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1 Regular rhythmic primes boost P600 in grammatical error processing

2 in dyslexic adults and matched controls

3 Laure-Hélène Canette<sup>1,2,3</sup>, Anna Fiveash<sup>1,2</sup>, Jennifer Krzonowski<sup>4</sup>, Alexandra Corneyllie<sup>1,2</sup>,

4 Philippe Lalitte<sup>3</sup>, Dave Thompson<sup>5,6</sup>, Laurel Trainor<sup>5,6</sup>, Nathalie Bedoin\*<sup>1,2,4</sup>

5 & Barbara Tillmann\*<sup>1,2</sup>

6 <sup>1</sup> CNRS, UMR5292; INSERM, U1028; Lyon Neuroscience Research Center, Auditory

7 Cognition and Psychoacoustics Team, Lyon, F-69000, France;

8 <sup>2</sup> University Lyon 1, Villeurbanne, F – 69000, France;

9 <sup>3</sup> LEAD-CNRS UMR 5022, Université de Bourgogne, Dijon, F – 21000 Dijon, France;

10 <sup>4</sup> Laboratory Dynamics of Language, UMR 5596, University Lyon 2, F – 69000 France;

11 <sup>5</sup> Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton,

12 ON

13 <sup>6</sup> McMaster Institute for Music and the Mind, McMaster University, Hamilton, ON

14  
15 \* shared last authors

16 Corresponding author:

17 Laure-Hélène Canette

18 LEAD

19 CNRS - Université Bourgogne Franche-Comté - UMR 5022

20 Institut Marey

21 I3M

22 64 rue de Sully

23 21000 Dijon

24 +33 (0)3 80 39 57 72

25 +33 (0)3 80 39 57 67

26 Laure-Helene.Canette@u-bourgogne.fr

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## Highlights

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- 1) Regular rhythmic stimulation benefits subsequent speech processing = 69
- 2) The P600 response to grammatical errors was enhanced after regular rhythms = 77
- 3) This benefit was observed in both dyslexic adults and matched controls = 73
- 4) It persisted despite dyslexics' temporal processing deficit and delayed P600 = 79
- 5) Findings encourage the use of rhythmic stimulation in rehabilitation and training = 84

## Abstract

Regular musical rhythms orient attention over time and facilitate processing. Previous research has shown that regular rhythmic stimulation benefits subsequent syntax processing in children with dyslexia and specific language impairment. The present EEG study examined the influence of a rhythmic musical prime on the P600 late evoked-potential, associated with grammatical error detection for dyslexic adults and matched controls. Participants listened to regular or irregular rhythmic prime sequences followed by grammatically correct and incorrect sentences. They were required to perform grammaticality judgments for each auditorily presented sentence while EEG was recorded. In addition, tasks on syntax violation detection as well as rhythm perception and production were administered. For both participant groups, ungrammatical sentences evoked a P600 in comparison to grammatical sentences and its mean amplitude was larger after regular than irregular primes. Peak analyses of the P600 difference wave confirmed larger peak amplitudes after regular primes for both groups. They also revealed overall a later peak for dyslexic participants, particularly at posterior sites, compared to controls. Results extend rhythmic priming effects on language processing to underlying electrophysiological correlates of morpho-syntactic violation detection in dyslexic adults and matched controls. These findings are interpreted in the theoretical framework of the Dynamic Attending Theory (Jones, 1976; 2019) and the Temporal Sampling Framework for developmental disorders (Goswami, 2011).

**Key words:** rhythmic priming, syntax processing, temporal attention, dyslexia, P600 evoked potential.

1 **1. Introduction**

2           The role of rhythm in speech and language processing and the potential application to  
3 rehabilitation have attracted increasing interest (e.g., Kotz & Schwartz, 2010; Schön &  
4 Tillmann, 2015). Investigating the potential influence of auditory rhythmic stimulation on  
5 language processing has been motivated by previously observed links between musical  
6 rhythm processing and speech processing. Given that these domains share neural resources  
7 and require similar rhythm perception and production capacities, rhythm-based training has  
8 been suggested to benefit language processing (e.g., Fiveash et al., submitted, for reviews;  
9 Fuji & Wan, 2014).

10           Numerous studies have demonstrated relations between rhythmic and linguistic skills.  
11 In typically-developing children, the ability to synchronize with the beat is associated with  
12 competences underlying reading acquisition, such as phonological awareness, verbal short-  
13 term memory, and rapid naming (Woodruff Carr, White-Schwoch, Tiernay, Strait & Kraus,  
14 2014). Rhythm perception abilities have also been reported to be associated with morpho-  
15 syntactic abilities in speech production (Gordon, Shivers, Wieland, Kotz, Yoder & McAuley,  
16 2015b). In children with developmental dyslexia and specific language impairment (SLI),  
17 rhythm competence has been associated with phonological awareness and reading skills (e.g.  
18 Corriveau & Goswami, 2009; Flaughnacco et al., 2014; Huss, Vernay, Fosker, Mead &  
19 Goswami, 2011; Thomson & Goswami, 2008). These links between rhythmic and linguistic  
20 skills have been further supported by studies demonstrating that musical training can benefit  
21 phonological and reading skills in dyslexic children (e.g., Overy, 2000; Flaughnacco et al.,  
22 2015).

23           The benefit of rhythm for speech processing has been shown not only with long-term  
24 musical training (e.g., Flaughnacco et al., 2015), but also with short-term exposure to musical  
25 material within an experimental session. Implemented as a priming paradigm, participants

1 listened to a rhythmic music-like sequence before performing a linguistic task (see Schön &  
2 Tillmann, 2015 for a review). The temporal structure of the music-like sequences was either  
3 exactly matched to the accent structure of the following sentence (and compared to a  
4 mismatched structure, e.g., Cason, Astésano & Schön, 2015; Cason, Hidalgo, Isoard, Roman  
5 & Schön, 2014) or contained a strongly metrical structure that primed a set of subsequently  
6 presented sentences (e.g., Chern, Tillmann, Vaughan & Gordon, 2018; Kotz, Gunter &  
7 Wonneberger, 2005; Przybylski et al., 2013). This latter approach is not based on a one-by-  
8 one matching of a given prime with its associated sentence, but taps into more general  
9 processes by stimulating temporal attention by the regular structures of the rhythmic prime  
10 (e.g., Jones, 1976). A beneficial effect of a regular metrical prime on subsequent sentence  
11 processing was first shown for patients with basal ganglia lesions. While the typically  
12 observed electrophysiological marker of grammatical error detection (the P600) has been  
13 reported to be missing in this population (Kotz, Frisch, von Cramon & Friederici, 2003),  
14 listening to regular march music for three minutes before listening to blocks of grammatical  
15 and ungrammatical sentences re-elicited this marker (Kotz et al., 2005). This approach was  
16 further developed by studying beneficial effects of rhythmic priming on language processing  
17 in children with developmental language disorders. Przybylski et al. (2013) showed that the  
18 regularity of a musical prime influenced subsequent grammatical processing (i.e., morpho-  
19 syntactic processing) in dyslexic children, SLI children and typically developing children. For  
20 all participant groups, grammaticality judgments were better after a metrically regular prime  
21 compared to a temporally irregular prime without a clear underlying meter (see also Chern et  
22 al., 2018). This effect of relative facilitation (i.e., comparing regular to irregular primes) was  
23 extended to the observation of a benefit of regular primes over baseline primes, implemented  
24 in environmental sound scenes or musical excerpts based on spectro-temporal patterns  
25 without rhythmic features (Bedoin, Brisseau, Molinier, Roch & Tillmann, 2016; Canette et

1 al., under revision). These findings support the hypothesis that the observed rhythmic priming  
2 effect relies on a benefit of the regular structure of the musical primes rather than a cost of the  
3 irregular primes. It is interesting to highlight that SLI and dyslexic children can benefit from  
4 the temporally regular structure of the primes despite their previously reported rhythm  
5 processing difficulties (e.g., Corriveau & Goswami, 2009; Muneaux, Ziegler, Truc,  
6 Thomson & Goswami, 2004). A recent study combined the rhythmic priming paradigm with a  
7 linguistic training program focusing on syntax processing and extended the beneficial effect  
8 of musically rhythmic primes to hearing-impaired children with cochlear implants (Bedoin,  
9 Bescombes, Escande, Dumont & Tillmann, 2017).

