://doi.org/10.1038/nn.4186

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

Elliott, J.G., Grigorenko, E.L., 2014. The Dyslexia Debate, Cambridge Studies in Cognitive and Perceptual Development. Cambridge University Press.

Fink, G.R., Markowitsch, H.J., Reinkemeier, M., Bruckbauer, T., Kessler, J., Heiss, W.-D., 1996. Cerebral Representation of One's Own Past: Neural Networks Involved in Autobiographical Memory. J. Neurosci. 16, 4275–4282. https://doi.org/10.1523/JNEUROSCI.16-13-04275.1996

Fischl, B., Salat, D. ~H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., van der Kouwe, A., Killiany, R., Kennedy, D., Klaveness, S., Montillo, A., Makris, N., Rosen, B., Dale, A. ~M., 2002. Whole brain segmentation: automated labeling of neuroanatomical structures in the human brain. Neuron 33, 341–355.

Fischl, B., Salat, D.H., van der Kouwe, A.J.W., Makris, N., Ségonne, F., Quinn, B.T., Dale, A.M., 2004. Sequence-independent segmentation of magnetic resonance images. Neuroimage 23, S69–S84. https://doi.org/DOI: 10.1016/j.neuroimage.2004.07.016

Fischl, B., Sereno, M.I., Dale, A., 1999a. Cortical Surface-Based Analysis: II: Inflation, Flattening, and a Surface-Based Coordinate System. Neuroimage 9, 195–207. https://doi.org/10.1006/nimg.1998.0396

Fischl, B., Sereno, M.I., Tootell, R.B.H., Dale, A.M., 1999b. High-resolution intersubject averaging and a coordinate system for the cortical surface. Hum. Brain Mapp. 8, 272–284. https://doi.org/10.1002/(SICI)1097-0193(1999)8:4<272::AID-HBM10>3.0.CO;2-4

Giraud, A., Poeppel, D., 2012. Cortical oscillations and speech processing: emerging computational principles and operations. Nat. Neurosci. 15, 511–517. https://doi.org/10.1038/nn.3063

Goswami, U., 2011. A temporal sampling framework for developmental dyslexia. Trends Cogn. Sci. 15, 3–10. https://doi.org/10.1016/j.tics.2010.10.001

Goswami, U., 2015. Sensory theories of developmental dyslexia: three challenges for research. Nat. Rev. Neurosci. 16, 43–54. https://doi.org/10.1038/nrn3836

Gramfort, A., Luessi, M., Larson, E., Engemann, D. a, Strohmeier, D., Brodbeck, C., Goj, R., Jas, M., Brooks, T., Parkkonen, L., Hämäläinen, M., 2013. MEG and EEG data analysis with MNE-Python. Front. Neurosci. 7, 267. https://doi.org/10.3389/fnins.2013.00267

Gramfort, A., Luessi, M., Larson, E., Engemann, D.A., Strohmeier, D., Brodbeck, C., Parkkonen, L., Hämäläinen, M.S., 2014. MNE software for processing MEG and EEG data. Neuroimage 86, 446–

460. https://doi.org/10.1016/j.neuroimage.2013.10.027

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, 2952–2961. https://doi.org/10.1016/j.neuroimage.2011.09.075

Hasson, U., Egidi, G., Marelli, M., Willems, R.M., 2018. Grounding the neurobiology of language in first principles: The necessity of non-language-centric explanations for language comprehension. Cognition 180, 135–157. https://doi.org/10.1016/j.cognition.2018.06.018

Hasson, U., Ghazanfar, A.A., Galantucci, B., Garrod, S., Keysers, C., 2012. Brain-to-brain coupling: A mechanism for creating and sharing a social world. Trends Cogn. Sci. 16, 114–121. https://doi.org/10.1016/j.tics.2011.12.007

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., Malach, R., 2004. Intersubject synchronization of cortical activity during natural vision. Science 303, 1634–40. https://doi.org/10.1126/science.1089506

Hentschke, H., Stüttgen, M.C., 2011. Computation of measures of effect size for neuroscience data sets. Eur. J. Neurosci. 34, 1887–1894. https://doi.org/10.1111/j.1460-9568.2011.07902.x

Hickok, G., Poeppel, D., 2007. The cortical organization of speech processing. Nat. Rev. Neurosci. 8, 393–402. https://doi.org/10.1038/nrn2113

Kessler, R.C., Adler, L., Ames, M., Demler, O., Faraone, S., Hiripi, E., Howes, M.J., Jin, R., Secnik, K., Spencer, T., Ustun, T.B., Walters, E.E., 2005. The World Health Organization Adult ADHD Self-Report Scale (ASRS): a short screening scale for use in the general population. Psychol. Med. 35, 245–56.

