Atypical beta power fluctuation while listening to an isochronous sequence in dyslexia

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Highlights

- Adults with dyslexia and matched controls listened to isochronous tone sequences.
- Dyslexia was associated with an atypical phase of beta (~20 Hz) power fluctuation.
- Atypical beta power fluctuation might reflect deficits in tracking auditory rhythm.

Abstract

Objective

Developmental dyslexia is a reading disorder that features difficulties in perceiving and tracking rhythmic regularities in auditory streams, such as speech and music. Studies on typical healthy participants have shown that power fluctuations of neural oscillations in beta band (15-25 Hz), which are likely related to predictive timing and attentional processes, reflect an essential mechanism for tracking rhythm or entrainment. Here we investigate whether adults with dyslexia have atypical beta power fluctuation.

Methods

The electroencephalographic activities of individuals with dyslexia (n = 13) and typical control participants (n = 13) were measured while they passively listened to an isochronous tone sequence (2 Hz presentation rate). The time-frequency neural activities generated from auditory cortices were analyzed.

Results

The phase of beta power fluctuation at the 2 Hz stimulus presentation rate differed and appeared opposite between individuals with dyslexia and controls.

Conclusions

Atypical beta power fluctuation might reflect deficits in perceiving and tracking auditory rhythm in dyslexia.

Significance

These findings extend our understanding of atypical neural activities for tracking rhythm in dyslexia and could inspire novel methods to objectively measure the benefits of training, and predict potential benefit of auditory rhythmic rehabilitation programs on an individual basis.

Keywords: Dyslexia, Electroencephalography (EEG), Beta oscillation, Auditory perception, Entrainment.

Abbreviations: electroencephalography (EEG), event-related potential (ERP), independent component analysis (ICA), standard deviation (SD).

Introduction

Developmental dyslexia is a common reading disorder with a prevalence rate of around 5 to 10% (Siegel, 2006), featuring impairments in phonological awareness, such as difficulties in identifying rhyming words or syllabic stress patterns in speech (Goswami et al., 2013). Beyond deficits in speech perception, this impairment is also associated with deficits of auditory processing of rhythmic temporal regularity (Goswami, 2011, 2015, 2019), including detecting amplitude envelope onset, perceiving and producing rhythm, and extracting auditory rhythmic regularity (Flaugnacco et al., 2014; Huss et al., 2011; Leong et al., 2011; Leong and Goswami, 2014). The association between these two domains of auditory processing are also observed among typically-developing children: rhythm perception and the ability to synchronize to a beat are associated with phonological awareness, verbal short-term memory, rapid naming, and morphosyntactic accuracy in speech production (e.g., Woodruff Carr et al., 2014). Despite this evidence, we know little about the neural processing that underlies the rhythmic deficits in dyslexia, the focus of the present paper.

Neural oscillations have been proposed as an essential mechanism for tracking rhythm (Haegens and Zion Golumbic, 2018; Trainor et al., 2018). The power fluctuations of high-frequency oscillations (beta band: 15–25 Hz) entrain to rhythmic regularity in sound streams. When participants listen to an isochronous tone sequence, the beta band power from auditory cortex decreases immediately following the onset of a tone, and then rebounds anticipatorily according to the onset time of the upcoming tone (Cirelli et al., 2014; Fujioka et al., 2012), consistent with a mechanism for predicting the onset time of the next expected tone. This entrainment activity can be modulated by hierarchical rhythmic structure or disrupted by a random sequence (Fujioka et al., 2009; 2015; Iversen et al., 2009; Snyder and Large, 2005), and it is associated with auditory prediction, attentional processing and perceptual performance (Chang et al., 2018, 2019; Morillon and Baillet, 2017). Atypical beta power entrainment activities have been observed in populations featuring deficits in rhythm perception and tracking, such as patients with Parkinson’s disease (te Woerd et al., 2017, 2018) and children with stuttering (Etchell et al., 2016). However, it is unknown whether atypical beta power entrainment to auditory rhythmicity is associated with dyslexia.

In the present study, we measured the electroencephalographic (EEG) activities of individuals with dyslexia while they passively listened to an isochronous tone sequence. We hypothesized that the beta power fluctuation generated from auditory cortex is different between individuals with dyslexia and typical controls.

Methods

Participants

Thirteen adults with developmental dyslexia (seven women, ten right-handed; mean age = 23.2 years, SD = 2.95 years) and 13 matched controls (seven women, seven right-handed, mean age = 22.5 years, SD = 2.07) participated in the current experiment. Although handedness was not perfectly matched in the current study, the higher proportion of non-right-handers appears to be a feature of dyslexia (e.g., Eglinton and Annett, 1994). All participants reported French as their native language, with one dyslexic participant reporting bilingualism with English. None reported auditory deficits. Education levels did not differ between the Dyslexic group (mean = 14.92 years; SD = 1.55) and the Control group (mean = 15.31 years, SD = 0.95), p = .45. Musical background, as measured by years of instrumental instruction, also did not differ between the Dyslexic group (mean = 2.00 years; SD = 2.16) and the Control group (mean = 1.69 years, SD = 2.13), p = 0.72.

Participants with dyslexia were part of a larger research project investigating dyslexia at the university level (Abadie and Bedoin, 2016; see Canette et al., 2020, Fiveash et al., 2020, for more information). As detailed in Table S2, they completed a set of language and neuropsychological tests, confirming the persistence of dyslexia for each participant. All participants with dyslexia reported having seen a speech therapist for a dyslexia diagnosis and for training designed to reduce reading difficulties for at least two years (and maximum 5 years) during childhood, which in France is generally defined as between 8 and 13 years old. They mainly have phonological difficulties (i.e., phonological or mixed forms of dyslexia, which are the most frequently observed forms of this neurodevelopmental pathology). Note that all participants with dyslexia had scores in the normal range for nonverbal intelligence (as measured by Raven’s Matrices) and they also performed in the normal range for reading comprehension (average z-score placed them above the mean = 1.91, SD = 0.60). None of the participants reported psychiatric or neurological diagnoses or attention disorder with/without hyperactivity. On the other hand, none of the controls reported a history of spoken or written language disorders. In particular we confirmed that, while at school, they did not have any difficulties in language understanding or production or learning to read, and none had been followed up by a speech therapist.

Written informed consent based on the French ethics procedure approval Committee (CPP Sud-Est II, 2007-009-3) was obtained from all participants prior to participating in the experiment, which was conducted in accordance with the guidelines of the Declaration of

Helsinki. Participants received a compensation of 12 Euros per hour for their participation in the study.

Stimulus

During the EEG recording, participants passively listened for 5 minutes to an isochronous sequence of piano tones with an inter-onset interval of 500 ms, which is in the tempo range that gives rise to a strong sense of the beat (Drake et al., 2000; Merchant et al., 2015). The tone was C4 (262 Hz), from the University of Iowa Musical Instrument Samples, and the amplitude envelope of the piano tone was percussive with 10 ms rise times. Tones were truncated to be 200 ms in duration, and a linear decay to zero was applied over the entire excerpt to remove offset artifact (Figure S3). For the behavioural post-test synchronization task, the same tone was played with the same inter-onset interval for either 10 repetitions (training trial) or 40 repetitions (experimental trials).

Procedure

To keep participants awake and still, they watched a silent black and white movie with Charlie Chaplin while they listened passively to the 5-minute isochronous tone sequence (and two other rhythmic patterns, not presented here) while EEG was continuously recorded[1]. This EEG recording was part of a longer experimental session and followed a priming experiment with an active task (reported in Canette et al., 2020 and Fiveash et al., 2020). After the EEG recording session, participants came back to the laboratory for a second testing session and

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[1] It is a common approach to have participants watch a silent movie during a passive listening task to keep them awake and reduce eyeblinks or eye movements during EEG/MEG recordings. As the movie is not time-locked to the tone sequence and is not rhythmic, its influence on EEG analyses is negligible (e.g., Kong et al., 2014; Luo and Ding, 2020).

completed a set of behavioural tests on syntax processing and rhythm perception and production based on the complex Beat Alignment Task (Einarson and Trainor, 2015; data presented in Canette et al., 2020) and two rhythmic patterns (except for one dyslexic participant who did not come back to this second session); these data were presented in Canette et al. (2020). In addition, relevant for the present experiment, participants performed a production task where they were required to tap along to the excerpts of the isochronous sequence used in the EEG session (i.e., inter-tone-onsets of 500 ms). Participants drummed with a stick on a drum pad (Roland, V-Drums) to each tone. Both the passive listening and production parts were implemented with the software Presentation (Neurobehavioural Systems), and stimuli were presented over headphones (Pioneer, HDJ-500). During a training trial, they tapped to a sequence of 10 tones. Following this, they completed two trials of 40 tones (i.e., 20 s duration) each.

EEG recording and preprocessing

The EEG signal was recorded with 95 Ag/AgCl active electrodes (actiCAP 96Ch Standard-2, Brain Products GmbH). The signal was recorded with a BrainAmp amplifier at a resolution of 16 bits, a sampling rate of 500 Hz, and with an analog low pass filter of 1000 Hz and high pass filter of 0.016 Hz. The ground electrode was placed at position AFz, the reference electrode on the tip of the nose, and an eye-movement monitoring electrode under the right eye at position Iz. Electrode impedances were kept below 20 kΩ, which is a well acceptable impedance levels for EEG recordings (e.g., Ferree et al., 2001; Luck, 2014). Continuous EEG data were transformed to an average reference offline. The EEG data was further processed in MATLAB with the FieldTrip toolbox (RRID: SCR_004849) (Oostenveld et al., 2011).

Independent component analysis (ICA) was used to remove artifact signals (Jung et al., 2000). To speed up the ICA performance, the continuous recordings were downsampled to 250 Hz, filtered between 0.7 and 83 Hz and then segmented into time window from -3 to 303 s time-locked to the first tone of the sequence. This window covered the entire stimulus sequence length. We went back to the unfiltered data, projected it to ICA space and the ICs reflecting artifact (identified by visual inspection, range of 2-13 ICs), including eye blinking, eye movement, electrocardiogram, and powerline noise, were excluded, and then the data in the ICA space was projected back to 95-channel space for all subsequent analyses.[2]

Modeling dipole sources for auditory cortex

In the present study, we focused on the responses generated from auditory cortex, as prior studies have shown that auditory beta oscillations are related to temporal prediction and rhythmic tracking (Chang et al., 2018, 2019; Cirelli et al., 2014; Fujioka et al., 2012, 2015). To achieve this goal, we used a dipole model as a spatial filter to largely separate the activities of auditory cortex from other sources, following the studies cited above, which is preferred to analyzing data on selected surface electrodes, as each surface electrode reflects a mixture of activities from many brain sources. The P1 ERP component (~60-90 ms) was used to localize bilateral auditory cortices, with the dipole locations (but not orientation) constrained to be bilaterally symmetric.

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[2] Although the electromagnetic field of the headphones was not masked, which might lead to some contamination of EEG recordings from sound waveforms, any potential headphone artifact should have had a negligible influence on our beta band findings because: (1) the observed beta power fluctuation shape was similar to those of previous studies (see *Power spectrum of beta power time series*); (2) we observed group differences (while a potential artefact would have equally affected recordings of each participant); and (3) this potential artifact was most likely attenuated by the ICA procedure. A potential artifact might have had more influence on early ERP analyses (reported in the *Supplementary Materials*), which showed somewhat atypical scalp topography in comparison with previous studies.

We used the multiple source probe scan algorithm and the four-shell ellipsoid model included in the Brain Electrical Source Analysis (BESA, RRID: SCR_009530) software package. We chose P1 because (1) it is primarily generated from primary auditory cortex (Godey et al., 2001), (2) it is the dominant peak at fast presentation rates while the N1 peak is strongly reduced at fast rates relevant to the current study (Näätänen and Picton, 1987), and (3) previous studies with similar experimental designs also used P1 for localizing auditory cortex (e.g., Fujioka et al., 2012). The mean locations (averaged across participants) of the fitted dipoles were [±44.23, -1.95, 7.26] (Talairach coordinates) with approximate mean orientations [0.2, 0.5, 0.8] (left) and [-0.2, 0.6, 0.8] (right). These locations are close to bilateral primary auditory cortices with orientations toward the mid-frontal surface area, consistent with typical auditory evoked potentials. The mean residual variances of the source fittings were 7.9% (range 3.4 to 16.3%) for the Control group and 7.0% (range 2.4 to 15.4%) for the Dyslexia group, and the residual variances were not different between groups (t(24) = 0.67, p = 0.509). Finally, the unfiltered continuous 95-channel EEG was projected into source-space EEG via the dipole model for further time-frequency analyses.

Note that it is important that we perform the analyses at dipole locations, as the MEG study of Fujioka et al. (2012) reported that the beta power generated in motor regions fluctuated at the opposite phase of the beta power in auditory cortex. As the spatial resolution of EEG is less precise than MEG, these two signals are likely to be mixed and potentially cancel each other in EEG analyzed from the surface channels.

Time-frequency analyses

The unfiltered continuous source-space EEG data was segmented to include non-overlapping epochs of 20 tones each. Each epoch was thus 11 s long, including 0.5 s prior to the first tone and 0.5 s following the twentieth tone as buffer periods to avoid edge artifacts for the time-frequency analysis. The first epoch at the beginning of each recording was excluded from further analysis, as the rhythmic temporal regularity might not yet be perceived. Subsequently, epochs were excluded that were greater than 150 μV to ensure artifacts were eliminated that were not removed by ICA. The mean number of usable trials was 23.8 in the Control group and 26.7 in Dyslexia group; this was not significantly different between groups ($t(24) = 1.20$, $p = 0.244$).

We focused on the induced (non-phase-locked) power in beta band, following our previous studies (e.g., Fujioka et al., 2012; Chang et al., 2016a, 2018, 2019; Cirelli et al., 2014). For each participant, the unfiltered mean ERP waveform (averaged across trials) was subtracted from each epoch to obtain induced waveforms (Fujioka et al., 2012; Cohen, 2014). We used a short-time Fourier transformation with overlapped time windows (moving successively by one sample) to perform the time-frequency transformation for 15-25 Hz (frequency bin size = 1 Hz). The window size was fixed at 500 ms and a Hanning taper was applied. For each frequency bin, the power was baseline corrected (percentage change) to the mean power for the 0-10 s window, then the beta power was obtained by averaging the power across 15-25 Hz bins. To further analyze the fluctuation of the beta power time series, we performed another Fourier transformation with a Hanning taper for the beta power time series for each 10 s epoch (single-trial), excluding the 0.5 s buffer periods at both ends.

Although some studies have defined the range of beta band to be as wide as 13-30 Hz, we defined it as 15-25 Hz for several reasons. (1) It is consistent with our previous studies (e.g., Fujioka et al., 2012; Chang et al., 2019). (2) Some other studies have interpreted activities below 15 Hz as alpha band (e.g., Ahveninen et al., 2017) and above 25 Hz as low-gamma band (e.g., Giroud et al., 2020). Therefore, it is debatable whether to include these frequencies as beta band. (3) Considering the imprecision of time-frequency analysis in terms of frequency resolution, activities closer to 13 or 30 Hz will be more likely contaminated by activities below 13 or above 30 Hz, respectively, compared to frequencies between 15 and 25 Hz.

For completeness, we also analyzed event-related potentials (ERPs) (see *Supplementary Materials*).

Tapping production task

We used circular statistics (Berens, 2009; Dalla Bella and Sowinski, 2015) to analyze the production performance of the synchronization task for isochronous sequences, leading to two measures related to the resulting vector R: its *angle*, representing synchronization accuracy and its *length*, representing synchronization consistency (ranging from 0 to 1, with 1 representing perfect consistency).

Statistics

We used a nonparametric cluster-based permutation test to analyze the EEG measure difference between groups with the FieldTrip toolbox (Oostenveld et al., 2011). In short, this procedure reduces the number of multiple comparisons by testing the statistical difference at the level of time and/or frequency clusters instead of individual time and/or frequency points, and it has been widely used for analyzing EEG and MEG data (see Maris and Oostenveld, 2007 for more details). Specifically, first we performed a two-sample t-test between the two groups

(Dyslexia, Control) for each time or frequency sample as the initial scan for clustering. Second, we grouped adjacent frequency (Figure 1B) or time (Figure S1A and S1C) samples reaching a threshold of $p < 0.05$ in the initial scan into single clusters and summed the t-values of all samples within each cluster as a cluster-level statistic. Third, we built a null distribution with 1000 random iterations. In each iteration, we pooled all 26 participants (13 in Dyslexia group and 13 in Control group), randomly split participants into 2 equal-size groups, and performed the same calculations as in the first two steps. The null distribution was composed by the summed t-values of the largest suprathreshold cluster of each iteration, and the final p-value was obtained by comparing the observed clustered summed t-value relative to the null distribution. In sum, if there was no group difference, the cluster(s) of the observed data should resemble the random-split data of the null distribution. The final p-value was corrected to two-tailed.

The circular statistics were computed in the Circular Statistics Toolbox for MATLAB (Berens, 2009). Participant group differences for *R angle* and *length* were assessed with two-tailed independent tests.

Note that the Watson-Williams test assumes the data to be distributed according to a von Mises distribution, i.e., with concentration parameter (κ) equal or above 1. Therefore, we examined whether our 2 Hz beta power fluctuation time series met this assumption. The κ parameter was similar between compared datasets (difference range: 0.05-0.14), with only κ parameters of the left and right auditory cortex of the Control group above 1. Although our data did not fully satisfy the assumptions, the Watson-Williams test is considered robust against deviations from these assumptions (Berens, 2009).

Results

Power spectrum of beta power time series

The beta power time series of left and right auditory cortex are visualized in Figure 1A. The Control group showed typical beta power fluctuations in that the peaks occurred at the approximate times of tone onsets (with anticipatory increase in power prior to tone onsets) and troughs between tones. This pattern is similar to those observed in previous studies (e.g., Chang et al., 2019; Fujioka et al., 2012, 2015). In contrast, the beta power fluctuations appear atypical in the Dyslexia group in that troughs occurred at the approximate times of tone onsets and peaks occurred between tones.

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Figure 1

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To examine the frequency characteristics of the beta power fluctuations, we frequency-transformed the beta power time series into a power spectrum for each participant. The spectra of beta power fluctuations (note that this is not the spectra of raw EEG waveform) are shown in Figure 1B. The cluster-based permutation tests on left or right auditory cortex did not show any significant differences in the power spectrum of beta power fluctuations between the Dyslexia and Control groups (range of power fluctuations 1-5 Hz). There was also no interaction between left/right auditory cortex and groups.

The frequency spectrum of beta power fluctuation (Figure 1B) did not show an obvious peak at 2 Hz as expected, despite the appearance of a power fluctuation around the 2 Hz tone onset rate in the averaged time domain waveforms (Figure 1A). Nevertheless, we speculated that the beta power fluctuations likely differed in phase between the two groups, and we extracted the phase of the beta power time series at 2 Hz (the stimulus presentation rate) from the frequency transformation above (Figure 1C) for subsequent exploratory analyses. Note that the phase of beta power time series refers to the peak/trough position of the fluctuations in the measured beta power relative to the onsets of the stimuli. A Watson-Williams two-sample test showed that the phase of the beta power time series differed significantly at right auditory cortex (F(1,24) = 12.90, p = .002), but not at left auditory cortex, although there was a trend for a difference (F(1,24) = 3.51, p = .073). The interaction between groups and left/right auditory cortex (taking the circular difference between hemispheres within each participant, and then performing a between-subject Watson-Williams test) was not significant (F(1,24) = 1.57, p = .222).

To investigate whether this significant right auditory cortex phase difference of beta power fluctuation between groups was specific to 2 Hz, we further performed the same analyses at 1 and 3 Hz in the right auditory cortex. At 3 Hz, there was no significant difference between groups, F(1,24) = 0.88, p = .356. Further, the group difference was larger at 2 Hz than at 3 Hz (taking the circular difference between frequencies within each participant, and then performing a between-subject Watson-Williams test), F(1,24) = 9.47, p = .005. Thus, the phase differences between groups were markedly larger at 2 Hz than at 3 Hz. At 1 Hz, the group difference was not significant, but there was a trend, F(1,24) = 3.33, p = .081. There was also a trend for larger group difference at 2 Hz than at 1 Hz, F(1,24) = 3.37, p = .079. Together these results suggest that the phase difference of beta band power fluctuation is likely specific to 2 Hz, the rate of tone presentation in the stimulus.

Tapping production task.

The two participant groups differed in neither synchronization consistency (vector length; t(23) = - 0.10, p =.93) nor synchronization accuracy (vector angle; Watson-Williams two-sample test: F(1,23) = 0.00, p =.99). Both control and dyslexic participants performed well on the tapping task, reaching synchronization consistency (vector length) close to one (controls: .95 ±.05; dyslexics: .95 ±.04) and synchronization accuracy (vector angle) suggesting weak anticipation of the next tone (controls: -11 ms ± 13; dyslexics: -15 ms ± 39).

Discussion

The results of the current study revealed that the phase of beta power fluctuation was different between adult university students with dyslexia and typical controls while listening to an isochronous tone sequence. To the best of our knowledge, this is the first study reporting atypical beta power entrainment in dyslexia.

The atypical beta power fluctuation in dyslexia might reflect deficits in tracking and/or perceiving auditory rhythms. Previous studies on typical healthy participants showed that the fluctuation of beta power reflects entrainment to the rhythmic regularity of an auditory sequence. Specifically, the peaks of the beta power align to the onset of the tones, and are associated with rhythm tracking and auditory perception and prediction (Chang et al., 2018, 2019; Cirelli et al., 2014; Fujioka et al., 2009, 2012, 2015; Snyder and Large, 2005; Iversen et al., 2009). Our neural findings are consistent with previous studies showing that individuals with dyslexia have deficits in perceiving the rhythmic modulation of nonverbal auditory streams and speech (Goswami et al., 2002; Goswami, 2011, 2015, 2019; Megnin-Viggars and Goswami, 2013). Nevertheless, it is important to note that we cannot eliminate all explanations based on factors beyond entrainment, such as, for example, that the participants in the Dyslexic group were more distracted by the visual movie, leading to less attention to the auditory stimuli.

It was unexpected that the frequency spectrum of beta power fluctuation (Figure 1B) did not show an obvious peak the at stimulus presentation rate (2 Hz). To the best of our knowledge, our study is the first one reporting the spectrum of beta power fluctuation, while most previous studies only reported its time-domain features. The lack of an obvious spectral peak could simply be due to a smaller signal-to-noise ratio in the current study, as the number of trials was smaller and the EEG recording time was shorter than in previous studies (e.g., Fujioka et al., 2012). It is also possible that the power fluctuation was not perfectly periodic; the moment-to-moment fluctuation rate might have drifted around 2 Hz on individual trials, and thus the 2 Hz peak was not obvious in the averaged spectrum with traditional Fourier-based time-frequency transformation approaches, which assume the signals to be stable over time. Future studies using more advanced cycle-by-cycle analysis approaches (e.g., Cole and Voytek, 2019) are needed to investigate the dynamic beta oscillatory activities.

There are a few studies reporting an association between beta oscillations and dyslexia. A previous study reported that auditory steady-state response synchronization is reduced in the beta frequency range in dyslexia, and that this response is associated with literacy skills (Van Hirtum et al., 2019). Differences in overall beta power at occipital channels between individuals with and without dyslexia have also been found during listening to noise-vocoded speech (Power et al., 2016). An atypical hemispheric asymmetry of beta power in response to linguistic tasks has also been associated with reading skill or processing phonological information in dyslexia (e.g., Penolazzi et al., 2010; Spironelli et al., 2008). The present study extends these studies by indicating that the beta oscillatory activity in response to a simple, rhythmic (isochronous) sound sequence is also atypical in dyslexia.

Atypical beta power fluctuation has also been observed in other disorders featuring deficits in perceiving or tracking auditory rhythm. For example, Parkinson's patients are known to have deficits in tracking auditory rhythms (Grahn and Brett, 2009; Grahn, 2012), and the phase of their beta power fluctuation while perceiving auditory or visual rhythms was opposite to that of the controls (te Woerd et al., 2017, 2018). Also, children with stuttering have deficits in perceiving auditory rhythm (Chang et al., 2016b; Falk et al., 2015; Wieland et al., 2015), and the phase of their beta power fluctuation was also opposite to that of controls (Etchell et al., 2016).

Although previous studies investigating children with dyslexia showed deficits in their ability to tap to a beat or perceive a beat (Muneaux et al., 2004, Thomson and Goswami, 2008), in the present study, performance on a simple metronome tapping task did not differ between adults with dyslexia and typical controls, and we failed to find any associations between atypical beta power fluctuation and tapping production performance to the same isochronous sequence (Figure S2). In addition to the relatively small sample size and thus potentially insufficient statistical power, it is possible that (1) our task was too easy and thus not sensitive enough to reflect a deficit in rhythm processing in dyslexia. Indeed, in another study, our participants with dyslexia were worse than controls (Canette et al., 2020) on performing more complex tapping task (e.g., tapping to the beat of musical excerpts). Furthermore, (2) individuals with dyslexia might find other ways and use different neural mechanisms to compensate as they get older (cf. Shaywitz et al., 2003; Law et al., 2015), making it challenging to directly associate beta oscillation with rhythmic abilities. In particular, previous behavioral studies have revealed greater deficits in tapping tasks for dyslexic adolescents than for dyslexic university students, who performed as well as controls on some of the measures (Wolff et al., 1990; see also Thomson et al., 2006). Furthermore, the observed variability of the dependent measures of the participants with dyslexia in our study suggests that individuals might use different neural mechanisms.

In additional analyses examining ERPs (presented in the *Supplementary Materials*), another common approach to examining auditory neural signature of dyslexia, we found a group difference in an early ERP component at the P1 latency at Fpz, and a marginal correlation between this component and the phase of beta power fluctuation (Figure S1). A possible post hoc explanation is that the atypical beta power fluctuation in dyslexia is associated with deficits in early auditory processing, such as encoding rise time and duration (Bamiou et al., 2001; Hämäläinen et al., 2013; Sharma et al., 2009; King et al., 2003). However, our study was not designed to examine this possibility, so future studies are needed with a larger sample size to investigate this possibility.

The current study did not investigate delta (1-3 Hz) oscillations or their cross-frequency coupling with beta oscillations, despite previously reported associations between delta oscillations and dyslexia. Both animal electrophysiology and human neuroimaging studies have shown that the delta oscillation phase time-locks and entrains to external rhythmic sensory input (see Haegens and Zion Golumbic, 2018 for a review) and it has been reported that atypical delta phase entrainment is associated with deficits of rhythm perception and tracking among individuals with dyslexia (Colling et al., 2017; Di Liberto et al., 2018; Molinaro et al., 2016; Power et al., 2013, 2016). However, recent studies have shown that it is challenging to reliably quantify delta phase entrainment because the frequency-domain signature of ERP activity typically overlaps with low-frequency oscillations in Fourier-based analysis (Doelling et al., 2019; Haegens and Zion Golumbic, 2018). For this reason, we have left the question of how delta and beta oscillations are related in dyslexia to future studies with materials and designs more appropriate for addressing this question. Note that the induced beta oscillations measured in the current study are unlikely to be confounded with ERPs because (1) the mean spectrum of the ERP showed that the power above 15 Hz was neglectable (Figure S4), and (2) we removed the phase-locked evoked activity from the induced activity in the beta band prior to conducting our analyses.

Understanding atypical beta power entrainment could potentially benefit individuals with dyslexia. Studies have shown that rhythmic auditory or musical training can improve the phonological awareness and reading skills in children with dyslexia, including randomized control trials (e.g., Cogo-Moreira et al., 2013; Flaugnacco et al., 2015; Habib et al., 2016; Thomson et al., 2013). The efficacy of longer-term musical rhythm training in language remediation is likely related to the importance of rhythm for decoding the speech stream (Flaugnacco et al., 2015; Kotz and Schwartze, 2010; Overy, 2000; Schön and Tillmann, 2015). In typically-developing children and in children with language disorders, presenting a rhythmic prime has been shown to immediately improve syntactic processing over the short term (Bedoin et al., 2016; Chern et al., 2018; Przybylski et al., 2013). Future studies are needed to investigate whether beta power entrainment is an underlying neural mechanism of these effects, and whether individual differences in beta power entrainment could predict the potential benefit of auditory rhythmic habilitation programs.

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Conflict of Interest Statement

None.

References

Abadie, R., & Bedoin, N. (2016). Les étudiants dyslexiques à l'Université: Quels déficits cognitifs et langagiers? Neurologies, 19, 298-303.

Ahveninen, J., Seidman, L. J., Chang, W. T., Hämäläinen, M., & Huang, S. (2017). Suppression of irrelevant sounds during auditory working memory. NeuroImage, 161, 1-8.

Bamiou, D. E., Musiek, F. E., & Luxon, L. M. (2001). Aetiology and clinical presentations of auditory processing disorders—a review. Arch Dis Child, 85, 361-365.

Bedoin, N., Brisseau, L., Molinier, P., Roch, D., & Tillmann, B. (2016). Temporally regular musical primes facilitate subsequent syntax processing in children with specific language impairment. Front Neurosci, 10, 245.

Berens, P. (2009). CircStat: A MATLAB toolbox for circular statistics. J Stat Softw, 31, 1-21.

Canette, L.-H., Fiveash, A., Krzonowski, J., Corneyllie, A., Lalitte, P., Thompson, D., Trainor, L., Bedoin, N., & Tillmann, B. (2020). Regular rhythmic primes boost P600 in grammatical error processing in dyslexic adults and matched controls. Neuropsychologia, 138, 107324.

Chang, A., Bosnyak, D. J., & Trainor, L. J. (2016a). Unpredicted pitch modulates beta oscillatory power during rhythmic entrainment to a tone sequence. Front Psychol, 7, 327.

Chang, A., Bosnyak, D. J., & Trainor, L. J. (2018). Beta oscillatory power modulation reflects the predictability of pitch change. Cortex, 106, 248-260

Chang, A., Bosnyak, D. J., & Trainor, L. J. (2019). Rhythmicity facilitates pitch discrimination: Differential roles of low and high frequency neural oscillations. NeuroImage, 198, 31-43.

Chang, S. E., Chow, H. M., Wieland, E. A., & McAuley, J. D. (2016b). Relation between functional connectivity and rhythm discrimination in children who do and do not stutter. Neuroimage Clin, 12, 442-450.

Chern, A., Tillmann, B., Vaughan, C., & Gordon, R. L. (2018). New evidence of a rhythmic priming effect that enhances grammaticality judgments in children. J Exp Child Psychol, 173, 371-379.

Cirelli, L. K., Bosnyak, D., Manning, F. C., Spinelli, C., Marie, C., Fujioka, T., et al. (2014). Beat-induced fluctuations in auditory cortical beta-band activity: using EEG to measure age-related changes. Front Psychol, 5, 742.

Cogo-Moreira, H., de Avila, C. R. B., Ploubidis, G. B., & de Jesus Mari, J. (2013). Effectiveness of music education for the improvement of reading skills and academic achievement in young poor readers: a pragmatic cluster-randomized, controlled clinical trial. PLoS One, 8(3).

Cohen, M. X. (2014). Analyzing neural time series data: theory and practice. MIT press.

Cole, S., & Voytek, B. (2019). Cycle-by-cycle analysis of neural oscillations. J Neurophysiol, 122, 849-861.

Colling, L. J., Noble, H. L., & Goswami, U. (2017). Neural entrainment and sensorimotor synchronization to the beat in children with developmental dyslexia: An EEG study. Front Neurosci, 11, 360.

Dalla Bella, S., & Sowiński, J. (2015). Uncovering beat deafness: detecting rhythm disorders with synchronized finger tapping and perceptual timing tasks. J Vis Exp, (97), e51761.

Di Liberto, G. M., Peter, V., Kalashnikova, M., Goswami, U., Burnham, D., & Lalor, E. C. (2018). Atypical cortical entrainment to speech in the right hemisphere underpins phonemic deficits in dyslexia. NeuroImage, 175, 70-79.

Doelling, K. B., Assaneo, M. F., Bevilacqua, D., Pesaran, B., & Poeppel, D. (2019). An oscillator model better predicts cortical entrainment to music. Proc Natl Acad Sci U S A, 116(20), 10113-10121.

Drake, C., Jones, M. R., & Baruch, C. (2000). The development of rhythmic attending in auditory sequences: attunement, referent period, focal attending. Cognition, 77(3), 251-288.

Eglinton, E., & Annett, M. (1994). Handedness and dyslexia: A meta-analysis. Percept Mot Skills, 79, 1611-1616.

Etchell, A. C., Ryan, M., Martin, E., Johnson, B. W., & Sowman, P. F. (2016). Abnormal time course of low beta modulation in non-fluent preschool children: a magnetoencephalographic study of rhythm tracking. NeuroImage, 125, 953-963.

Falk, S., Müller, T., & Dalla Bella, S. (2015). Non-verbal sensorimotor timing deficits in children and adolescents who stutter. Front Psychol, 6, 847.

Ferree, T. C., Luu, P., Russell, G. S., & Tucker, D. M. (2001). Scalp electrode impedance, infection risk, and EEG data quality. Clin Neurophysiol, 112, 536-544.

Fiveash, A., Schön, D., Canette, L.-H., Morillon, B., Bedoin, N., & Tillmann, B. (2020). A stimulus-brain coupling analysis of regular and irregular rhythms in adults with dyslexia and controls. Brain Cogn, 140. doi: 10.1016/j.bandc.2020.105531

Flaugnacco, E., Lopez, L., Terribili, C., Montico, M., Zoia, S., & Schön, D. (2015). Music training increases phonological awareness and reading skills in developmental dyslexia: A randomized control trial. PLoS One, 10(9), e0138715.

Flaugnacco, E., Lopez, L., Terribili, C., Zoia, S., Buda, S., Tilli, S., Monasta, L, Montico, M., Sila, A., Ronfani, L., & Schön, D. (2014). Rhythm perception and production predict reading abilities in developmental dyslexia. Front Human Neurosci, 8, 392.

Fujioka, T., Ross, B., & Trainor, L. J. (2015). Beta-band oscillations represent auditory beat and its metrical hierarchy in perception and imagery. J Neurosci, 35(45), 15187-15198.

Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. J Neurosci, 32(5), 1791-1802.

Fujioka, T., Trainor, L., Large, E., & Ross, B. (2009). Beta and gamma rhythms in human auditory cortex during musical beat processing. Ann NY Acad Sci, 1169, 89-92.

Giroud, J., Trébuchon, A., Schön, D., Marquis, P., Liegeois-Chauvel, C., Poeppel, D., & Morillon, B. (2020). Asymmetric sampling in human auditory cortex reveals spectral processing hierarchy. PLoS Biol, 18(3), e3000207.

Goswami, U. (2011). A temporal sampling framework for developmental dyslexia. Trends Cogn Sci, 15, 3-10.

Goswami, U. (2015). Sensory theories of developmental dyslexia: Three challenges for research. Nat Rev Neurosci, 16, 43–54.

Goswami, U. (2019). A neural oscillations perspective on phonological development and phonological processing in developmental dyslexia. Lang Linguist Compass, 13, e12328.

Goswami, U., Mead, N., Fosker, T., Huss, M., Barnes, L., & Leong, V. (2013). Impaired perception of syllable stress in children with dyslexia: A longitudinal study. J Mem Lang, 69, 1-17.

Goswami, U., Thomson, J., Richardson, U., Stainthorp, R., Hughes, D., Rosen, S., & Scott, S. K. (2002). Amplitude envelope onsets and developmental dyslexia: A new hypothesis. P Natl Acad Sci USA, 99(16), 10911–10916.

Goswami, U., Wang, H.-L., Cruz, A., Fosker, T., Mead, N., & Huss, M. (2011). Language-universal sensory deficits in developmental dyslexia: English, Spanish and Chinese. J Cogn Neurosci, 23, 325–337.

Grahn, J. A. (2012). Neural mechanisms of rhythm perception: current findings and future perspectives. Top Cogn Sci, 4, 585-606.

Grahn, J. A., & Brett, M. (2009). Impairment of beat-based rhythm discrimination in Parkinson's disease. Cortex, 45(1), 54-61.

Habib, M., Lardy, C., Desiles, T., Commeiras, C., Chobert, J., & Besson, M. (2016). Music and dyslexia: A new musical training method to improve reading and related disorders. Front Psychol, 7, 26.

Haegens, S., & Zion Golumbic, E. (2018). Rhythmic facilitation of sensory processing: A critical review. Neurosci Biobehav Rev, 86, 150-165.

Hämäläinen, J. A., Salminen, H. K., & Leppänen, P. H. (2013). Basic auditory processing deficits in dyslexia: Systematic review of the behavioral and event-related potential/field evidence. J Learn Disabil, 46, 413-427.

Huss, M., Verney, J. P., Fosker, T., Mead, N., & Goswami, U. (2011). Music, rhythm, rise time perception and developmental dyslexia: Perception of musical meter predicts reading and phonology. Cortex, 47(6), 674

Iversen, J., Repp, B., & Patel, A. (2009). Top-down control of rhythm perception modulates early auditory responses. Ann NY Acad Sci, 1169(1), 58-73.

King, W. M., Lombardino, L. J., Crandell, C. C., & Leonard, C. M. (2003). Comorbid auditory processing disorder in developmental dyslexia. Ear Hearing, 24(5), 448-456.

Kong, Y. Y., Mullangi, A., & Ding, N. (2014). Differential modulation of auditory responses to attended and unattended speech in different listening conditions. Hearing Res, 316, 73-81.

Kotz, S. A., & Schwartze, M. (2010). Cortical speech processing unplugged: A timely subcortico-cortical framework. Trends Cognitive Sci, 14, 392-399.

Law, J. M., Wouters, J. & Ghesquiere, P. (2015). Morphological Awareness and Its Role in Compensation in Adults with Dyslexia. Dyslexia, 21, 254-72.

Leong, V., & Goswami, U. (2014). Impaired extraction of speech rhythm from temporal modulation patterns in speech in developmental dyslexia. Front Human Neurosci, 8, 96.

Leong, V., Hämäläinen, J., Soltész, F., & Goswami, U. (2011). Rise time perception and detection of syllable stress in adults with developmental dyslexia. J Mem Lang, 64(1), 59-73.

Luck, S. J. (2014). An introduction to the event-related potential technique. MIT press.

Luo, C., & Ding, N. (2020). Cortical encoding of acoustic and linguistic rhythms in spoken narratives. eLife, 9, e60433.

Megnin-Viggars, O., & Goswami, U. (2013). Audiovisual perception of noise vocoded speech in dyslexic and nondyslexic adults: The role of low-frequency visual modulations. Brain Lang, 124(2), 165–173.

Merchant, H., Grahn, J., Trainor, L., Rohrmeier, M., & Fitch, W. T. (2015). Finding the beat: a neural perspective across humans and non-human primates. Philos Trans R Soc Lond B Biol Sci, 370, 20140093.

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.

Morillon, B., & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. Proceedings of the National Academy of Sciences, 114(42), E8913-E8921.

Muneaux, M., Ziegler, J. C., Truc, C., Thomson, J., & Goswami, U. (2004). Deficits in beat perception and dyslexia: Evidence from French. NeuroReport, 15, 1255–1259.

Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. Psychophysiology, 24(4), 375-425.

Overy, K. (2000). Dyslexia, temporal processing and music: The potential of music as an early learning aid for dyslexic children. Psychol of Music, 28, 218-229.

Penolazzi, B., Spironelli, C., Vio, C., & Angrilli, A. (2010). Brain plasticity in developmental dyslexia after phonological treatment: A beta EEG band study. Behavl Brain Res, 209, 179-182.

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.

Power, A. J., Mead, N., Barnes, L., & Goswami, U. (2013). Neural entrainment to rhythmic speech in children with developmental dyslexia. Front Human Neurosci, 7, 777.

Przybylski, L., Bedoin, N., Krifi-Papoz, S., Herbillon, V., Roch, D., Léculier, L., Kotz, S. A., & Tillmann, B. (2013). Rhythmic auditory stimulation influences syntactic processing in children with developmental language disorders. Neuropsychology, 27(1), 121-131.

Schön, D., & Tillmann, B. (2015). Short- and long-term rhythmic interventions: Perspectives for language rehabilitation. Ann NY Acad Sci, 1337, 32-39.

Sharma, M., Purdy, S. C., & Kelly, A. S. (2009). Comorbidity of auditory processing, language, and reading disorders. J Speech Lang Hearing Res, 52, 706-722

Shaywitz, S. E., Shaywitz, B. A., Fulbright, R. K., Skudlarski, P., Mencl, W. E., Constable, R. T., Pugh, K. R., Holahan, J. M., Marchione, K. E., Fletcher, J. M. & Lyon, G. R. (2003). Neural systems for compensation and persistence: young adult outcome of childhood reading disability. Biol Psychiat, 54, 25-33.

Siegel, L. S. (2006). Perspectives on dyslexia. Paed Child Health, 11(9), 581-587.

Snyder, J. S., & Large, E. W. (2005). Gamma-band activity reflects the metric structure of rhythmic tone sequences. Cogn Brain Res, 24, 117-126.