10         The reported beneficial priming effects of regular musical structures on language  
11 processing can be interpreted within the framework of the Dynamic Attending Theory (Jones,  
12 1976, 2019; Jones & Boltz, 1989; Large & Jones, 1999). According to this framework,  
13 attention is not distributed equally across time, but aligns with external regularities (for  
14 example, to beat onsets in musical structures). This allows listeners to develop expectations  
15 about when future events will occur (i.e., predictive timing), leading to facilitated event and  
16 structure processing at expected time points thanks to enhanced attentional resources. In the  
17 rhythmic priming paradigm, the hypothesis is that the entrainment to the regular musical  
18 prime benefits subsequent language processing, aiding sequencing and structural integration.  
19 More specifically, the regular events in the musical prime provide predictable cues that may  
20 allow for boosting and entraining of internal oscillators. These oscillators then persist after the  
21 musical prime has stopped and facilitate entrainment to the less regular speech signal.  
22 Consequently, this entrainment then benefits sentence processing by facilitating segmentation  
23 and sequencing of the speech signal and thus favoring the processing of its syntactic structure.

24         The present study investigated the beneficial effect of regular rhythmic musical primes  
25 on syntax processing in dyslexic adults and their matched controls by measuring event-related

1 potentials (ERPs). Based on Kotz et al. (2005), in which a regular musical prime evoked a  
2 P600 to grammatical errors in subsequently presented sentences in patients with basal ganglia  
3 lesions (who are missing this component without the prime, see Kotz et al., 2003), we  
4 predicted an enhanced P600 after regular musical primes in comparison to irregular primes.  
5 The P600 component is of particular interest as a biomarker because several studies have  
6 shown P600 abnormalities in dyslexic adults in response to morpho-syntactic violations (e.g.,  
7 subject-verb agreement), as used here (Cantiani, Lorusso, Perego & Guasti, 2013; Rispen,  
8 Been & Zwarts, 2006). In particular, the P600 peaked later for dyslexic participants in  
9 comparison to control participants.

10         Our study recorded EEG during the rhythmic priming paradigm in dyslexic adults and  
11 their matched control participants. The effect of regular primes was compared to that of  
12 irregular primes within the same participants, thus avoiding a comparison across studies and  
13 patient groups (as in Kotz et al., 2015). The rhythmic priming paradigm was implemented as  
14 in Przybylski et al (2013), but with four main changes. First, we measured not only behavioral  
15 performance of grammaticality processing, but also recorded EEG, aiming to observe an  
16 enhanced P600 in response to grammatical errors after the regular primes. Second, we  
17 elaborated a set of new musical primes (instead of using only one prime pair), which were  
18 also musically more attractive and complex. Third, we constructed new sentence material that  
19 controlled error positions to be optimal for the ERP measurements and that was  
20 complemented with filler sentences. Fourth, in addition to the grammaticality judgments  
21 performed on the sentences presented after the primes, participants performed behavioral tests  
22 to (1) assess complex morpho-syntactic skills and (2) measure rhythm perception and  
23 production skills. Rhythm skills were assessed with tapping tasks (i.e., free spontaneous  
24 tapping, synchronization) and an adaptation of the complex Beat Alignment Test (Einarson &  
25 Trainor, 2016; based on Iversen & Patel, 2008).



1

## 2 **2. Methods**

### 3 **2.1. Participants**

4           Twenty-six adults participated in the study: 13 dyslexic adults (7 women, 10 right-  
5 handed, mean age = 23.2 years, SD = 2.95) and 13 matched control adults (7 women, 10  
6 right-handed, mean age = 22.5 years, SD = 2.07). All participants reported French as their  
7 native language, with one dyslexic participant reporting bilingualism with English. None  
8 reported auditory deficits. Education levels did not differ between the dyslexic group (M =  
9 14.92 years; SD = 1.55) and the control group (M = 15.31 years, SD = 0.95),  $p = .45$ . Musical  
10 background, as measured by years of instrumental instruction, did not differ between the  
11 dyslexic group (M = 2.00 years; SD = 2.16) and the control group (M = 1.69 years, SD =  
12 2.13),  $p = .72$ .

13           As part of a larger research project investigating dyslexia at the university (Abadie &  
14 Bedoin, 2016), dyslexic participants completed a set of language and neuropsychological  
15 tests. All dyslexic participants had developmental dyslexia and reported having seen a speech  
16 therapist for the diagnosis and for training sessions designed to reduce reading difficulties for  
17 at least two years during childhood, while none of the controls reported this<sup>1</sup>. None of the  
18 controls reported history of spoken or written language disorders. All dyslexics had scores in  
19 the normal range for Raven's matrices (mean standard score = 10.31, SD = 3.25) and for  
20 reading comprehension (average z-score placed them above the mean = 1.91, SD = 0.60).  
21 None had any current or past psychiatric or neurological diagnosis nor attention disorder with  
22 or without hyperactivity (ADHD). Eleven dyslexics had a pathological score in reading and/or  
23 orthographic skills for pseudo-words and/or irregular words according to the *ECLA-16+*  
24 battery (Gola-Asmussen, Lequette, Pouget, Rouyer & Zorman, 2010), a set of standardized

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<sup>1</sup> One control participant reported to have consulted a speech therapist for tongue position correction.

1 tests adapted for adult assessment and broadly based on the *Batterie Analytique du Langage*  
2 *Ecrit* (BALE, Jacquier-Roux, Valdois & Zorman, 2010), which is widely used in France to  
3 assess dyslexia in children. It is difficult to precisely categorize the form of dyslexia in adults  
4 because of successful compensation mechanisms – especially in the case of students. Among  
5 these eleven dyslexics, four had a pathological score in phonological awareness, two had a  
6 pathological score in a visual attention skill, which is frequently disturbed in surface dyslexia  
7 (measured with *EVADYS* test, Valdois, Guinet & Embs, 2014, see Bosse, Tainturier &  
8 Valdois, 2007), and four had a pathological score in both phonological awareness and visual  
9 attention skill<sup>2</sup>. The remaining two dyslexics did not have scores currently reaching the  
10 pathological threshold in reading or orthographic skills, despite having been diagnosed as  
11 dyslexic children when they were at school, and while still experiencing reading difficulties.  
12 However, they had pathological scores in phonological awareness (a persistent deficit  
13 underlying phonological and mixed forms of dyslexia) and/or a visual-attentional deficit  
14 (frequently observed in surface dyslexia). Therefore, our dyslexic participants were mainly  
15 experiencing phonological difficulties (i.e., phonological or mixed forms of dyslexia, which  
16 are the most frequently observed forms of this neurodevelopmental pathology).

17 Each participant performed the EEG experiment in one testing session and the  
18 behavioral tests on syntax processing and rhythm perception and production in a second  
19 testing session (except for one dyslexic participant who did not come back to the second  
20 session). Written informed consent based on French ethics procedure approval Committee  
21 (CPP Sud-Est II, 2007-009-3: *Processing of Music and Language*) was obtained from all  
22 participants prior to the experiment, which was conducted in accordance with the guidelines  
23 of the Declaration of Helsinki.

24

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<sup>2</sup> Information about phonology and visual attention skills is missing for one dyslexic participant.

1 Table 1. Means and standard deviations (SD) of the dyslexic participants' results reported in  
2 z-scores for language abilities and visual-attentional span, and in standard scores for one  
3 measure of nonverbal intelligence (Raven's Matrices). Pathological z-scores are defined as  
4 scores that place the participant at least 1.65 SD below the mean of the normative group in  
5 linguistic tests (i.e., the usual criterion for speech therapists) and at least 2.00 SD below the  
6 mean of the normative group in the test of visual attention span (global report of five-letter  
7 strings). For the Matrix test, a standard score at or below 4 is considered as pathological.  
8 Reading, orthographic and phonological skills were assessed with the test *ECLA 16+* (Gola-  
9 Asmussen et al., 2010); reading comprehension was assessed with the test *Le Vol du PC*  
10 (Boutard, Claire, & Gretchanovsky, 2004); and visual attention span was assessed with the  
11 test *EVADYS* (Valdois et al., 2014). A star (\*) indicates pathological scores.

		Mean z-score	SD
Reading times	Pseudo-words	-2.23*	2.20
	Irregular words	-1.72*	1.93
Reading comprehension	Text	1.91	0.60
Spelling	Pseudo-words	-1.59	1.19
	Irregular words	-1.40	1.25
Phonology (time)	Suppression of initial phoneme	-2.47*	1.28
Visual attention span	Global report (correct letters)	-1.55	2.15
		Mean standard score	SD
Non-verbal fluid intelligence and abstract reasoning	Raven's matrices	10.31	3.25

12

## 13 **2.2. Materials**

### 14 *2.2.1. Rhythmic material*

15 Twenty-two rhythmic sequences were used. In addition to the regular and irregular  
16 sequences of Przybylski et al. (2013), 20 new sequences were constructed (10 regular, 10

1 irregular) with the same features related to meter as in Przybylski et al. (2013), but with more  
2 temporal and timbral variety with the aim of creating more musical and diverse material. The  
3 regular sequences were constructed on the basis of a 4/4 meter and a 120 BPM tempo (i.e.,  
4 inter-beat-interval of 500 ms or 2 Hz). The new sequences were formed by four overlaid  
5 rhythmic patterns. To vary and characterize the sequences in timbre, each layer was played by  
6 one (and sometimes two) percussion instrument(s) (i.e. bass drum, snare drum, tom-tom, and  
7 cymbal). All sequences were played with MIDI VST instrument timbres. Four of the  
8 sequences also contained some samples of electronic percussions. Each sequence was  
9 composed of one cycle of 16 beats that was repeated four times, thus leading to a duration of  
10 32 seconds. At the end of a cycle, a short rhythmic pattern or a percussion sound was added to  
11 reinforce the sensation of formal periodicity. To create a feeling of completion at the end of  
12 the sequence, the first beat of the cycle was added at the end, thus adding about 2 seconds  
13 with a short reverberation effect, leading to the total duration of 34 seconds.

14 The irregular sequences were derived from the regular sequences. The percussion  
15 sounds, the total duration and the durations of each event were identical. For each of the four  
16 rhythm patterns, the number of percussive events was the same as for the regular sequences,  
17 but reordered across the sequence to obtain a maximum of rhythmic irregularity. In this way,  
18 it was not possible to perceptually extract an underlying pulse or a regular metric. Each  
19 rhythmically regular sequence led to the construction of one rhythmically irregular sequence.  
20 All sequences were recorded with Cubase 4 and Kontakt 3 VST instruments. A short reverb  
21 effect was added (reverb time 1.75 s, mixed at 25%). They were exported in 16 bits/48 000  
22 Hz mono wav files and normalized in loudness.

23

### 24 2.2.2. *Linguistic material*

25 The experimental material was composed of 768 French sentences that were

1 grammatically correct (384) or incorrect (384). Grammatical and ungrammatical sentences  
2 were composed of an average of 9.15 syllables (range = 7-12; SD = 1.12). All sentences were  
3 composed of five words (average duration of the sentences = 1996 ms  $\pm$ 199 ms) and had the  
4 same syntactic construction (i.e., pronoun, verb, determiner, adjective and noun or noun and  
5 adjective). Incorrect sentences contained a subject-verb (i.e., number) agreement error (e.g.,  
6 Je finirai/\*finirons les derniers exercices – *I will finish*<sub>[singular, plural] *the last exercises* or Nous  
7 finirons/\*finirai les derniers exercices – *We will finish*<sub>[plural, singular] *the last exercises*). Verbs  
8 were in future tense, allowing for time-locking the ERPs to the critical morpheme (i.e., just  
9 after the phoneme [ʁ]) always at the same location regardless of the verb. For the construction  
10 of the sentence set, 192 different sentences were used as the basis and for each sentence, four  
11 versions were constructed: two correct versions (with either *Je* (I) or *Nous* (we) as the subject)  
12 and the two derived grammatically incorrect versions. The resulting 768 sentences were split  
13 into four lists of 192 sentences, with one of the four versions per list. In each list, there were  
14 48 correct sentences with *Je* (I) as the subject, 48 correct sentences with *Nous* (we) as the  
15 subject, 48 incorrect sentences with *Je* (I) as the subject, and 48 incorrect sentences with *Nous*  
16 (we) as the subject. Each participant heard one of the lists with 48 sentences in each  
17 experimental condition (i.e., four experimental conditions, crossing Rhythmic Prime and  
18 Grammaticality as factors), thus hearing only one of the four versions of each sentence, and  
19 never the same sentence in its grammatically correct and incorrect versions.</sub></sub>

20         Additionally, 192 filler sentences, grammatically correct (96) or incorrect (96), were  
21 constructed to avoid participants focusing only on the verb agreement manipulation in the  
22 experimental sentences. The incorrect filler sentences contained gender agreement errors on  
23 other words within the sentence, such as a determiner or adjective (e.g., Je garerai la/\*le  
24 voiture grise – *I will park the*<sub>[f., m.] *grey car*). The filler sentences also contained on average  
25 9.00 syllables (range = 7-11; SD = 1.04), were composed of five words with the same</sub>

1 syntactic construction, and had an average duration of 2041 ms  $\pm$ 216 ms.

2 For experimental and filler sentences, word frequency was controlled using lemma  
3 frequency per million according to the movies corpus (Lexique 3; New, Pallier, Ferrand &  
4 Matos, 2001). Mean frequency of verbs, adjectives and nouns used for experimental and filler  
5 sentences were 188.7 (SD = 460.4). Sentences were recorded by a native female speaker of  
6 French with a natural speed of production with the Rocme! Software (Ferragne, Flavier &  
7 Fressard, 2012).

8 The experiment was run using the software Presentation (Neurobehavioural Systems).  
9 Stimuli were presented via headphones (Pioneer, HDJ-500).

10

### 11 *2.2.3. Material for additional behavioral tests*

12 **2.2.3.1. Syntax test.** To evaluate morpho-syntactic processing in speech perception, a new test  
13 was created with subtle morpho-syntactic errors, covering errors regarding tense, prepositions  
14 and person agreement (in French). We first created 48 correct sentences and derived one  
15 incorrect sentence from each correct sentence. Sentences were spread into two lists of 48  
16 sentences (24 correct sentences and 24 incorrect sentences) to avoid participants listening to  
17 the same sentence in its correct and incorrect versions. Each correct sentence of the first list  
18 was matched in number of words, number of syllables and word's lexical frequency (Lexique  
19 3; New et al., 2001) to a correct sentence of the second list. Half of the participants heard the  
20 correct sentences of one list and the incorrect sentences of the other list, and the reverse for  
21 the other half of the participants. Sentences were recorded by a native female speaker of  
22 French with the same material and procedure as for the sentences used in the EEG recording.  
23 The experiment was run using the software Open Sesame (Mathôt, Schreij, & Theeuwes,  
24 2012) and stimuli were presented via headphones.

25

1 **2.2.3.2. Temporal processing test.** For the synchronization tasks, isochronous sequences of a  
2 duration of 20 seconds (played with a metronome sound, duration = 100 ms) were created at  
3 three tempi, notably with inter-sound-intervals of 400 ms, 550 ms and 700 ms. The cBAT  
4 (complex Beat Alignment Task) contained eleven musical excerpts that were used for  
5 perception and production tasks, and an additional one as an example (see Einarson &  
6 Trainor, 2015, for details). These musical excerpts had an average target inter-beat-interval of  
7 500 ms (ranging from 366 ms to 692 ms across the excerpts).

8 For the perception task, an isochronous sequence with a woodblock sound was  
9 superimposed on the musical excerpts. This superimposition was either correctly aligned with  
10 the beat of the musical excerpt (“on the beat”) or misaligned in either phase (shifting the  
11 isochronous woodblock sequence to be 25% too early or 25% too late relative to the beat of  
12 the music) or tempo (increasing or decreasing the tempo of the woodblock sequence by 10%  
13 compared to the tempo of the music). Thus, there were three versions of each of the 9 musical  
14 excerpts. Participants responded on a computer keyboard as to whether the woodblock was  
15 aligned with the excerpt on each trial.

16 For the production task, participants drummed with a stick on a drum pad (Roland, V-  
17 Drums) to the beat of each excerpt. Both the perception and production parts of the temporal  
18 processing task were implemented with the software Presentation (Neurobehavioural  
19 Systems) and stimuli were presented over headphones.

20

21

## 22 **2.3. Procedure**

### 23 *2.3.1. EEG experiment*

24 The experimental material was presented over 48 blocks, each block consisting of one  
25 rhythmic sequence followed by six sentences. In each block of six sentences, there were four  
26 experimental sentences (two correct and two incorrect) and two filler sentences (one correct

1 and one incorrect). Sentence distribution in the blocks, sentence order in each block and block  
2 order were randomized for each participant. Similarly, the presentation order of the rhythmic  
3 sequences was pseudo-randomly determined with the constraint that within the 48 blocks,  
4 four consecutive blocks presented the same type of musical sequences (regular or irregular),  
5 followed by the other type for the following four blocks (e.g., RRRRIIIIRRRR...). Half of the  
6 participants started with regular sequences and half with irregular sequences.

7 Participants were comfortably seated in a sound-attenuated booth in front of a monitor  
8 with a computer mouse. Participants wore headphones and were asked to listen to the music  
9 while looking at a fixation cross on the computer screen. At the end of the musical sequence,  
10 they judged each of the six following sentences for grammaticality by pressing one of two  
11 buttons on the computer mouse. Participants were able to respond one second after the end of  
12 the sentence when response choices were indicated on the screen by the words *grammatical*  
13 and *ungrammatical*. After the participant had responded, the next sentence was triggered after  
14 an average delay of 750 ms (randomly determined from a distribution between 500 and 1000  
15 ms). This type of jittered delay was also inserted before each musical sequence and the first  
16 sentence of the set. Participants were told to look at the fixation cross and to blink as little as  
17 possible during the experiment, and were instructed to avoid blinking during the sentences in  
18 particular. There was a short break after every 12 blocks. The experiment lasted 50 minutes.

19

20

### 21 2.3.2. Behavioral post-tests

22 For the rhythm perception and production tests, participants first performed the  
23 production tasks: (1) spontaneous regular tapping at their preferred rate for a duration of 30  
24 seconds, (2) tapping along to the isochronous sequences with the three different tempi (see  
25 above), and (3) tapping along to the beat of nine musical excerpts from the cBAT production



1 test. Then, participants performed the perception test of the cBAT and judged whether the  
2 sound of a metronome was aligned or not with the beat of 24 musical excerpts (8 correctly  
3 aligned, 8 phase-shifted, 8 tempo-shifted). Participants could respond during the musical  
4 excerpt. After responding, participants indicated their confidence level in their response (on a  
5 scale from 1 to 3). These tests lasted about 30 minutes.

6 For the syntax test, participants were asked to judge the grammaticality of each  
7 sentence by pressing one of two keys on the computer keyboard. Participants were alerted  
8 about the difficulty of the test and to be careful and rigorous in their judgments. A fixation  
9 point was displayed on the screen during the presentation of the sentence, and it disappeared  
10 when participants gave their response. A new sentence was triggered after each response.  
11 Presentation order of the sentences was randomized for each participant. This test lasted about  
12 five minutes.

13

## 14 ***2.4. Data acquisition and analyses***

### 15 *2.4.1. EEG recording and analyses*

16 The EEG signal was recorded with 95 Ag/AgCl active electrodes (ActiCAP, Brain  
17 Products GmbH) configured according to the international 10–20 system. The signal was  
18 recorded with a BrainAmp amplifier at a resolution of 16 bits, a sampling rate of 500 Hz, and  
19 with an analog low pass of 1000 Hz and high pass of 0.016 Hz. The ground electrode was  
20 placed at position AFz, the reference electrode on the tip of the nose, and an eye-movement  
21 monitoring electrode under the right eye with the electrode Iz. Electrode impedances were  
22 kept below 20 k $\Omega$ .

23 The EEG signals were analyzed using EEGLAB/ERPLAB (Lopez-Calderon & Luck,  
24 2014). Datasets were bandpass-filtered between 0.1 and 30 Hz. Data were segmented into  
25 1200 ms epochs beginning 200 ms before the critical morpheme and ending 1000 ms after. A

1 semi-automatic artifact rejection was done: artifact rejection was performed automatically  
2 using a  $\pm 100 \mu\text{V}$  rejection threshold throughout all electrodes except Iz, and manually by  
3 removing any trials contaminated with eye movements or muscle activity on any of the  
4 electrodes. The mean percentage of rejected trials was 24.56 (SD = 16.02) for the dyslexic  
5 group and 25.84 (SD = 16.06) for the control group, leading to on average 36.22 trials per  
6 condition (SD = 0.76) for the dyslexic group and on average 35.58 trials per condition (SD =  
7 0.40) for the control group. Epochs were averaged for each condition and each participant and  
8 then averaged across participants for visual display.

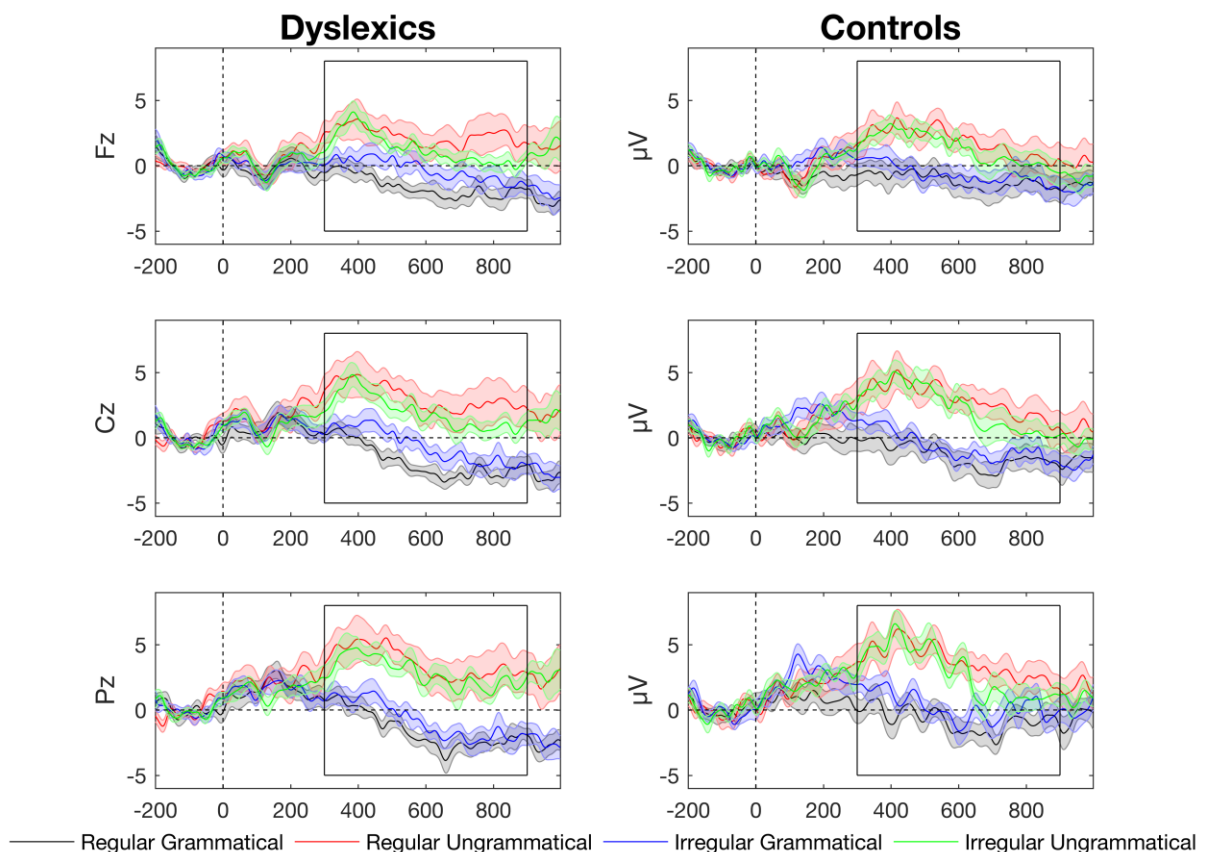
9 ERP data were analyzed based on Regions of interest (ROIs) as well as for the midline  
10 electrodes (Fz, Cz, Pz) to cover most of the recorded scalp area. ROIs were defined on the  
11 basis of Mathias, Palmer, Perrin & Tillmann (2014): (1) left frontal region (F1, F3, F5, F7,  
12 AF3, AF7, AFF1h), (2) right frontal region (F2, F4, F6, F8, AF4, AF8, AFF2h), (3) left  
13 central region (C1, C3, C5, T7, FCC3h, FTT7h, CCP1h, CCP5h), (4) right central region (C2,  
14 C4, C6, T8, FCC4h, FTT8h, CCP2h, CCP6h), (5) left posterior region (P1, P3, P5, P7, PO3,  
15 PO7, PPO1h), (6) right posterior region (P2, P4, P6, P8, PO4, PO8, PPO2h).

16 The time windows for the analysis of the P600 component were chosen based on  
17 previous studies (e.g., Rispens et al., 2006), and visual inspection of grand averages for Cz, Fz  
18 and Pz (Figure 1) and shifted earlier in time as our trigger was not located at the onset of the  
19 critical verb, but shifted to the occurrence of the phoneme [ʁ] (i.e., the first acoustic cue for  
20 the number agreement) inside the critical verb. We calculated the mean amplitude within the  
21 post-stimulus time window [300-900 ms]. ANOVAs were computed in an analysis based on  
22 the ROIs as well as in an analysis based on the midline electrodes. For the ROI analysis, we  
23 ran a  $2 \times 2 \times 3 \times 2 \times 2$  ANOVA with Rhythmic Prime (regular, irregular), Grammaticality (correct,  
24 incorrect), Region (frontal, central, posterior) and Hemisphere (left, right) as within-  
25 participant factors, and Group (dyslexic, control) as a between-participants factor. For the

1 midline analysis, we ran the same ANOVA, except that the factor Region was defined as (Fz,  
2 Cz, Pz) and the factor Hemisphere was removed.

3 In addition, we calculated the difference wave between grammatical and  
4 ungrammatical sentences and extracted peak amplitude and latency in the P600 time window  
5 for midline electrodes. We used a custom-made MATLAB script from Fiveash, Thompson,  
6 Badcock, and McArthur (2018): <https://github.com/nicalbee/erpPeak>. Amplitude and latency  
7 were separately analyzed with a 2x3x2 ANOVA with Rhythmic Prime (regular, irregular),  
8 Region (Fz, Cz, Pz) as within-participant factors and Group (dyslexic, control) as a between-  
9 participants factor.

10 For all analyses, we calculated partial  $\eta^2$  (Cohen, 1988) to estimate effect sizes, and  
11 Greenhouse-Geisser correction was applied when necessary.



12  
13 Figure 1. Grand-averages of ERPs mean amplitude for grammatical and ungrammatical  
14 sentences depending on the Rhythmic Prime (regular, irregular), for Fz, Cz and Pz electrodes,

1 in each participant Group (control and dyslexic). The square represents the time window  
2 defined for the analyses. Shaded error bars represent one standard error on either side of the  
3 mean.

4

#### 5 *2.4.2. Behavioral data analyses*

6 Grammaticality judgments were analyzed with signal detection theory, calculating  
7 discrimination sensitivity  $d'$  and response bias  $c$  for each participant (based on hits; i.e.,  
8 correct responses for ungrammatical sentences) and false alarms (FAs; i.e., errors for  
9 grammatical sentences) (Macmillan & Creelman, 1991)<sup>3</sup>. For grammaticality judgments  
10 acquired during the EEG recording, 2x2 ANOVAs with Rhythmic Prime (regular, irregular)  
11 as a within-participant factor and Group (dyslexics, controls) as a between-participants factor  
12 were performed for  $d'$  and  $c$ , separately. For the syntax post-test, participant group differences  
13 for  $d'$  and  $c$  were assessed with two-sided independent  $t$ -tests. In addition, performance was  
14 also analyzed with proportion of correct responses, with a 2x2x2 ANOVA, with Group,  
15 Grammaticality and Rhythmic Prime as factors for data acquired during the EEG recording,  
16 and a 2x2 ANOVA with Group and Grammaticality as factors for the syntax post-test. To  
17 estimate effect sizes, we calculated partial  $\eta^2$  (Cohen, 1988).

18 For the rhythm perception and production tests, group differences were investigated  
19 with two-sided independent  $t$ -tests on the following measures: 1) Free tapping data were  
20 analyzed with average Inter-Tap-Interval (ITIs), within-trial variability (standard deviation of  
21 ITIs), and coefficient of variation (CV), defined as the standard deviation divided by the mean  
22 ITI; 2) The production performance of the synchronization tasks for isochronous sequences  
23 and musical excerpts were analyzed with circular statistics (see Berens, 2009; Dalla Bella &

---

<sup>3</sup> The correction of the  $d'$  and  $c$  measures used .01 for cases without false alarms and .99 for the maximum number of hits.

1 Sowinski, 2015), leading to two measures related to the resulting vector  $R$ : its *angle*<sup>4</sup> (with  
2 degrees being transformed back into ms), representing synchronization accuracy (negative  
3 values indicate that, on average, participants' taps precede the beat (leading), whereas positive  
4 values indicate average taps followed the stimuli (lagging)), and its *length* (ranging from 0 to  
5 1), representing synchronization consistency (with 1 representing perfect consistency); 3) For  
6 the cBAT perception task, data were analyzed with  $d'$  and  $c$ , as well as with response times  
7 (for correct responses) and subjective confidence judgments (scale from 1 to 3).

8

9

10

### 11 **3. Results**

#### 12 **3.1. Electrophysiological data**

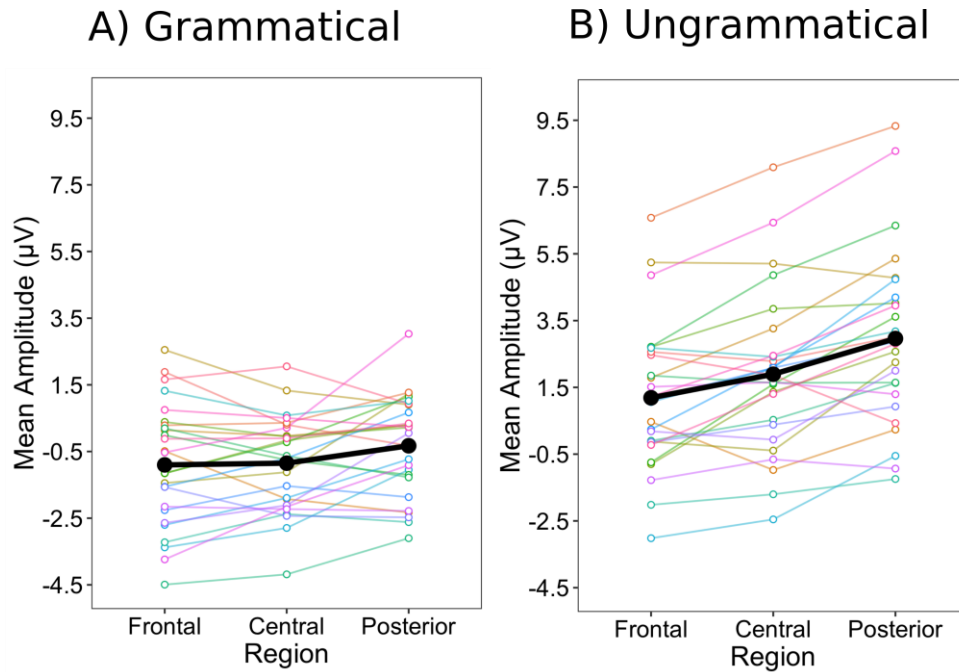
##### 13 *3.1.1. Mean amplitude*

14 The main effect of *Grammaticality* was significant for the ROI analysis,  $F(1, 24) =$   
15  $60.21, p < .001, \eta_p^2 = .72$ , and the midline analysis,  $F(1, 24) = 61.13, p < .001, \eta_p^2 = .72$ , with  
16 a larger P600 for ungrammatical than grammatical sentences. The main effect of *Region* was  
17 significant for the ROI analysis and the midline analysis [ $F(1.23, 29.60) = 15.59, p < .001, \eta_p^2 =$   
18  $.39$ , and  $F(1.33, 31.96) = 7.47, p = .006, \eta_p^2 = .24$ , respectively]: The P600 was larger in  
19 posterior regions than central regions, and larger in central regions than in frontal regions. The  
20 *Grammaticality x Region* interaction was significant for the ROI analysis,  $F(1.21, 29.02) =$   
21  $13.85, p < .001, \eta_p^2 = .37$ , and the midline analysis,  $F(1.36, 32.76) = 16.80, p < .001, \eta_p^2 = .41$ .  
22 Even though significant for all regions, the difference between grammatical and  
23 ungrammatical sentences was strongest for the posterior region (ROI:  $F(1, 24) = 70.32, p <$   
24  $.01, \eta_p^2 = .75$ ; midline:  $F(1, 24) = 77.77, p < .01, \eta_p^2 = .76$ ), followed by the central region

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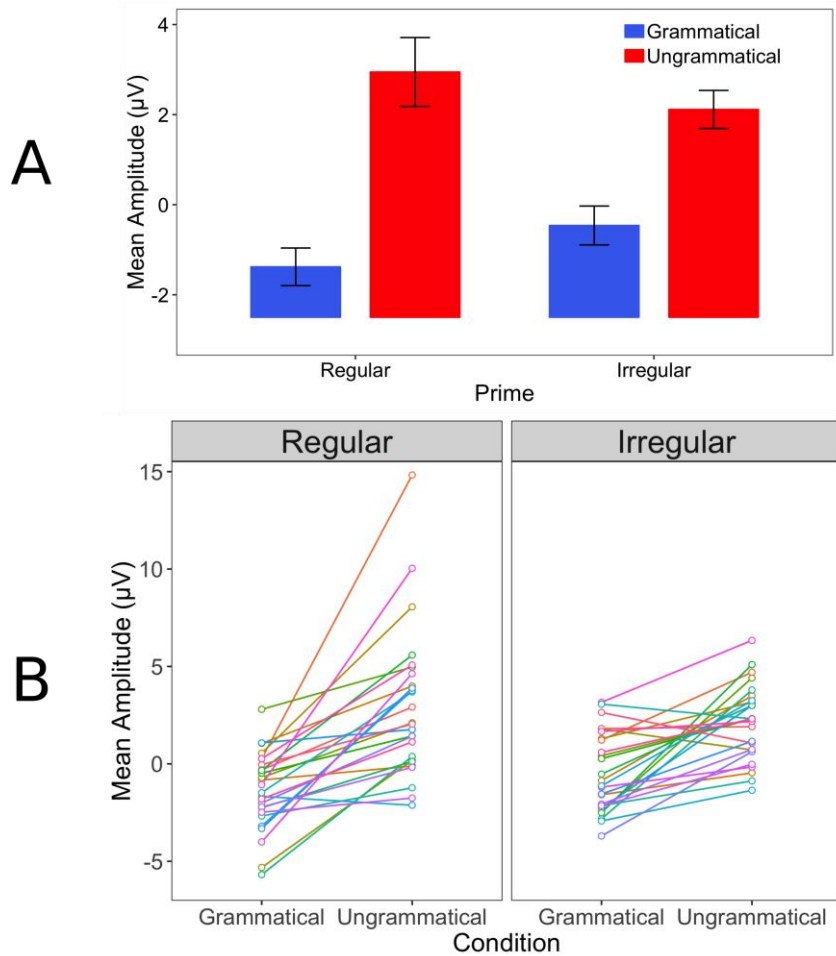
<sup>4</sup> Note that further analyses (including vector length analyses) were based only on trials where the Rayleigh test yielded significant results.

1 (ROI:  $F(1, 24) = 52.63, p < .01, \eta_p^2 = .69$ ; midline:  $F(1, 24) = 57.91, p < .01, \eta_p^2 = .71$ ), and  
 2 then the frontal region (ROI:  $F(1, 24) = 36.20, p < .01, \eta_p^2 = .60$ ; midline:  $F(1, 24) = 34.41, p$   
 3  $< .01, \eta_p^2 = .59$ ) (Figure 2).



4  
 5 Figure 2. Representation of the Region x Grammaticality interaction for the analyses of the  
 6 ROIs in the defined time window. Mean amplitudes (µV) were presented as a function of  
 7 Grammaticality (grammatical vs. ungrammatical) and Region (frontal, central, posterior).  
 8 Individual colored lines represent individual participant data. The black line represents the  
 9 mean.

10  
 11 Most importantly, the factor *Rhythmic Prime* interacted with the factor  
 12 *Grammaticality*: the difference between grammatical and ungrammatical sentences was  
 13 stronger after the regular prime than after the irregular prime (see Figure 3). For the midline  
 14 analysis, this interaction was significant,  $F(1, 24) = 4.78, p = .039, \eta_p^2 = .17$ . For the ROI  
 15 analysis, the same pattern was observed, but less strongly, as reflected in the marginally  
 16 significant interaction,  $F(1, 24) = 3.41, p = .077, \eta_p^2 = .12$ .



1  
2 Figure 3. A) Mean amplitude ( $\mu\text{V}$ ) for grammatical and ungrammatical sentences depending  
3 on Rhythmic Prime (regular, irregular), in the time window for midline electrodes. B)  
4 individual participant data.

5  
6 In addition, for the ROI analysis, there was a main effect of *Hemisphere* (i.e., overall  
7 larger amplitude in the left than right hemisphere),  $F(1, 24) = 9.03, p = .006, \eta_p^2 = .27$ , and it  
8 interacted with *Grammaticality and Region*:  $F(1.74, 41.71) = 5.67, p = .009, \eta_p^2 = .19$ .  
9 Ungrammatical sentences led to increased amplitude in comparison to grammatical sentences,  
10 but differences in laterality (with increased amplitude for the left hemisphere) were observed  
11 only for the grammatical sentences, not the ungrammatical ones. Additionally, amplitude  
12 increased for the parietal regions for ungrammatical sentences for both hemispheres, but for  
13 grammatical sentences only in the right hemisphere. Finally, the ROI analysis also showed a

1 marginally significant interaction between *Rhythmic Prime, Region, Hemisphere and Group*,  
2  $F(1.73, 41.43) = 3.28, p = .054, \eta_p^2 = .12$ . For the control group, the amplitude was stronger in  
3 the left hemisphere than in the right hemisphere in the frontal region after the regular prime,  
4  $F(1, 24) = 4.70, p = .040, \eta_p^2 = .16$ , and in the central region after regular and irregular  
5 primes,  $F(1, 24) = 4.98, p = .035, \eta_p^2 = .16$  and  $F(1, 24) = 6.50, p = .018, \eta_p^2 = .21$ ,  
6 respectively. In the dyslexic group, the amplitude was also stronger numerically in the left  
7 hemisphere, but not significantly in each region.

8

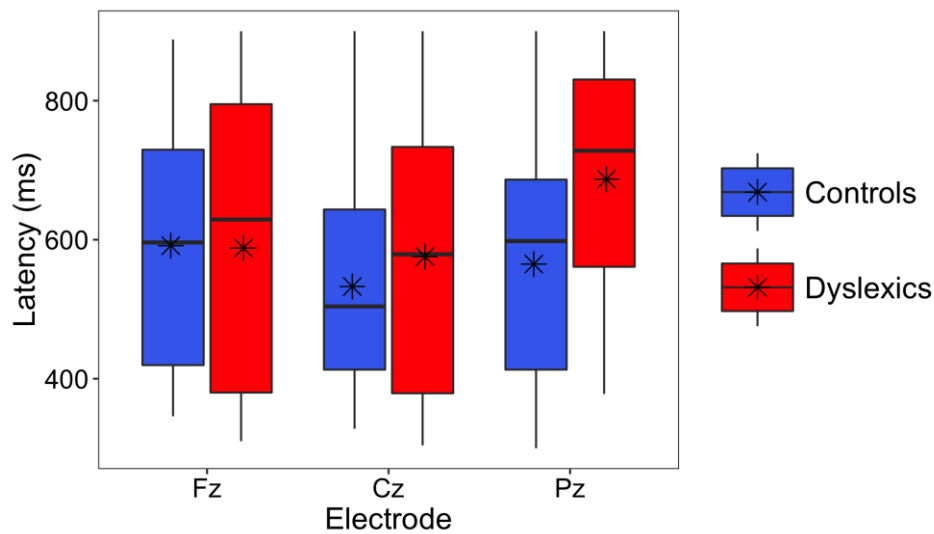
### 9 3.1.2. Peak amplitude and latency

10 The peak *amplitude* midline analysis showed a main effect of *Rhythmic Prime*,  $F(1,$   
11  $24) = 5.96, p = .02, \eta_p^2 = .20$ , and a main effect of *Region*,  $F(2, 48) = 33.09, p < .001, \eta_p^2 =$   
12  $.58$ , revealing that peak amplitudes were larger after regular primes ( $M = 10.07, SD = 4.36$ )  
13 compared to irregular primes ( $M = 7.90, SD = 3.48$ ), and that amplitude increased from the  
14 frontal Fz electrode ( $M = 7.46, SD = 3.15$ ) to the central Cz electrode ( $M = 9.19, SD = 3.40$ )  
15 to the posterior Pz electrode ( $M = 10.30, SD = 3.62$ ). There were no other significant effects,  
16 all  $p$ -values  $> .30$ .

17 For the peak *latency* midline analysis, the main effect of *Region* was significant,  $F(2,$   
18  $48) = 4.71, p = .01, \eta_p^2 = .16$ , and it interacted significantly with *Group*,  $F(2, 48) = 3.67, p =$   
19  $.03, \eta_p^2 = .13$ , as well as with *Rhythmic Prime*,  $F(1.48, 35.46) = 4.98, p = .02, \eta_p^2 = .17$ . The  
20 *Region x Group* interaction (see Figure 4) revealed that dyslexic participants reached the peak  
21 of the P600 later than did the control participants, in particular for the posterior Pz electrode,  
22 while they did not differ for the frontal Fz electrode. The *Region x Rhythmic Prime* interaction  
23 revealed that the latency after regular primes was longer ( $644\text{ms} \pm 189.53$ ) than after irregular  
24 primes ( $535\text{ms} \pm 191.35$ ),  $t(25) = 2.55, p = .017, d = 0.50$ , for the frontal Fz electrode, in  
25 particular, but less so for Cz ( $586\text{ ms} \pm 182$  for regular;  $521\text{ ms} \pm 178$  for irregular,  $p = .13$ ) and



1 not for Pz (610 ms  $\pm$ 193 for regular; 641 ms  $\pm$ 177 for irregular,  $p = .46$ ). Together with the  
 2 peak amplitude analyses, these results suggest that while the peak was higher in amplitude  
 3 after the regular prime, it was reached later after regular primes, in particular for the frontal  
 4 site. Note that the main effects of *Rhythmic Prime* ( $p = .16$ ) and *Group* ( $p = .31$ ) were not  
 5 significant. No other effects were significant, all  $p$ -values  $> .61$ .



7  
 8 **Figure 4.** Latency values for the P600 difference wave across the three midline electrodes  
 9 depending on Group, averaged across both Rhythmic Prime types. Boxplots represent the  
 10 interquartile range of the data (the 25<sup>th</sup> percentile to the 75<sup>th</sup> percentile). The black line  
 11 represents the median, and the asterisk represents the mean. The whiskers of the boxplot  
 12 represent the largest value that lies within 1.5 times the 75<sup>th</sup> or 25<sup>th</sup> percentile respectively.

13  
 14 **3.2. Behavioral data**

15 **3.2.1. Grammaticality judgments during EEG recording**

16 Response accuracy was high overall (97%, see Table 2), but higher for grammatical  
 17 than ungrammatical sentences, as reflected in the main effect of *Grammaticality*,  $F(1, 24) =$   
 18  $7.84$ ,  $p = .010$ ,  $\eta_p^2 = .25$ . Dyslexics performed worse than controls, in particular for  
 19 ungrammatical sentences, but the main effect of *Group*,  $F(1, 24) = 3.45$ ,  $p = .075$ ,  $\eta_p^2 = .13$ ,

1 and its interaction with *Grammaticality*,  $F(1, 24) = 3.86$ ,  $p = .061$ ,  $\eta_p^2 = .14$ , showed only  
 2 marginal significance. There were no other significant effects (all  $p$ -values  $> .26$ ). These  
 3 results were confirmed by  $d'$  analyses:  $d'$  was higher in the control group ( $4.02 \pm 0.43$ ) than  
 4 the dyslexic group ( $3.76 \pm 0.52$ ), even though not significantly,  $F(1, 24) = 2.63$ ,  $p = .12$ ,  $\eta_p^2 =$   
 5  $.10$ . The main effect of *Rhythmic Prime* and its interaction with *Group* were not significant  
 6 ( $p$ -values  $> .38$ ). Response bias  $c$  differed only marginally between the two groups, with  
 7 dyslexics tending more strongly to respond “grammatical” (0.16) than controls (0.03),  $F(1,$   
 8  $24) = 3.43$ ,  $p = .076$ ,  $\eta_p^2 = .13$ . No other effects were significant (all  $p$ -values  $> .45$ ).

9

10 Table 2. Mean percentage of correct responses (and Standard Deviation) for each group  
 11 (control, dyslexic) for grammatical and ungrammatical sentences, presented as a function of  
 12 the Rhythmic Prime (regular, irregular).

	Regular prime		Irregular prime	
	Grammatical sentences	Ungrammatical sentences	Grammatical sentences	Ungrammatical sentences
Dyslexic group	97.92 (2.82)	95.51 (3.28)	97.76 (1.99)	93.75 (5.89)
Control group	97.76 (1.99)	97.60 (3.16)	98.08 (2.32)	97.12 (2.17)

13

### 14 3.2.2. Complex syntax processing post-test

15 Percentages of correct responses were higher for grammatical than ungrammatical  
 16 sentences, as reflected in the main effect of *Grammaticality*,  $F(1, 23) = 28.16$ ,  $p < .001$ ,  $\eta_p^2 =$   
 17  $.55$  (see Table 3). The main effect of *Group* was significant, with lower performance for  
 18 dyslexic participants than control participants,  $F(1, 23) = 17.09$ ,  $p < .001$ ,  $\eta_p^2 = .43$ .  
 19 Dyslexics’ performance was particularly low for ungrammatical sentences, but the interaction  
 20 between *Grammaticality and Group* just fell short of significance,  $F(1, 23) = 3.95$ ,  $p = .059$ ,  
 21  $\eta_p^2 = .15$ .

22  $d'$  was significantly lower in the dyslexic group ( $M = 1.91$ ,  $SD = 0.58$ ) than in the

1 control group ( $M = 2.80$ ,  $SD = 0.62$ ),  $F(1, 23) = 13.96$ ,  $p = .001$ ,  $\eta_p^2 = .38$ . Response bias  $c$   
 2 did not differ between the two groups ( $-0.34$  for dyslexics;  $-0.46$  for controls,  $p = .37$ ). Note  
 3 that  $d'$  for this post-test correlated positively with  $d'$  for the grammaticality judgment task  
 4 during the EEG recording,  $r(25) = .50$ ,  $p = .01$ .

5  
 6 Table 3. Mean percentage of correct responses (and Standard Deviation) for each group  
 7 (control, dyslexic) for grammatical and ungrammatical sentences.

	Grammatical sentences	Ungrammatical sentences
Dyslexic group	90.63 (6.19)	65.97 (19.85)
Control group	95.51 (2.67)	84.89 (7.64)

8  
 9 *3.2.3. Rhythm perception and production*

10 In the production tasks (Table 4), the two participant groups did not differ in the free  
 11 tapping task ( $p$ -values  $> .56$ ) on any of ITI, within-trial variability and CV, or in the  
 12 synchronization task to the isochronous sequences at an IOI of 400 and 700 ms in either  
 13 synchronization accuracy (vector angle) or synchronization consistency (vector length). Only  
 14 for the synchronization task to the isochronous sequence with an IOI of 550 ms was the  
 15 synchronization accuracy (vector angle) of the dyslexics ( $+2$  ms) significantly different from  
 16 that of the controls ( $-72$  ms);  $t(23) = -2.16$ ,  $p = .042$ ,  $d = 0.80$ . Notably, only the taps of  
 17 controls anticipated the beat, suggesting entrainment. For the musical excerpts (cBAT), the  
 18 dyslexics were less precise in their tapping, notably with weaker synchronization consistency  
 19 (vector length) than the controls ( $.72$  versus  $.87$ ;  $t(23) = 2.43$ ,  $p = .023$ ,  $d = 0.89$ ). They also  
 20 anticipated less than did the controls (vector angle), but not significantly,  $t(23) = -1.68$ ,  $p =$   
 21  $.107$ ,  $d = 0.65$ .

22 For the perception part of the cBAT (Table 4), participant groups did not differ  
 23 significantly for  $d'$  or  $c$ . Even though the mean  $d'$  of dyslexics was inferior to that of controls,

1 this difference was not significant,  $t(23) = 1.51, p = .144, d = 0.59$ . However, the groups  
 2 differed significantly in confidence judgments, with dyslexics being less confident in their  
 3 responses,  $t(23) = 2.85, p = .009, d = 1.00$ , and there was a marginally significant difference  
 4 for response times on correct trials, with dyslexics needing more time to respond,  $t(23) = -$   
 5  $1.96, p = .062, d = 0.74$ .

6 For the cBAT production task with musical excerpts, synchronization consistency  
 7 (vector length) correlated positively with  $d'$  for grammaticality judgments during EEG  
 8 recording,  $r(23) = .41, p = .049$  and with  $d'$  for complex syntax processing in the post-test,  
 9  $r(23) = .44, p = .033$ . For the cBAT perception task,  $d'$  correlated positively with  $d'$  for  
 10 grammaticality judgments during the EEG recording,  $r(23) = .42, p = .037$ , but not with  $d'$  for  
 11 complex syntax processing in the post-test,  $p = .23$ .

12

13 Table 4. Mean results (and Standard Deviation) of the dyslexic group and the control group  
 14 for free tapping and for the cBAT.

			Dyslexics		Controls	
			Mean	SD	Mean	SD
Production	Free tapping	Mean	490.73	187.87	514.85	173.72
		SD	17.07	4.33	18.69	8.67
		CV	0.04	0.01	0.04	0.01
	Tapping ISI 400 ms	R	0.87	0.07	0.85	0.05
		Angle	-34.08	8.37	-46.09	9.91
	Tapping ISI 550 ms	R	0.84	0.09	0.87	0.05
		Angle	2.02	24.21	-72.80	22.91
	Tapping ISI 700 ms	R	0.87	0.07	0.85	0.05
		Angle	-5.80	26.52	-51.70	19.44
	Music cBAT	R	0.72	0.05	0.87	0.04
		Angle	-4.60	7.21	-22.59	7.87
	Perception	Music	$d'$	2.60	0.29	3.20

cBAT	<i>c</i>	0.37	0.16	0.37	0.16
	Confidence judgments	2.47	0.07	2.72	0.06
	Correct response times	7488.73	547.62	5838.20	631.39

---

1

2 **4. Discussion**

3         The current EEG study aimed to extend the previously observed rhythmic priming  
4 effects on behavioral grammaticality judgments (Chern et al., 2018; