

Atypical neural synchronization to speech envelope modulations in dyslexia



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ABSTRACT

A fundamental deficit in the synchronization of neural oscillations to temporal information in speech could underlie phonological processing problems in dyslexia. In this study, the hypothesis of a neural synchronization impairment is investigated more specifically as a function of different neural oscillatory bands and temporal information rates in speech. Auditory steady-state responses to 4, 10, 20 and 40 Hz modulations were recorded in normal reading and dyslexic adolescents to measure neural synchronization of theta, alpha, beta and low-gamma oscillations to syllabic and phonemic rate information. In comparison to normal readers, dyslexic readers showed reduced non-synchronized theta activity, reduced synchronized alpha activity and enhanced synchronized beta activity. Positive correlations between alpha synchronization and phonological skills were found in normal readers, but were absent in dyslexic readers. In contrast, dyslexic readers exhibited positive correlations between beta synchronization and phonological skills. Together, these results suggest that auditory neural synchronization of alpha and beta oscillations is atypical in dyslexia, indicating deviant neural processing of both syllabic and phonemic rate information. Impaired synchronization of alpha oscillations in particular demonstrated to be the most prominent neural anomaly possibly hampering speech and phonological processing in dyslexic readers.

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1. Introduction

Developmental dyslexia refers to a hereditary neurological disorder characterized by severe and persistent difficulties in reading and spelling despite normal intelligence, education and intense remedial effort. Depending on the used criteria, dyslexia is thought to affect between 5 and 10% of the population (Vellutino, Fletcher, Snowling, & Scanlon, 2004). Although it is widely agreed that the majority of dyslexic individuals show difficulties in one or several aspects of phonological processing, the underlying cause of these phonological problems remains debated. Recent evidence suggests that a fundamental deficit in synchronization of neural oscillations to temporal information in speech could underlie the phonological processing problems found in dyslexia (Goswami, 2011).

Abbreviations: ASSR(s), auditory steady-state response(s); SNR, signal-to-noise ratio.

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Temporal information in speech, most prominently represented as amplitude modulations in the speech envelope between 2 and 50 Hz (Rosen, 1992), is crucial for accurate speech perception (Shannon, Zeng, Kamath, Wygonski, & Ekelid, 1995). The lower end of the speech envelope modulation range (between 2 and 12 Hz) hereby provides information on syllabic patterns (Edwards & Chang, 2013; Greenberg, Carvey, Hitchcock, & Chang, 2003), whereas the higher end of this range (between 12 and 50 Hz) provides information on phonemic patterns (Chait, Greenberg, Arai, Simon, & Poeppel, 2015; Leong & Goswami, 2014). Given the importance of temporal information for speech perception, it is of particular interest to understand how these syllabic and phonemic modulation rates are processed in the human auditory cortex. In this context, recent studies have assigned a fundamental role to neural oscillations by means of neural synchronization (Giraud & Poeppel, 2012; Peelle & Davis, 2012). It has been shown that neural populations in the auditory cortex synchronize their oscillatory activity in a rate-dependent manner to incoming temporal information. More specifically, the neural theta band (4–8 Hz) has been associated with sampling of events of

lower temporal precision, coinciding with the typical rates of syllabic patterns (Doelling, Arnal, Ghitza, & Poeppel, 2014; Ghitza, 2013; Ghitza, Giraud, & Poeppel, 2012; Luo & Poeppel, 2007), whereas the neural beta (13–30 Hz) and gamma (> 30 Hz) band sample events that require higher temporal precision, such as phonemic rate patterns (Bidelman, 2015; Han, Mody, & Ahlfors, 2012).

To examine whether an impairment in synchronization of neural oscillations to phonologically relevant patterns in speech could be related to the phonological processing problems in dyslexia, previous studies have focused on different oscillatory ranges. As a measure for syllable rate processing, modulations around 4 Hz are typically used. In general, results from these studies indicate no deviances in neural synchronization of theta oscillations in adults with dyslexia (Hämäläinen, Rupp, Soltész, Szűcs, & Goswami, 2012; Poelmans, Luts, Vandermosten, Boets, et al., 2012) nor in pre-reading children with a hereditary risk for dyslexia (Vanvooren, Poelmans, Hofmann, Ghesquière, & Wouters, 2014). On the other hand, modulations of 20 Hz and higher have been used as a measure for phoneme rate processing. Regarding these beta and low-gamma ranges, inconsistent results have been found, with dyslexic readers showing reduced synchronization in the left hemisphere (Lehongre, Ramus, Villiermet, Schwartz, & Giraud, 2011; Poelmans, Luts, Vandermosten, Boets, et al., 2012), increased synchronization in the right hemisphere (Lizarazu et al., 2015) or no synchronization deficit (Hämäläinen et al., 2012). Based on these findings, the dyslexic brain seems to be characterized by atypical synchronizing behavior of beta or low-gamma neural oscillations, while no clear impairments are found regarding theta synchronization.

Strikingly, research in dyslexia is characterized by a lack of interest in auditory neural synchronization of alpha rates (8–13 Hz). The lower end of the speech envelope modulation range, representing syllable rate information, however includes modulations up to 12 Hz. Next to theta oscillations, an additional role for encoding of syllable rate information therefore seems to be attributable to auditory alpha range oscillatory activity. Initial evidence for this hypothesis is provided by Shahin and Pitt (2012), who found that alpha, not theta, oscillations supported neurophysiological mechanisms of speech segmentation. Additionally, a growing number of studies suggests that alpha oscillations are not only implicated in speech perception by means of bottom-up neural encoding, but also by exerting excitatory and inhibitory influences controlled by top-down processes (Kayser, Ince, Gross, & Kayser, 2015; Obleser & Weisz, 2012; Weisz, Hartmann, Müller, Lorenz, & Obleser, 2011; Weisz, Müller, Jatzew, & Bertrand, 2014; Weisz & Obleser, 2014; for a more general review, see Klimesch, Sauseng, & Hanslmayr, 2007). More specifically, alpha oscillations are thought to regulate auditory selective attention, a top-down process facilitating neural tracking of speech by selectively attending to relevant information and ignoring irrelevant information. Auditory selective attention has been related to speech-in-noise perception (Strauß, Wöstmann, & Obleser, 2014) as well as phonological skills (Yoncheva, Maurer, Zevin, & McCandliss, 2014). Given that dyslexic readers exhibit both speech and phonological processing problems, these novel insights urge for an investigation of auditory alpha oscillations in dyslexia.

In the present study, auditory neural synchronization is evaluated in a group of normal reading and dyslexic adolescents in four oscillatory bands (theta, alpha, beta and low-gamma), corresponding to two speech envelope frequency ranges (syllabic and phonemic). Besides neural synchronization to specific modulation frequencies, we also investigate the behavior of surrounding neural band activity during auditory processing. Despite recent findings assigning a unique role to alpha oscillations for speech perception in normal readers, alpha rate synchronization has not yet been

extensively examined in dyslexia. Our study is the first to address four different oscillatory bands, including alpha, to examine whether a fundamental deficit in the functional role of neural oscillations is related to the phonological processing problems found in dyslexia.

2. Materials and methods

2.1. Participants

Fifty-three adolescents participated in this study, 21 normal reading adolescents (10 male, 11 female) and 32 dyslexic adolescents (15 male, 17 female; Table 1). All participants had bilateral normal hearing (pure tone average at 500, 1000 and 2000 Hz < 25 dB HL), normal nonverbal intelligence (IQ score $\geq$ 80; Kort et al., 2005; Wechsler, 1991) and no history of brain injury or neurological disorders. Participants were classified as normal or dyslexic readers based on their history of reading problems and their current reading performance. Dyslexic readers were required to (1) dispose of a formal clinical dyslexia diagnosis or report a life-long history of reading problems, and (2) score below percentile 10 on both a standardized word reading (Brus & Voeten, 1973) and pseudoword reading test (van den Bos, Spelberg, Scheepstra, & De Vries, 1994). Normal readers were required to (1) report no history of reading problems, and (2) score above percentile 10 on both reading tests. In addition to word and pseudoword reading, phonological awareness was also assessed by means of a spoonerisms test (Poelmans et al., 2011).

