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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 recorded¹. 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

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 & 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 Ω , 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.²

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.

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.

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 [± 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 μ 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 (κ) equal or above 1. Therefore, we
279 examined whether our 2 Hz beta power fluctuation time series met this assumption. The κ
280 parameter was similar between compared datasets (difference range: 0.05-0.14), with only κ
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

285 **Results**

286 *Power spectrum of beta power time series*

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

294 =====

295 Figure 1

296 =====

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

304 The frequency spectrum of beta power fluctuation (Figure 1B) did not show an obvious
305 peak at 2 Hz as expected, despite the appearance of a power fluctuation around the 2 Hz tone
306 onset rate in the averaged time domain waveforms (Figure 1A). Nevertheless, we speculated that
307 the beta power fluctuations likely differed in phase between the two groups, and we extracted the

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