Laasonen, M., Service, E., Virsu, V., 2002. Crossmodal temporal order and processing acuity in developmentally dyslexic young adults. Brain Lang. 80, 340–54. https://doi.org/10.1006/brln.2001.2593

Lankinen, K., Saari, J., Hari, R., Koskinen, M., 2014. Intersubject consistency of cortical MEG signals during movie viewing. Neuroimage 92, 217–224. https://doi.org/10.1016/j.neuroimage.2014.02.004

Lefly, D.L., Pennington, B.F., 2000. Reliability and Validity of the Adult Reading History Questionnaire. J. Learn. Disabil. 33, 286–296. https://doi.org/10.1177/002221940003300306

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, 1080–1090. https://doi.org/10.1016/j.neuron.2011.11.002

Luo, H., Poeppel, D., 2007. Phase patterns of neuronal responses reliably discriminate speech in human auditory cortex. Neuron 54, 1001–10. https://doi.org/10.1016/j.neuron.2007.06.004

Mai, G., Minett, J.W., Wang, W.S.Y., 2016. Delta, theta, beta, and gamma brain oscillations index levels of auditory sentence processing. Neuroimage 133, 516–528. https://doi.org/10.1016/j.neuroimage.2016.02.064

Mantel, N., 1967. The Detection of Disease Clustering and a Generalized Regression Approach. Cancer Res. 27, 209–220.

Marinkovic, K., Dhond, R.P., Dale, A.M., Glessner, M., Carr, V., Halgren, E., 2003. Spatiotemporal Dynamics of Modality-Specific and Supramodal Word Processing. Neuron 38, 487–497. https://doi.org/10.1016/S0896-6273(03)00197-1

Meyer, L., 2018. The neural oscillations of speech processing and language comprehension: state of the art and emerging mechanisms. Eur. J. Neurosci. 48, 2609–2621. https://doi.org/10.1111/ejn.13748

Molinaro, N., Lizarazu, M., Lallier, M., Bourguignon, M., Carreiras, M., 2016. Out-of-synchrony speech entrainment in developmental dyslexia. Hum. Brain Mapp. 37, 2767–2783. https://doi.org/10.1002/hbm.23206

Morillon, B., Liégeois-Chauvel, C., Arnal, L.H., Bénar, C.-G., Giraud, A.-L., 2012. Asymmetric Function of Theta and Gamma Activity in Syllable Processing: An Intra-Cortical Study. Front. Psychol. 3, 1–9. https://doi.org/10.3389/fpsyg.2012.00248

Nevala, J., Kairaluoma, L., Ahonen, T., Aro, M., Holopainen, L., 2006. Lukemis- ja kirjoittamistaitojen yksilötestistö nuorille ja aikuisille. Niilo Mäki Instituutti, Jyväskylä.

Nourski, K. V., Reale, R.A., Oya, H., Kawasaki, H., Kovach, C.K., Chen, H., Howard, M.A., Brugge, J.F., 2009. Temporal Envelope of Time-Compressed Speech Represented in the Human Auditory Cortex. J. Neurosci. 29, 15564–15574. https://doi.org/10.1523/JNEUROSCI.3065-09.2009

Obleser, J., Weisz, N., 2012. Suppressed alpha oscillations predict intelligibility of speech and its acoustic

details. Cereb. Cortex 22, 2466–2477. https://doi.org/10.1093/cercor/bhr325

Peelle, J.E., Davis, M.H., 2012. Neural oscillations carry speech rhythm through to comprehension. Front. Psychol. 3, 1–17. https://doi.org/10.3389/fpsyg.2012.00320

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 Lang. 160, 1–10. https://doi.org/10.1016/j.bandl.2016.06.006

Pulvermüller, F., Eulitz, C., Pantev, C., Mohr, B., Feige, B., Lutzenberger, W., Elbert, T., Birbaumer, N., 1996. High-frequency cortical responses reflect lexical processing: an MEG study. Electroencephalogr. Clin. Neurophysiol. 98, 76–85. https://doi.org/10.1016/0013-4694(95)00191-3