Spironelli, C., Penolazzi, B., & Angrilli, A. (2008). Dysfunctional hemispheric asymmetry of theta and beta EEG activity during linguistic tasks in developmental dyslexia. Biol Psychol, 77, 123-131.

Stefanics, G., Fosker, T., Huss, M., Mead, N., Szucs, D., & Goswami, U. (2011). Auditory sensory deficits in developmental dyslexia: a longitudinal ERP study. NeuroImage, 57, 723-732.

te Woerd, E. S., Oostenveld, R., de Lange, F. P., & Praamstra, P. (2017). Impaired auditory-to-motor entrainment in Parkinson's disease. J Neurophysiol, 117, 1853-1864.

te Woerd, E., Oostenveld, R., de Lange, F., and Praamstra, P. (2018). Entrainment for attentional selection in Parkinson's disease. Cortex, 166–178.

Thomson, J. M., & Goswami, U. (2008). Rhythmic processing in children with developmental dyslexia: Auditory and motor rhythms link to reading and spelling. J Physiol-Paris, 102(1-3), 120-129.

Thomson, J. M., Fryer, B., Maltby, J. & Goswami, U. (2006). Auditory and motor rhythm awareness in adults with dyslexia. J Res Read, 29, 334–348.

Thomson, J. M., Leong, V., & Goswami, U. (2013) Auditory processing interventions and developmental dyslexia: A comparison of phonemic and rhythmic approaches. Read Writ, 26,139-161.

Trainor, L.J., Chang, A., Cairney, J., Li, Y.C. (2018). Is auditory perceptual timing a core deficit of developmental coordination disorder? Ann NY Acad Sci, 1423, 30-39

Van Hirtum, T., Ghesquière, P., & Wouters, J. (2019). Atypical neural processing of rise time by adults with dyslexia. Cortex, 113, 128-140.

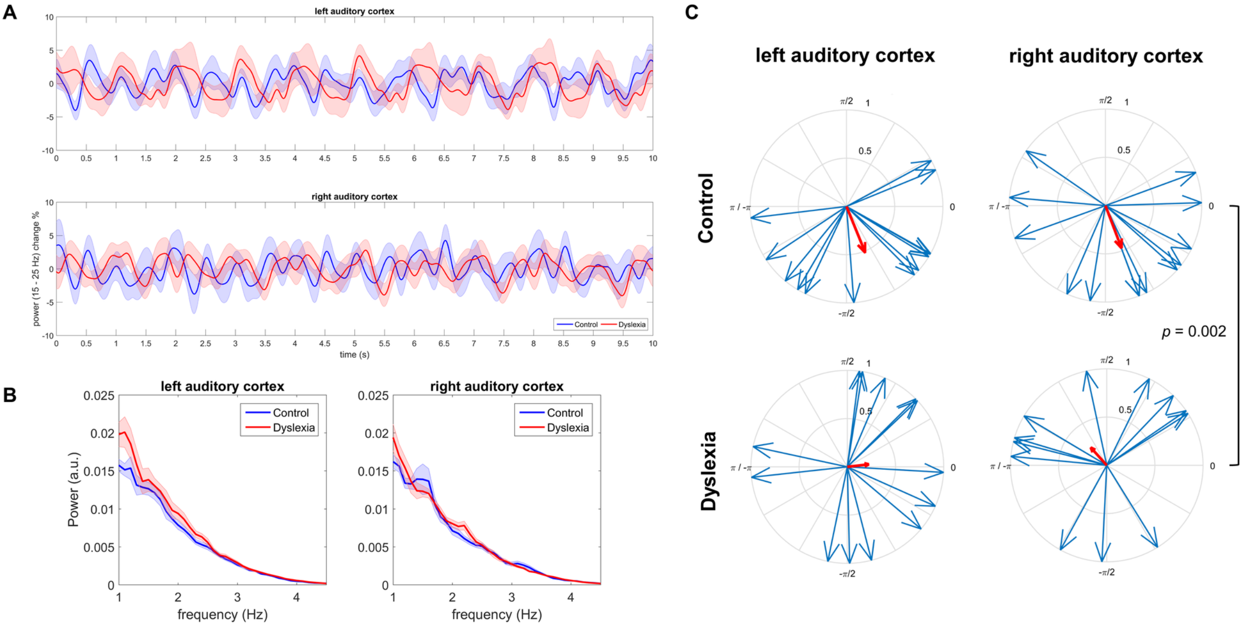
Wieland, E. A., McAuley, J. D., Dilley, L. C., & Chang, S. E. (2015). Evidence for a rhythm perception deficit in children who stutter. Brain Lang, 144, 26-34.

Wolff, P. H., Michel, G. F., Ovrut, M., & Drake, C. (1990). Rate and timing precision of motor coordination in developmental dyslexia. Dev Psychol, 26, 349.

Woodruff Carr, K., White-Schwoch T., & Tiernay A. T. (2014). Beat synchronization predicts neural speech encoding and reading readiness in preschoolers. P Natl Acad Sci USA, 111(40), 14559-14564.

Figure Legend

Figure 1. The beta (15-25 Hz) power at bilateral auditory cortices. (A) The beta power time series are presented as the mean ± standard error across typical (control) and dyslexic participants. (B) The spectra of beta power fluctuation (note that this is not the spectra of the raw EEG waveform). (C) The phases of beta power time series at 2 Hz. Each blue arrow represents the phase angle of beta power for a single participant; the phase angles and lengths of the red arrows represent the group-averaged angle and consistency of the angle distribution, respectively. The phase angles differed significantly between groups at the right auditory cortex. (p: p-value; a.u.: arbitrary unit)


A
left auditory cortex
right auditory cortex
power (15 - 25 Hz) change %
10
5
0
-5
-10
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8
8.5
9
9.5
10
time (s)
Control
Dyslexia
B
left auditory cortex
right auditory cortex
Power (a.u.)
0.025
0.02
0.015
0.01
0.005
0
frequency (Hz)
1
2
3
4
Control
Dyslexia
C
left auditory cortex
right auditory cortex
Control
Dyslexia
π/2
1
0.5
π / -π
0
-π/2
p = 0.002