This study was approved by the Medical Ethical Committee of the University Hospitals of Leuven. All participants and their parents gave written informed consent.

2.2. Auditory steady-state responses

Auditory-steady-state responses (ASSRs) provide an interesting neurophysiological paradigm to measure synchronization of neural oscillations in the auditory cortex. ASSRs are defined as frequency and phase locked (i.e. synchronized) responses, which appear in the EEG when a stimulus with a periodic character is presented to the auditory system (Picton, John, Dimitrijevic, & Purcell, 2003). Because the periodic parameters of ASSR stimuli can be controllably adjusted to match the temporal rates at which meaningful phonological components occur in speech, ASSRs have been suggested to offer an objective measure for the ability of the auditory system to encode the different time scales represented in the speech envelope (e.g. Miyazaki, Thompson, Fujioka, & Ross, 2013; Tang, Brock, & Johnson, 2016; Tang, Crain, & Johnson, 2016). A number of studies have indeed demonstrated significant correlations between ASSRs and speech perception (Alaerts, Luts, Hofmann, & Wouters, 2009; Dimitrijevic, John, & Picton, 2004; Manju, Gopika, & Arivudai Nambi, 2014; Poelmans, Luts, Vandermosten, Boets, et al., 2012), thereby consolidating the link between low-level auditory temporal processing and speech perception.

2.2.1. Stimulus parameters

The stimuli used in the present study consisted of amplitude modulated speech-weighted noise. The carrier noise was adopted from the “Leuven Intelligibility Sentence Test” (van Wieringen & Wouters, 2008) and represents the long-term average speech spectrum of 730 sentences of a female speaker. The speech-weighted carrier noise was 100% amplitude modulated at approximately 4, 10, 20 and 40 Hz to measure neural synchronization of theta, alpha, beta and gamma oscillations respectively. The spectrum (dB/Hz) of the carrier wave, as well as the time signals of the

Table 1
Participant characteristics.

	Normal readers (N = 21)		Dyslexic readers (N = 32)		Group comparisons
	M (SD)	Range	M (SD)	Range	
Age (months)	177 (3)	172; 182	176 (4)	167; 181	$t_{(51)} = 0.66, p = 0.515$
Nonverbal IQ ^a	100 (10)	90; 125	100 (20)	80; 125	$U = 332.00, p = 0.944$
Reading					
Word reading					
Raw score	83 (11)	66; 111	62 (11)	31; 79	$t_{(51)} = 6.79, p < 0.001$
Z score ^b	−0.48 (0.84)		−2.10 (0.86)		
Pseudoword reading					
Raw score	77 (13)	55; 104	50 (15)	16; 80	$t_{(51)} = 7.04, p < 0.001$
Z score ^b	−0.34 (0.67)		−1.76 (0.76)		
Composite score ^c	−0.41 (0.69)		−1.93 (0.77)		$t_{(51)} = 7.33, p < 0.001$
Phonological awareness					
Accuracy					
Raw score	0.85 (0.11)	0.52; 1.00	0.74 (14)	0.18; 0.97	$t_{(51)} = 2.81, p = 0.007$
Z score ^d	0.00 (1.00)		−0.94 (1.31)		
Reaction time					
Raw score (s)	4.70 (3.13)	2.08; 8.51	8.03 (4.53)	3.87; 38.05	$U = 108.00, p < 0.001$
Z score ^d	0.16 (1.64)		−1.58 (2.37)		
Composite score ^e	0.20 (1.37)		−1.48 (1.77)		$U = 114.00, p < 0.001$

Note. For non-normally distributed data (i.e. nonverbal IQ, phonological awareness reaction time and phonological awareness composite score), the median and interquartile range are presented instead of the mean (M) and standard deviation (SD), and group comparisons are calculated using Mann-Whitney *U*-tests instead of independent *t*-tests.

^a Standard scores were calculated based on the conversion of raw scores to scaled scores by means of the normative data of Kort et al. (2005).

^b Z scores were computed using normative data of 15- to 16-year-old Dutch students, which were weighted by educational level (word reading: $M = 89.3$, $SD = 13.2$; pseudoword reading: $M = 83.8$, $SD = 19.3$; Kuijpers et al., 2003).

^c For each participant, the composite score was calculated as $[(Z_{\text{word reading}} + Z_{\text{pseudoword reading}})/2]$.

^d Z scores were calculated with respect to the current group of normal readers. The raw score of reaction time was first multiplied by (-1) , so that accuracy and reaction time were interpretable in the same direction.

^e For each participant, the composite score was calculated as $[(Z_{\text{PA accuracy}} + Z_{\text{PA reaction time}}(-1))/2]$.

modulated stimuli are shown in Fig. 1. All stimuli were presented at 70 dB SPL through insert earphones in three modalities: monaurally to the left ear, monaurally to the right ear and bilaterally.

2.2.2. Recording parameters

EEGs were recorded with the BioSemi ActiveTwo system using 64 active Ag/AgCl electrodes mounted in head caps according to the 10–10 electrode system. Electrode offsets were kept below

30 mV. All recordings were administered in a double-walled soundproof booth with Faraday cage. Participants were asked to lie down on a bed while watching a soundless movie. From our preceding ASSR studies in children (Vanvooren et al., 2014) and adult populations (Goossens, Vercammen, Wouters, & van Wieringen, 2016; Poelmans, Luts, Vandermosten, Boets, et al., 2012; Poelmans, Luts, Vandermosten, Ghesquière, & Wouters, 2012; Vanvooren, Hofmann, Poelmans, Ghesquière, & Wouters,

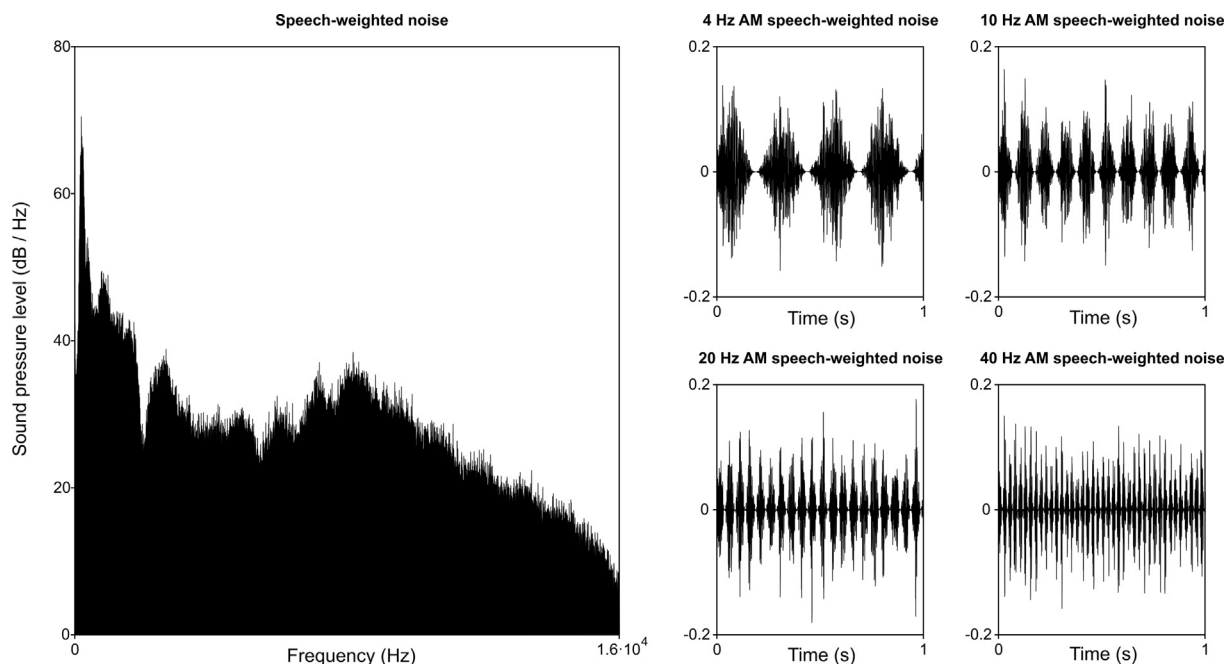


Fig. 1. Stimulus parameters. The panel on the left shows the spectrum (dB/Hz) of the speech-weighted carrier noise adopted from the “Leuven Intelligibility Sentence Test” (van Wieringen & Wouters, 2008). The panels on the right show a 1 s time signal of each of the amplitude modulated stimuli, i.e. 4 and 10 Hz syllabic rate modulations (top) and 20 and 40 Hz phonemic rate modulations (bottom).

