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

2

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28 **Highlights**

- 29
- Adults with dyslexia and matched controls listened to isochronous tone sequences.
- 30
- Dyslexia was associated with an atypical phase of beta (~20 Hz) power fluctuation.
- 31
- Atypical beta power fluctuation might reflect deficits in tracking auditory rhythm.
- 32

33 **Abstract**

34 *Objective*

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

41

42 *Methods*

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

47

48 *Results*

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

51

52 *Conclusions*

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

55

56 *Significance*

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

60

61 **Keywords:** Dyslexia, Electroencephalography (EEG), Beta oscillation, Auditory perception,  
62 Entrainment

63

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

66

67

## 68 **Introduction**

69           Developmental dyslexia is a common reading disorder with a prevalence rate of around 5  
70 to 10% (Siegel, 2006), featuring impairments in phonological awareness, such as difficulties in  
71 identifying rhyming words or syllabic stress patterns in speech (Goswami et al., 2013). Beyond  
72 deficits in speech perception, this impairment is also associated with deficits of auditory  
73 processing of rhythmic temporal regularity (Goswami, 2011, 2015, 2019), including detecting  
74 amplitude envelope onset, perceiving and producing rhythm, and extracting auditory rhythmic  
75 regularity (Flaugnacco et al., 2014; Huss et al., 2011; Leong et al., 2011; Leong and Goswami,  
76 2014). The association between these two domains of auditory processing are also observed  
77 among typically-developing children: rhythm perception and the ability to synchronize to a beat  
78 are associated with phonological awareness, verbal short-term memory, rapid naming, and  
79 morphosyntactic accuracy in speech production (e.g., Woodruff Carr et al., 2014). Despite this  
80 evidence, we know little about the neural processing that underlies the rhythmic deficits in  
81 dyslexia, the focus of the present paper.

82           Neural oscillations have been proposed as an essential mechanism for tracking rhythm  
83 (Haegens and Zion Golumbic, 2018; Trainor et al., 2018). The power fluctuations of high-  
84 frequency oscillations (beta band: 15–25 Hz) entrain to rhythmic regularity in sound streams.  
85 When participants listen to an isochronous tone sequence, the beta band power from auditory  
86 cortex decreases immediately following the onset of a tone, and then rebounds anticipatorily  
87 according to the onset time of the upcoming tone (Cirelli et al., 2014; Fujioka et al., 2012),  
88 consistent with a mechanism for predicting the onset time of the next expected tone. This  
89 entrainment activity can be modulated by hierarchical rhythmic structure or disrupted by a  
90 random sequence (Fujioka et al., 2009; 2015; Iversen et al., 2009; Snyder and Large, 2005), and

91 it is associated with auditory prediction, attentional processing and perceptual performance  
92 (Chang et al., 2018, 2019; Morillon and Baillet, 2017). Atypical beta power entrainment  
93 activities have been observed in populations featuring deficits in rhythm perception and tracking,  
94 such as patients with Parkinson's disease (te Woerd et al., 2017, 2018) and children with  
95 stuttering (Etchell et al., 2016). However, it is unknown whether atypical beta power entrainment  
96 to auditory rhythmicity is associated with dyslexia.

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

101

## 102 **Methods**

### 103 *Participants*

104 Thirteen adults with developmental dyslexia (seven women, ten right-handed; mean age  
105 = 23.2 years, SD = 2.95 years) and 13 matched controls (seven women, seven right-handed,  
106 mean age = 22.5 years, SD = 2.07) participated in the current experiment. Although handedness  
107 was not perfectly matched in the current study, the higher proportion of non-right-handers  
108 appears to be a feature of dyslexia (e.g., Eglinton and Annett, 1994). All participants reported  
109 French as their native language, with one dyslexic participant reporting bilingualism with  
110 English. None reported auditory deficits. Education levels did not differ between the Dyslexic  
111 group (mean = 14.92 years; SD = 1.55) and the Control group (mean = 15.31 years, SD = 0.95),  
112  $p = .45$ . Musical background, as measured by years of instrumental instruction, also did not



113 differ between the Dyslexic group (mean = 2.00 years; SD = 2.16) and the Control group (mean  
114 = 1.69 years, SD = 2.13),  $p = 0.72$ .

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

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

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

137

### 138 *Stimulus*

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

148

### 149 *Procedure*

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

---

<sup>1</sup> 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 & Ding, 2020).

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

167

#### 168 *EEG recording and preprocessing*

169 The EEG signal was recorded with 95 Ag/AgCl active electrodes (actiCAP 96Ch  
170 Standard-2, Brain Products GmbH). The signal was recorded with a BrainAmp amplifier at a  
171 resolution of 16 bits, a sampling rate of 500 Hz, and with an analog low pass filter of 1000 Hz  
172 and high pass filter of 0.016 Hz. The ground electrode was placed at position AFz, the reference  
173 electrode on the tip of the nose, and an eye-movement monitoring electrode under the right eye  
174 at position Iz. Electrode impedances were kept below 20 k $\Omega$ , which is a well acceptable  
175 impedance levels for EEG recordings (e.g., Ferree et al., 2001; Luck, 2014). Continuous EEG  
176 data were transformed to an average reference offline. The EEG data was further processed in  
177 MATLAB with the FieldTrip toolbox (RRID: SCR\_004849) (Oostenveld et al., 2011).

178 Independent component analysis (ICA) was used to remove artifact signals (Jung et al.,  
179 2000). To speed up the ICA performance, the continuous recordings were downsampled to 250  
180 Hz, filtered between 0.7 and 83 Hz and then segmented into time window from -3 to 303 s time-  
181 locked to the first tone of the sequence. This window covered the entire stimulus sequence  
182 length. We went back to the unfiltered data, projected it to ICA space and the ICs reflecting  
183 artifact (identified by visual inspection, range of 2-13 ICs), including eye blinking, eye  
184 movement, electrocardiogram, and powerline noise, were excluded, and then the data in the ICA  
185 space was projected back to 95-channel space for all subsequent analyses.<sup>2</sup>

186

### 187 *Modeling dipole sources for auditory cortex*

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

---

<sup>2</sup> 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.

196 We used the multiple source probe scan algorithm and the four-shell ellipsoid model included in  
197 the Brain Electrical Source Analysis (BESA, RRID: SCR\_009530) software package. We chose  
198 P1 because (1) it is primarily generated from primary auditory cortex (Godey et al., 2001), (2) it  
199 is the dominant peak at fast presentation rates while the N1 peak is strongly reduced at fast rates  
200 relevant to the current study (Näätänen and Picton, 1987), and (3) previous studies with similar  
201 experimental designs also used P1 for localizing auditory cortex (e.g., Fujioka et al., 2012). The  
202 mean locations (averaged across participants) of the fitted dipoles were [ $\pm 44.23$ , -1.95, 7.26]  
203 (Talairach coordinates) with approximate mean orientations [0.2, 0.5, 0.8] (left) and [-0.2, 0.6,  
204 0.8] (right). These locations are close to bilateral primary auditory cortices with orientations  
205 toward the mid-frontal surface area, consistent with typical auditory evoked potentials. The mean  
206 residual variances of the source fittings were 7.9% (range 3.4 to 16.3%) for the Control group  
207 and 7.0% (range 2.4 to 15.4%) for the Dyslexia group, and the residual variances were not  
208 different between groups ( $t(24) = 0.67$ ,  $p = 0.509$ ). Finally, the unfiltered continuous 95-channel  
209 EEG was projected into source-space EEG via the dipole model for further time-frequency  
210 analyses.

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

216

217 *Time-frequency analyses*

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

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

238           Although some studies have defined the range of beta band to be as wide as 13-30 Hz, we  
239 defined it as 15-25 Hz for several reasons. (1) It is consistent with our previous studies (e.g.,

240 Fujioka et al., 2012; Chang et al., 2019). (2) Some other studies have interpreted activities below  
241 15 Hz as alpha band (e.g., Ahveninen et al., 2017) and above 25 Hz as low-gamma band (e.g.,  
242 Giroud et al., 2020). Therefore, it is debatable whether to include these frequencies as beta band.  
243 (3) Considering the imprecision of time-frequency analysis in terms of frequency resolution,  
244 activities closer to 13 or 30 Hz will be more likely contaminated by activities below 13 or above  
245 30 Hz, respectively, compared to frequencies between 15 and 25 Hz.

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

248

#### 249 *Tapping production task*

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

255

#### 256 *Statistics*

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

263 (Dyslexia, Control) for each time or frequency sample as the initial scan for clustering. Second,  
264 we grouped adjacent frequency (Figure 1B) or time (Figure S1A and S1C) samples reaching a  
265 threshold of  $p < 0.05$  in the initial scan into single clusters and summed the t-values of all  
266 samples within each cluster as a cluster-level statistic. Third, we built a null distribution with  
267 1000 random iterations. In each iteration, we pooled all 26 participants (13 in Dyslexia group  
268 and 13 in Control group), randomly split participants into 2 equal-size groups, and performed the  
269 same calculations as in the first two steps. The null distribution was composed by the summed t-  
270 values of the largest suprathreshold cluster of each iteration, and the final p-value was obtained  
271 by comparing the observed clustered summed t-value relative to the null distribution. In sum, if  
272 there was no group difference, the cluster(s) of the observed data should resemble the random-  
273 split data of the null distribution. The final p-value was corrected to two-tailed.

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

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

284





308 phase of the beta power time series at 2 Hz (the stimulus presentation rate) from the frequency  
309 transformation above (Figure 1C) for subsequent exploratory analyses. Note that the phase of  
310 beta power time series refers to the peak/trough position of the fluctuations in the measured beta  
311 power relative to the onsets of the stimuli. A Watson-Williams two-sample test showed that the  
312 phase of the beta power time series differed significantly at right auditory cortex ( $F(1,24) =$   
313  $12.90, p = .002$ ), but not at left auditory cortex, although there was a trend for a difference  
314 ( $F(1,24) = 3.51, p = .073$ ). The interaction between groups and left/right auditory cortex (taking  
315 the circular difference between hemispheres within each participant, and then performing a  
316 between-subject Watson-Williams test) was not significant ( $F(1,24) = 1.57, p = .222$ ).

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

328

329 *Tapping production task.*

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

336

### 337 **Discussion**

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

342           The atypical beta power fluctuation in dyslexia might reflect deficits in tracking and/or  
343 perceiving auditory rhythms. Previous studies on typical healthy participants showed that the  
344 fluctuation of beta power reflects entrainment to the rhythmic regularity of an auditory sequence.  
345 Specifically, the peaks of the beta power align to the onset of the tones, and are associated with  
346 rhythm tracking and auditory perception and prediction (Chang et al., 2018, 2019; Cirelli et al.,  
347 2014; Fujioka et al., 2009, 2012, 2015; Snyder and Large, 2005; Iversen et al., 2009). Our neural  
348 findings are consistent with previous studies showing that individuals with dyslexia have deficits  
349 in perceiving the rhythmic modulation of nonverbal auditory streams and speech (Goswami et  
350 al., 2002; Goswami, 2011, 2015, 2019; Megnin- Viggars and Goswami, 2013). Nevertheless, it  
351 is important to note that we cannot eliminate all explanations based on factors beyond

352 entrainment, such as, for example, that the participants in the Dyslexic group were more  
353 distracted by the visual movie, leading to less attention to the auditory stimuli.

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

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

374 indicating that the beta oscillatory activity in response to a simple, rhythmic (isochronous) sound  
375 sequence is also atypical in dyslexia.

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

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

397 who performed as well as controls on some of the measures (Wolff et al., 1990; see also  
398 Thomson et al., 2006). Furthermore, the observed variability of the dependent measures of the  
399 participants with dyslexia in our study suggests that individuals might use different neural  
400 mechanisms.

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

410 The current study did not investigate delta (1-3 Hz) oscillations or their cross-frequency  
411 coupling with beta oscillations, despite previously reported associations between delta  
412 oscillations and dyslexia. Both animal electrophysiology and human neuroimaging studies have  
413 shown that the delta oscillation phase time-locks and entrains to external rhythmic sensory input  
414 (see Haegens and Zion Golumbic, 2018 for a review) and it has been reported that atypical delta  
415 phase entrainment is associated with deficits of rhythm perception and tracking among  
416 individuals with dyslexia (Colling et al., 2017; Di Liberto et al., 2018; Molinaro et al., 2016;  
417 Power et al., 2013, 2016). However, recent studies have shown that it is challenging to reliably  
418 quantify delta phase entrainment because the frequency-domain signature of ERP activity  
419 typically overlaps with low-frequency oscillations in Fourier-based analysis (Doelling et al.,

420 2019; Haegens and Zion Golumbic, 2018). For this reason, we have left the question of how  
421 delta and beta oscillations are related in dyslexia to future studies with materials and designs  
422 more appropriate for addressing this question. Note that the induced beta oscillations measured  
423 in the current study are unlikely to be confounded with ERPs because (1) the mean spectrum of  
424 the ERP showed that the power above 15 Hz was neglectable (Figure S4), and (2) we removed  
425 the phase-locked evoked activity from the induced activity in the beta band prior to conducting  
426 our analyses.

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

440

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451

452 **Conflict of Interest Statement**

453 None

454

455 **References**

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- 650

651 **Figure Legends**

652 **Figure 1. The beta (15-25 Hz) power at bilateral auditory cortices.** (A) The beta power time  
653 series are presented as the mean  $\pm$  standard error across typical (control) and dyslexic  
654 participants. (B) The spectra of beta power fluctuation (note that this is not the spectra of the raw  
655 EEG waveform). (C) The phases of beta power time series at 2 Hz. Each blue arrow represents  
656 the phase angle of beta power for a single participant; the phase angles and lengths of the red  
657 arrows represent the group-averaged angle and consistency of the angle distribution,  
658 respectively. The phase angles differed significantly between groups at the right auditory cortex.  
659 (p: p-value; a.u.: arbitrary unit)  
660