Ramus, F., Rosen, S., Dakin, S.C., Day, B.L., Castellote, J.M., White, S., Frith, U., 2003. Theories of developmental dyslexia: Insights from a multiple case study of dyslexic adults. Brain 126, 841–865. https://doi.org/10.1093/brain/awg076

Rommers, J., Dickson, D.S., Norton, J.J.S., Wlotko, E.W., Federmeier, K.D., 2017. Alpha and theta band dynamics related to sentential constraint and word expectancy. Lang. Cogn. Neurosci. 32, 576–589. https://doi.org/10.1080/23273798.2016.1183799

Schulte-Körne, G., Bruder, J., 2010. Clinical neurophysiology of visual and auditory processing in dyslexia: A review. Clin. Neurophysiol. 121, 1794–1809. https://doi.org/10.1016/j.clinph.2010.04.028

Ségonne, F., Dale, a M., Busa, E., Glessner, M., Salat, D., Hahn, H.K., Fischl, B., Segonne, F., Dale, a M., Busa, E., Glessner, M., Salat, D., Hahn, H.K., Fischl, B., 2004. A hybrid approach to the skull stripping problem in MRI. Neuroimage 22, 1060–1075. https://doi.org/10.1016/j.neuroimage.2004.03.032

Sled, J.G., Zijdenbos, A.P., Evans, A.C., 1998. A nonparametric method for automatic correction of intensity nonuniformity in MRI data. IEEE Trans Med Imaging 17, 87–97.

Suppanen, E., 2014. Inter-subject correlation of MEG data during movie viewing. Master's thesis, Aalto University School of Electrical Engineering.

Taulu, S., Simola, J., 2006. Spatiotemporal signal space separation method for rejecting nearby interference in MEG measurements. Phys. Med. Biol. 51, 1759–1768.

https://doi.org/10.1088/0031-9155/51/7/008

Tesche, C.D., Uusitalo, M.A., Ilmoniemi, R.J., Huotilainen, M., Kajola, M., Salonen, O., 1995. Signal-space projections of MEG data characterize both distributed and well-localized neuronal sources. Electroencephalogr. Clin. Neurophysiol. 95, 189–200.

Thiede, A., 2014. Magnetoencephalographic (MEG) Inter-subject Correlation using Continuous Music Stimuli. Master's thesis, Aalto University School of Science.

Thiede, A., Suppanen, E., Glerean, E., Kliuchko, M., Brattico, E., Parkkonen, L., 2019. Magnetoencephalographic (MEG) Inter-subject Correlation using Continuous Music Stimuli. Manuscript in preparation.

Tzourio, N., Crivello, F., Mellet, E., Nkanga-Ngila, B., Mazoyer, B., 1998. Functional anatomy of dominance for speech comprehension in left handers vs right handers. Neuroimage 8, 1–16. https://doi.org/10.1006/nimg.1998.0343

Uusitalo, M.A., Ilmoniemi, R.J., 1997. Signal-space projection method for separating MEG or EEG into components. Med. Biol. Eng. Comput. 35, 135–40.

Vilberg, K.L., Rugg, M.D., 2008. Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. Neuropsychologia 46, 1787–1799. https://doi.org/10.1016/j.neuropsychologia.2008.01.004

Ward, L.M., 2003. Synchronous neural oscillations and cognitive processes. Trends Cogn. Sci. 7, 553–559. https://doi.org/10.1016/j.tics.2003.10.012

Wechsler, D., 2008. Wechsler Memory Scale (Third Edition). The Psychological Corporation, New York : Wechsler, D. Psykologien Kustannus Oy, Helsinki.

Wechsler, D., 2005. Wechsler Adult Intelligence Scale (Third Edition), III. ed. The Psychological Corporation, New York: Wechsler, D. Psykologien Kustannus Oy, Helsinki.

Wilson, S.M., Molnar-Szakacs, I., Iacoboni, M., 2008. Beyond superior temporal cortex: intersubject correlations in narrative speech comprehension. Cereb. Cortex 18, 230–242. https://doi.org/10.1093/cercor/bhm049

Wolf, M., 1986. Rapid alternating stimulus naming in the developmental dyslexias. Brain Lang. 27, 360–

79.