2015), we have learned that a passive listening paradigm warrants the same level of alertness and attention throughout the EEG measurement. For each subject, we collected a total of 12 EEG measurements (4 modulation frequencies $\times$ 3 modes of stimulation). Each measurement consisted of a 5-min (300-s) EEG recording.

2.2.3. Preprocessing

A sequence of pre-processing steps was applied per EEG recording. First, the EEG signal was segmented into epochs of 1.024 s. This resulted in 292 epochs per electrode (300 s/1.024 s). Next, BESA Research 6.0 software was used for artefact rejection. The amplitude rejection level was determined on an individual basis, but never exceeding 150 μ V, until exactly 256 epochs per electrode were retained. Each artefact-free recording was then imported into Matlab R2013a and referenced to electrode Cz. The remaining 256 artefact-free epochs of each electrode were clustered into sweeps of 64 consecutive epochs. This resulted in four sweeps (256 epochs/64 epochs), which were subsequently averaged into one sweep per electrode. In the following step, sweeps were averaged across a pre-selected electrode configuration. Nine electrodes over the left hemisphere (TP7, P1, P3, P5, P7, P9, PO3, PO7 and O1) and nine electrodes over the right hemisphere (TP8, P2, P4, P6, P8, P10, PO4, PO8 and O2) were included in the inter-electrode averaging, resulting in one “channel” representing the averaged time signal recorded over the left temporo-parietal hemispheric region and one “channel” representing the averaged time signal recorded over the right temporo-parietal hemispheric region. Our electrode configuration was based on previous research showing that these electrodes are the most sensitive to pick up ASSRs in children (Vanvooren et al., 2014) as well as adults (Vanvooren et al., 2015). The topographic maps in Fig. 2 confirm the suitability of this electrode configuration in the current adolescent dataset. In the final step, a Fast Fourier Transformation (FFT) algorithm was used to convert the time signals of the two channels into a set of complex values that vary with frequency. From the complex values of the FFT, power values were calculated in discrete frequency bins. Fig. 3 shows the resulting FFT spectra for a randomly selected normal reading participant.

2.2.4. Outcome measures

The signal-to-noise ratio (SNR) was used as a measure for the degree of neural synchronization to the modulation frequency. The SNR was calculated from the FFT using the following formula:

$$\text{SNR} = \frac{P_f}{P_{f \pm 1 \text{ Hz}}}$$

P_f represents the power of the Fourier component in the frequency bin corresponding to the modulation frequency f , also referred to as the response power (μV^2). For example, the response power for 4 Hz stimulation was calculated as the power of the Fourier component in the 4 Hz frequency bin. The response amplitude (μV) was derived from the response power as $\sqrt{P_f}$. Response power and amplitude represent the amount of neural activity that synchronized (i.e. frequency and phase locked) to the modulation frequency.

$P_{f \pm 1 \text{ Hz}}$ represents the average power of the Fourier components in an approximately 2 Hz wide frequency band around the modulation frequency f (i.e. 60 frequency bins or approximately 1 Hz on each side), further referred to as the surrounding power (μV^2). For example, the surrounding power for 4 Hz stimulation was calculated as the average power in the 3–5 Hz frequency band, excluding the 4 Hz frequency bin. The surrounding amplitude (μV) was derived from the surrounding power as $\sqrt{P_{f \pm 1 \text{ Hz}}}$. Surrounding power and amplitude represent the amount of non-synchronized neural background activity. Note that, even though we chose the narrowest frequency interval that allowed for an adequate

estimation of the surrounding amplitude, a possible influence of delta range activity needs to be taken into account in the analysis and interpretation of effects in the 3–5 Hz range. The SNR, as well as the amplitude measures, were converted to dB using a logarithmic transformation with reference to 1 μV .

In summary, this study applied three different outcome measures to describe the synchronizing behavior of neural oscillations in normal and dyslexic readers. As a measure for the degree of neural synchronization, the SNR was used. However, the SNR is determined by the strength of both synchronized and non-synchronized activity. Each group difference in SNR can therefore be explained by a difference in synchronized activity, a difference in non-synchronized background activity, or a combination of both. To distinguish between these factors underlying SNR differences, additional analyses of response amplitude and surrounding amplitude were also performed.

2.3. Statistical analyses

All statistical analyses were performed with IBM SPSS Statistics 23.0. The assumption of normality was assessed with a Kolmogorov-Smirnov test for all groups and conditions separately. Mauchly's test was used to examine the assumption of sphericity and the Greenhouse-Geisser correction was applied if necessary. Levene's test confirmed homogeneity of variance for all levels of the within subject variables. The significance level for exploring assumptions was set at $p < 0.01$ to adjust for multiple comparisons. For post hoc comparisons, the more conservative Bonferroni correction procedure was used. All analyses were two-tailed ($\alpha = 0.05$), unless otherwise stated.

To examine possible group differences between normal and dyslexic readers in terms of response amplitudes, surrounding amplitudes and SNRs, a series of three-way factorial mixed analyses of variance (FM-ANOVA) was carried out for each modulation frequency separately. Hemisphere (two levels: left hemisphere and right hemisphere) and stimulation mode (three levels: left ear, both ears, right ear) were defined as within-subject variables. Reading group (two levels: normal readers and dyslexic readers) was included as between-subject variable. The results presented here will focus on the main effects of reading group and possible interaction effects of reading group with hemisphere or stimulation mode. The main effects of and interaction effects between hemisphere and stimulation mode will not be discussed. The latter effects, by definition, apply to both reading groups and therefore provide no added value to our research questions.

For those EEG outcome measures where the FM-ANOVA revealed the strongest group differences between normal and dyslexic readers, Spearman's rho (r_s) correlation coefficients with behavioral measures of reading and phonological awareness were calculated. A False Discovery Rate (FDR) correction (Benjamini & Hochberg, 1995) was applied for the number of correlational analyses performed. The significance of the difference between correlation coefficients in the normal reading and dyslexic group was assessed using a Fisher z transformation. In addition to the FM-ANOVA, these correlational analyses allow to evaluate whether neural auditory processing relates to reading and phonological skills, and whether the relation is different in normal and dyslexic readers.

3. Results

3.1. SNR

In normal readers mean SNRs were 8.5 dB, 9.9 dB, 12.4 dB and 20.6 dB for 4, 10, 20 and 40 Hz respectively. In dyslexic readers,

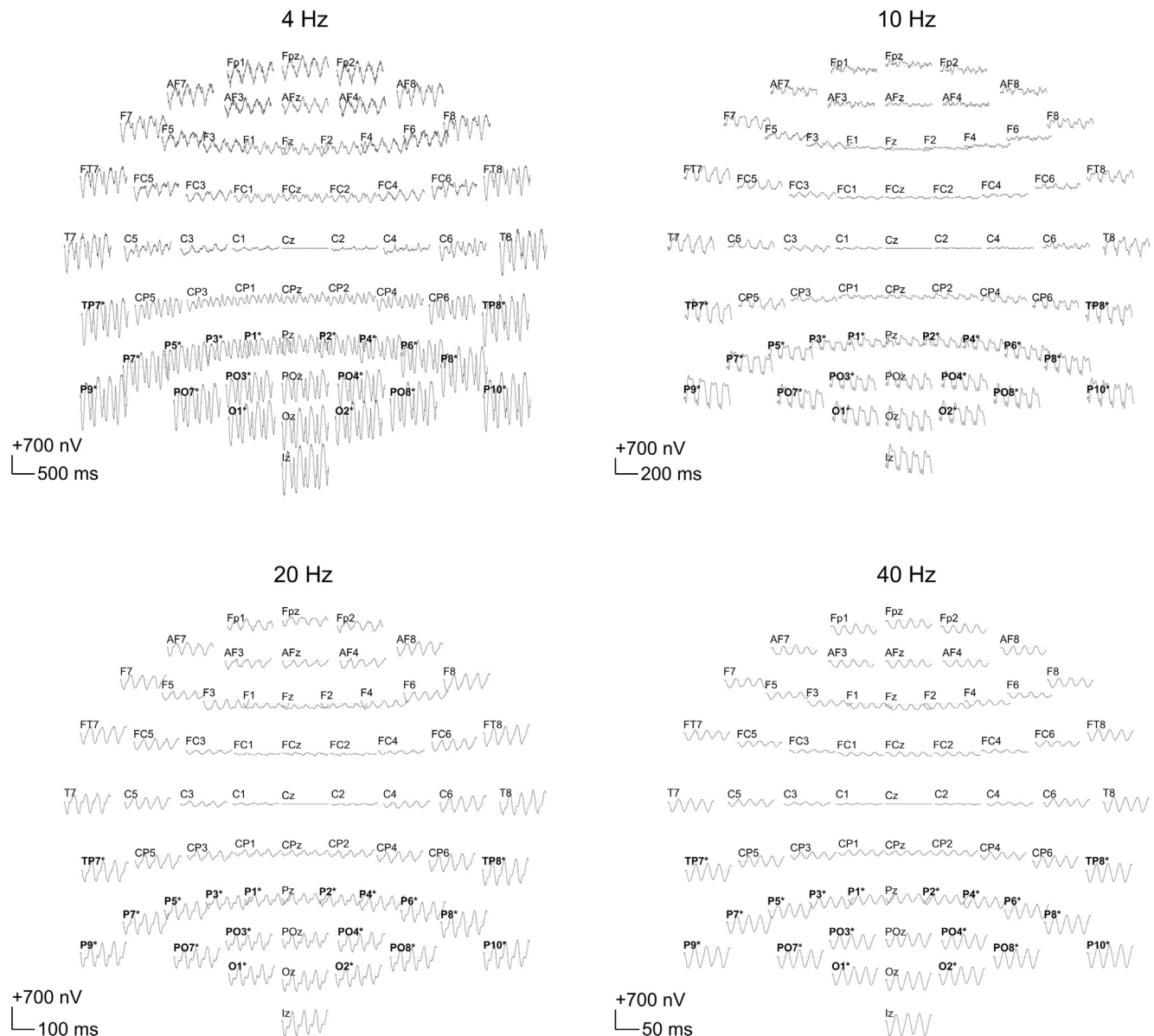


Fig. 2. Topographic maps. Grand mean averaged response waveforms for 4, 10, 20 and 40 Hz ASSRs were constructed using BESA Research 6.0 software by averaging each recording's 256 artefact-free Cz-referenced epochs over all participants ($N = 53$) and stimulation modes (left ear, both ears and right ear). The response waveforms are displayed at the approximate electrode locations viewed from the top of the head with the nose at the top of the figure, and with positivity at the electrode location relative to the reference electrode shown by an upward deflection. The electrodes that were included in further analyses are indicated with an asterisk.

mean SNRs were 9.9 dB, 7.6 dB, 13.8 dB and 20.9 dB for 4, 10, 20 and 40 Hz respectively (Fig. 4).

For 4 Hz SNRs, a trend towards a main effect of reading group ($F_{(1,51)} = 3.08$, $p = 0.085$) was found. Although not significant, dyslexic readers seemed to show higher 4 Hz SNRs than normal readers (mean difference = 1.4 dB, $SE = 0.09$ dB). No interaction effects of reading group with hemisphere or stimulation mode were found (all $p > 0.1$). For 10 Hz SNRs, a significant main effect of reading group ($F_{(1,51)} = 4.89$, $p = 0.032$) was found. Overall, dyslexic readers showed significantly lower 10 Hz SNRs than normal readers (mean difference = 2.4 dB, $SE = 1.1$ dB). No interaction effects of reading group with hemisphere or stimulation mode were found (all $p > 0.1$). For 20 Hz SNRs, no main effect of reading group was found ($F_{(1,51)} = 1.66$, $p = 0.203$), but there was a significant interaction between reading group and stimulation mode ($F_{(1,73)} = 5.03$, $p = 0.017$). Post hoc testing for the effect of reading group revealed higher 20 Hz SNRs in dyslexic readers for left ear (mean

difference = 2.1 dB, $SE = 1.1$ dB, $p = 0.053$) and right ear stimulation (mean difference = 2.3 dB, $SE = 1.1$ dB, $p = 0.043$), but not for stimulation of both ears (mean difference = 0.3 dB, $SE = 1.3$ dB, $p = 0.808$). For 40 Hz SNRs, no main effects of reading group (all $p > 0.1$) or any interaction effects with reading group (all $p > 0.1$) were found.

3.2. Surrounding amplitude

In normal readers, mean surrounding amplitudes were 12.9 dB, 16.0 dB, 23.2 dB and 32.6 dB for 3–5, 9–11, 19–21 and 39–41 Hz respectively. In dyslexic readers, mean surrounding amplitudes were 13.7 dB, 16.8 dB, 23.5 dB and 32.3 dB for 3–5, 9–11, 19–21 and 39–41 Hz respectively (Fig. 5, dashed lines).

For amplitudes between 3 and 5 Hz (surrounding 4 Hz), a significant main effect of reading group ($F_{(1,51)} = 4.47$, $p = 0.039$) was found. Overall, dyslexic readers showed significantly smaller 3–

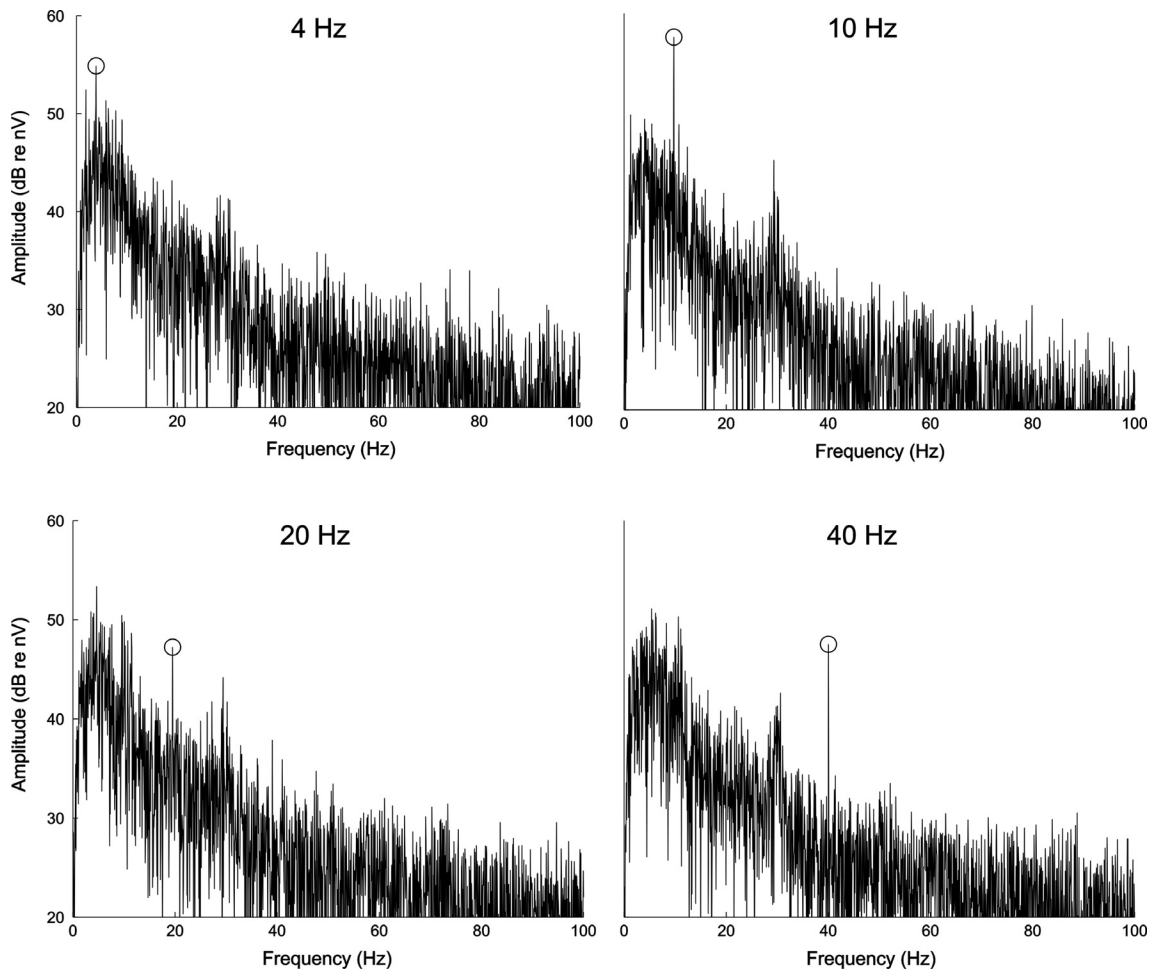


Fig. 3. FFT spectra. Exemplary FFT spectra for 4, 10, 20 and 40 Hz ASSRs in the left hemisphere during right ear stimulation are displayed for a randomly selected normal reading participant. The circle indicates the response amplitude defined as the root of the power of the Fourier component in the frequency bin corresponding to the modulation frequency. The surrounding amplitude was defined as the root of the average power of the Fourier components in an approximately 2 Hz wide frequency band around the modulation frequency (i.e. 60 frequency bins or approximately 1 Hz on each side). Amplitudes were converted to dB using a logarithmic transformation with reference to 1 nV for graphical reasons.

5 Hz amplitudes than normal readers (mean difference = 0.8 dB, SE = 0.4 dB). Although not significant, a trend appeared towards an interaction effect of reading group with hemisphere ($F_{(1,51)} = 3.04$, $p = 0.087$) and stimulation mode ($F_{(2,102)} = 2.74$, $p = 0.069$). Post hoc testing however shows similar group difference in both hemispheres (left hemisphere: mean difference = 0.9 dB, SE = 0.4 dB, $p = 0.027$; right hemisphere: mean difference = 0.7 dB, SE = 0.4 dB, $p = 0.061$) and for unilateral stimulation modes (left ear: mean difference = 0.8 dB, SE = 0.4 dB, $p = 0.058$; right ear: mean difference = 1.0 dB, SE = 0.4 dB, $p = 0.011$), although maybe not as clear for bilateral stimulation (mean difference = 0.6 dB, SE = 0.4 dB, $p = 0.117$). For amplitudes between 9–11 Hz (surrounding 10 Hz), 19–21 Hz (surrounding 20 Hz) and 39–41 Hz (surrounding 40 Hz) no main effects of reading group (all $p > 0.1$) or any interaction effects with reading group (all $p \geq 0.1$) were found.

3.3. Response amplitude

In normal readers, mean response amplitudes were −4.7 dB, −6.4 dB, −10.8 dB and −12.0 dB for 4, 10, 20 and 40 Hz respectively. In dyslexic readers, mean response amplitudes were −3.9 dB, −9.5 dB, −9.8 dB and −11.4 dB for 4, 10, 20 and 40 Hz respectively (Fig. 5, solid lines).

For 10 and 20 Hz response amplitudes, results were the same as for SNRs, showing an overall group difference for 10 Hz ($F_{(1,51)} = 5.20$, $p = 0.027$) and a significant interaction effect between reading group and stimulation mode for 20 Hz ($F_{(1,75)} = 5.99$, $p = 0.008$). For 4 and 40 Hz response amplitudes, no main effects of reading group (all $p > 0.1$) or any interaction effects with reading group (all $p > 0.1$) were found. Hence, the group differences that were found for 4 Hz SNRs are mainly driven by a difference in the underlying non-synchronized neural background activity, while the group differences observed for 10 and 20 Hz SNRs are determined by a difference in the amount of synchronized neural activity.

3.4. Correlations between EEG outcome measures and behavioral measures of reading and phonology

For 4 Hz conditions, no significant correlations were found between 3 and 5 Hz surrounding amplitudes and reading or phonological awareness (all $r_s < |0.28|$, $p > 0.1$). For 10 Hz conditions, significantly positive correlations were found between 10 Hz response amplitudes and phonological awareness in normal readers ($r_s = 0.48$, $p = 0.029$), suggesting that higher synchronization of alpha activity is related to better phonological skills. The latter relation was not found in dyslexic readers ($r_s = -0.05$,

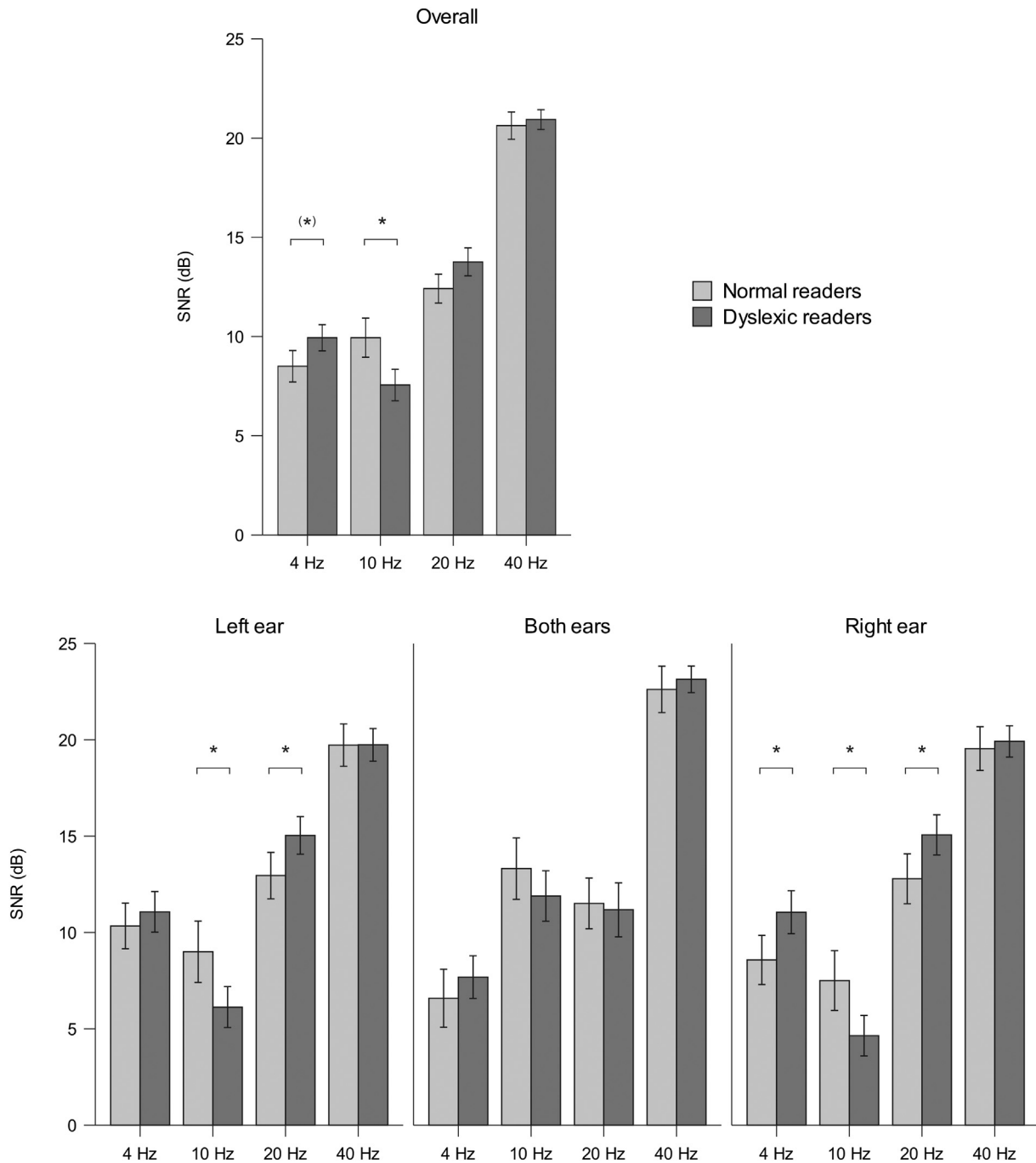


Fig. 4. SNRs. SNRs (dB) for 4, 10, 20 and 40 Hz ASSRs are displayed for normal readers (light grey) and dyslexic readers (dark grey). Top panel: Overall SNRs (dB) averaged over factors hemisphere and stimulation mode. Bottom panels: SNRs (dB) separate for each stimulation mode, averaged over left and right hemisphere. Error bars indicate 95% confidence intervals. Bonferroni corrected two-tailed significances are indicated using (*) for $p \leq 0.1$ and * for $p \leq 0.05$. Note that, for some specific conditions, synchronization of alpha oscillations was not only reduced, but also absent in the dyslexic reading group. Synchronization is considered to be present if the F-ratio statistic shows a significant difference ($p < 0.05$) between P_f and $P_{f \pm 1 \text{ Hz}}$, corresponding to an SNR of 4.8 dB (Dobie & Wilson, 1996; John & Picton, 2000). Whereas normal readers exhibited SNRs that were clearly higher than the significance level of 4.8 dB for all 10 Hz stimulation modes, dyslexic readers were not able to reach this criterion, in particular for unilateral stimulation modes.

$p = 0.779$). For 20 Hz conditions, significantly positive correlations were found between 20 Hz SNRs and phonology in dyslexic readers ($r_s = 0.36$, $p = 0.042$), indicating that higher synchronization of beta activity relates to better phonological skills in dyslexic readers, whereas no such relation was present in normal readers ($r_s = 0.17$, $p = 0.454$). A summary of all correlation coefficients is presented in Table 2, and scatter plots of significant correlations are provided in Fig. 6.

4. Discussion

The objective of this study was to investigate neural synchronization of theta, alpha, beta and low-gamma range oscillations in dyslexia. EEGs were recorded during auditory stimulation with 4, 10, 20 and 40 Hz amplitude modulated speech-weighted noise in a group of normal reading and dyslexic adolescents. These modulation rates were specifically selected from the modulation spec-

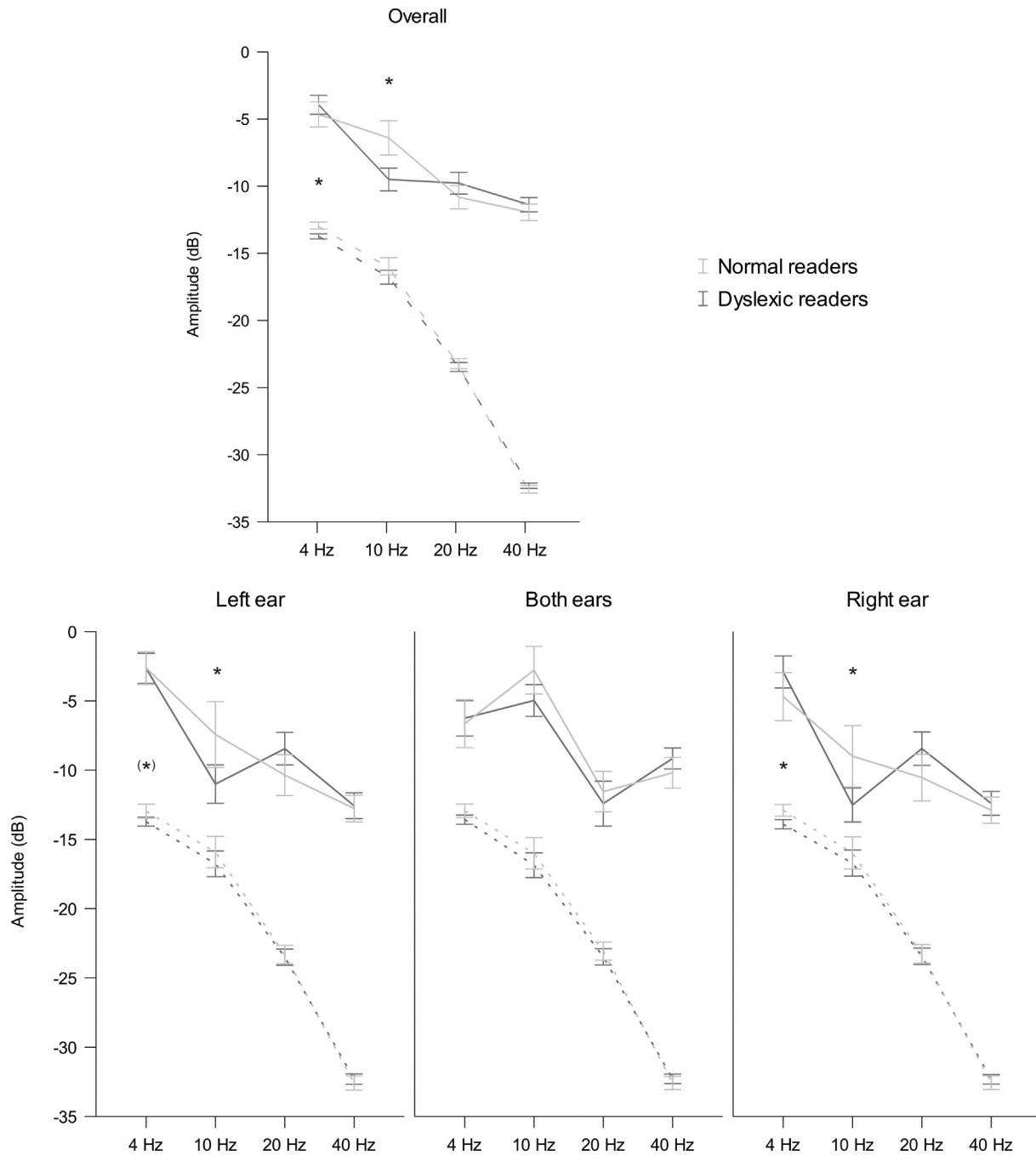


Fig. 5. Surrounding and response amplitudes. Surrounding amplitudes (dB re μ V) between 3–5, 9–11, 19–21 and 39–40 Hz (dashed lines) and response amplitudes (dB re μ V) for 4, 10, 20 and 40 Hz ASSRs (solid lines) are displayed for normal readers (light grey) and dyslexic readers (dark grey). Top panel: Overall amplitudes averaged over factors hemisphere and stimulation mode. Bottom panels: Amplitudes separate for each stimulation mode, averaged over left and right hemisphere. Error bars indicate 95% confidence intervals. Bonferroni corrected two-tailed significances are indicated using (*) for $p \leq 0.1$ and * for $p \leq 0.05$.

Table 2

Spearman rho correlation coefficients between EEG outcome measures and behavioral measures of reading and phonology.

	Reading			Phonological awareness		
	NR	DR	NR vs. DR	NR	DR	NR vs. DR
4 Hz surrounding amplitude	0.27 ($p = 0.230$)	−0.05 ($p = 0.781$)	$p = 0.138$	0.00 ($p = 1.000$)	−0.28 ($p = 0.115$)	$p = 0.169$
10 Hz response amplitude	0.33 ($p = 0.145$)	0.04 ($p = 0.837$)	$p = 0.156$	0.48 ($p = 0.029^*$)	−0.05 ($p = 0.779$)	$p = 0.028$
20 Hz SNR	−0.23 ($p = 0.320$)	0.23 ($p = 0.214$)	$p = 0.059$	−0.17 ($p = 0.454$)	0.36 ($p = 0.042$)	$p = 0.034$

Note. Spearman's rho correlational analyses were two-tailed ($\alpha = 0.05$) and Fisher z analyses were one-tailed ($\alpha = 0.01$). P values that survived FDR correction, which was applied for the execution of two correlational analyses, i.e. within the normal reading group (NR) and within the dyslexic reading group (DR), are indicated with an asterisk.

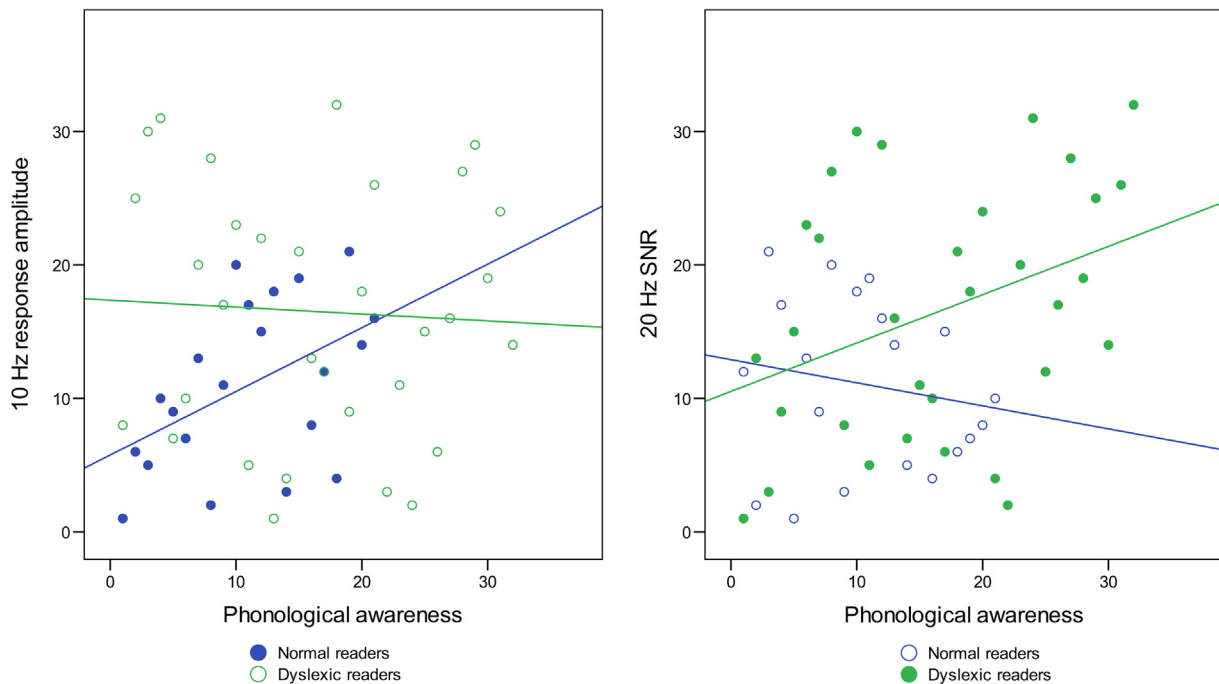


Fig. 6. Spearman rho correlations between EEG outcome measures and behavioral measures. The relation between 10 Hz response amplitudes and phonological awareness (left panel) and 20 Hz SNRs and phonological awareness (right panel) is displayed by means of scatter plots of ranked values for the normal reading and dyslexic reading group. Filled symbols represent a significant within-group correlation.

trum of the speech envelope to measure if and how different bands of neural oscillations in the auditory cortex were able to synchronize their activity to syllabic (4 and 10 Hz) and phonemic (20 and 40 Hz) rate information. To our knowledge, this is the first EEG study to examine auditory synchronization of neural oscillations using such a broad range of speech envelope rates. In particular the inclusion of alpha rate modulations, which have not previously been investigated in dyslexia, makes this study unique.

Our results revealed atypical neural synchronization to both syllabic and phonemic rate information in dyslexic readers. More specifically, deviances were observed in synchronized activity of alpha and beta range oscillations. No evidence for a deficit in theta or low-gamma synchronization was found. However, dyslexic readers did show significantly smaller non-synchronized neural background activity in the theta range. Regarding the relation between auditory neural synchronization and dyslexia, our results hence assign an important role to (1) synchronization of neural activity in the alpha and beta frequency band, and (2) non-synchronized background activity in the theta frequency band.

4.1. Neural synchronization to syllable rate information

4.1.1. Less synchronized activity in the alpha frequency band

Dyslexic readers showed significantly smaller response amplitudes as well as lower SNRs to 10 Hz modulations in comparison to normal readers. Additionally, neural synchronization of alpha oscillations correlated positively with reading and phonological skills in normal readers, while this relation was absent in dyslexic readers. Together, these results provide strong evidence that adolescents with dyslexia show an impairment in the neural synchronization of alpha oscillations during auditory processing.

There are several reasons why an auditory alpha range synchronization deficit could be a crucial mechanism underlying speech and phonological processing problems in dyslexia. If neural oscillations encode temporal information in a rate-dependent manner, alpha oscillations are responsible for encoding information in the

corresponding 8–13 Hz frequency range. As described by Drullman, Festen, and Plomp (1994a, 1994b) and Shannon et al. (1995), the most important modulation frequencies for accurate speech perception are situated between 4 and 16 Hz. In addition, modulation rates around 10 Hz have been associated with (the upper limit of) temporal rates at which syllables occur in speech (Edwards & Chang, 2013; Greenberg et al., 2003). The inability of neural oscillations to follow alpha rate modulations could therefore imply less accurate encoding of important speech related, in this case syllabic, components. In dyslexia, syllabic rate processing deficits have been specifically suggested in the theta range (Goswami, 2011). Yet, we and others have never been able to show a theta rate synchronization deficit in adults with dyslexia (Hämäläinen et al., 2012; Poelmans, Luts, Vandermosten, Boets, et al., 2012) nor in pre-reading children with a hereditary risk for dyslexia (Vanvooren et al., 2014). The absence of group differences in theta range synchronization possibly suggests that encoding of other frequency ranges than the theta range might be more important for accurate syllabic processing. According to our current results, the underlying neural deficit leading to syllabic encoding problems seems to be an alpha, not theta, related impairment. This bottom-up hypothesis is supported by the findings of Shahin and Pitt (2012), who have provided the first evidence for a supporting role of alpha oscillations in speech segmentation.

Besides the possibility that alpha oscillations are related to speech processing through bottom-up neural encoding, a more tentative explanation might be provided by top-down controlled mechanisms. In a recent perspective article, Strauß et al. (2014) assign a crucial role to alpha oscillations during speech processing in challenging listening situations by means of auditory selective inhibition. More specifically, Strauß et al. advocate that the enhancement of alpha activity selectively inhibits the processing of task-irrelevant information, such as noise interference, thereby protecting task-relevant information in the speech signal. A dysfunction in alpha synchronization is suggested to result in a lack of selective inhibition, obstructing the process of auditory selective

attention during speech processing in adverse listening conditions. Since our results demonstrate that participants with dyslexia exhibit a significant impairment in the neural synchronization of alpha oscillations, we are inclined to hypothesize that this inability to enhance alpha activity might be related to the speech-in-noise perception deficits have been established in dyslexia (Boets, Ghesquière, van Wieringen, & Wouters, 2007; Dole, Hoen, & Meunier, 2012; Poelmans et al., 2011; Ziegler, Pech-Georgel, George, & Lorenzi, 2009).

We should note that the link between our experimental design and either bottom-up or top-down speech processing necessarily remains indirect, as we did not implement speech stimuli nor challenging listening conditions. Nevertheless, we are convinced that our results contribute significantly to the ongoing discussion on the relation between neural auditory processing, phonology and reading, and provide the first indications for a crucial role of deviant synchronization of alpha activity in dyslexia. Experimental set-ups specifically designed to measure the role of alpha range ASSRs during speech processing promise to provide highly interesting results that will shed new light on the present findings.

4.1.2. Less non-synchronized background activity in the theta frequency band

No group differences were found between normal reading and dyslexic adolescents in the neural synchronization of theta oscillations, but dyslexic readers did show significantly lower non-synchronized theta range background activity during auditory stimulation. However, non-synchronized theta activity was not related to reading or phonological awareness skills in either normal or dyslexic readers.

In contrast to our results, resting-state EEG studies have shown no differences between normal and dyslexic readers in theta range resting-state activity (Babiloni et al., 2012; Pagnotta et al., 2015; Schiavone et al., 2014) or differences were found in the other direction, with dyslexic readers showing higher theta activity than normal readers (Arns, Peters, Breteler, & Verhoeven, 2007; Marosi et al., 1995). This apparent discrepancy is however not unexpected if we assume that the presence of auditory stimulation influences the behavior of the surrounding theta band. Normal reading adolescents indeed showed significantly increased non-synchronized theta range activity, suggesting that the background activity in the surrounding frequency bins is in some way interacting with the synchronized activity at the modulation frequency. The oscillatory band around the modulation frequency seems to be co-activated, resulting in significantly higher non-synchronized theta range activity in comparison to dyslexic readers. This interpretation corresponds with results of Howard and Poeppel (2012), who also showed similar co-modulation of the theta band in normal reading adults. Yet, the current data do not allow to determine whether the increase in non-synchronized theta activity is as such related to the presence of (temporal information in) the stimulus, hence, further speculation seems unjustifiable. Moreover, the importance of the observed group difference is tempered by the absence of significant correlations between non-synchronized theta activity and reading or phonological awareness skills. To understand the functional relevance of the observed group difference, further research would be needed on the role of non-synchronized background activity in the theta range.

4.2. Neural synchronization to phoneme rate information

4.2.1. More synchronized activity in the beta frequency band

Dyslexic readers showed a trend towards larger response amplitudes as well as significantly higher SNRs to 20 Hz modulations. The latter also correlated positively with phonological skills, specifically in dyslexic readers. Based on these results, it seems

that adolescents with dyslexia do not only show deviant neural synchronization to syllable rate information, but also demonstrate atypical neural synchronization of beta oscillations to phoneme rate information.

While studies examining alpha synchronization during auditory processing are rather scarce, auditory neural synchronization of beta oscillations has been extensively investigated in dyslexia before. In adults with dyslexia, MEG studies generally found no clear beta range deficits in neural synchronization (Hämäläinen et al., 2012; Lehongre et al., 2011). Also in 5-year-old preschoolers, an EEG study by Vanvooren et al. (2014) revealed no group differences in beta synchronization between children with and without a hereditary risk for dyslexia. However, their results did show an immature hemispheric specialization pattern, suggesting that beta range synchronization was still developing in prereaders (see also Vanvooren et al. (2015)). This crucial finding leaves open the possibility that beta range synchronization differences might still emerge in later stages of reading development, reflective of an atypical maturation of beta oscillations. Indeed, in a recent MEG study, Lizarazu et al. (2015) reported group differences in school-aged children (and adults) with dyslexia, which could be related to beta range synchronization. In their study, participants with dyslexia demonstrated significantly enhanced right hemispheric neural synchronization to 30 Hz stimulation in comparison to normal readers. Together with our results, these findings suggest that enhanced beta synchronization emerges in dyslexic readers during reading development, possibly due to the influence of explicit reading instruction and the development of phonemic awareness. Because these atypical patterns arise at a later age, they seem to reflect the consequential effects, rather than the underlying cause for emerging reading problems in dyslexia. Enhanced beta synchronization could therefore be the manifestation of a compensatory mechanism, by which the dyslexic brain attempts to improve phonemic rate processing. This hypothesis is confirmed by a series of ERP studies demonstrating enhanced responses to phonemic rate alterations in speech and non-speech stimuli in school-aged children and adults with dyslexia (Helenius, Salmelin, Richardson, Leinonen, & Lyytinen, 2002; Lohvansuu et al., 2014). Similar to our correlational results, Lohvansuu et al. (2014) found that enhanced ERPs were significantly associated with better phonological, reading and writing skills, confirming the interpretation of compensatory speech perception mechanisms in dyslexia.

4.2.2. Normal activity in the low-gamma frequency band

Regarding low-gamma neural synchronization, our results show no group differences between normal reading and dyslexic adolescents. We included low-gamma modulation rates because the speech envelope supposedly contains modulations up to 50 Hz (Rosen, 1992). Nevertheless, the main energy in the modulation spectrum of the speech envelope is situated between 4 and 16 Hz (Drullman, Festen, & Plomp, 1994a, 1994b; Shannon et al., 1995). The relative contribution of 40 Hz modulations in comparison to lower modulation rates hence seems to be rather limited to exert a significant influence on speech perception. This conjecture is supported by the results of a study by Alaerts et al. (2009), who demonstrated significant correlations between speech perception and 4, 10 and 20 Hz ASSRs, while speech perception did not relate to 40 Hz ASSRs. Yet, other studies have related neural processing of low-gamma modulation rates to speech perception skills in normal readers (Dimitrijevic et al., 2004) and to phonological skills in dyslexic readers (Lehongre et al., 2011). Together with recent evidence on oscillatory cross-frequency coupling mechanisms (Hyafil, Fontolan, Kabdebon, Gutkin, & Giraud, 2015; Wang et al., 2014), a potential role for low-gamma oscillations is thus not to be excluded.

4.3. Overall effects of hemisphere and stimulation mode

The hemispheric lateralization of ASSRs is characterized by a complex interaction between the modulation frequency and the stimulation mode. Although we did not elaborate on the overall effects of hemisphere, our results regarding hemispheric differences are in good agreement with our previous studies (Poelmans, Luts, Vandermosten, Ghesquière, et al., 2012; Vanvooren et al., 2015), as well as reports from others (e.g. Keceli, Okamoto, & Kakigi, 2015; Lamminmäki, Parkkonen, & Hari, 2014; Ross, Herdman, & Pantev, 2005), by showing a lateralization towards the right hemisphere for 4, 20 and 40 Hz responses. Note that the absence of significant interaction effects between reading group and hemisphere indicates that hemispheric effects were not significantly different between normal and dyslexic readers, suggesting that both reading groups show similar lateralization patterns.

While unilateral stimulation modes generated clear group differences, effects during bilateral stimulation were generally less pronounced or absent. Instead, bilateral stimulation exhibited a rather interesting influence on synchronization of neural oscillations in both participant groups. In comparison to unilateral stimulation, we found larger synchronization for 10 and 40 Hz and lower synchronization for 4 and 20 Hz during bilateral stimulation. In a previous study comparing unilateral and bilateral stimulation modes for different stimulation frequencies, Poelmans, Luts, Vandermosten, Ghesquière, et al. (2012) suggested frequency-dependent constructive and destructive interference processes during bilateral stimulation as an explanation for these phenomena. However, as long as the underlying neural effects are not better understood, it remains difficult to speculate about what exactly occurs in the brain during bilateral stimulation, and the reason why this condition behaves somewhat differently than unilateral stimulation.

5. Conclusion

In this study, we investigated neural synchronization of theta, alpha, beta and low-gamma range oscillations in normal and dyslexic readers. In contrast to a recent model suggesting that speech perception and phonological problems in dyslexia are caused by an impairment in the neural synchronization of theta and low-gamma range oscillations, our results in adolescents with dyslexia demonstrate atypical alpha and beta range synchronization. Our most prominent finding, showing that dyslexic readers exhibited significantly reduced neural synchronization of alpha oscillations, is novel in dyslexia research. We advocate that this neural impairment could be related to syllabic rate speech and phonological processing problems in dyslexia through bottom-up neural encoding as well as top-down inhibitory processes associated with selective attention. On the other hand, dyslexic adolescents showed significantly enhanced neural synchronization of beta oscillations, suggesting that over-synchronization of beta range oscillations may be a compensatory mechanism to improve processing of phonemic rate information.

In sum, this study provides evidence for differential impairments in auditory neural synchronization to both syllable and phoneme rate information in dyslexic readers. Since our results assign a key role to the synchronizing behavior of alpha oscillations, we hope that these findings may guide future research on the role of neural alpha synchronization in dyslexia.

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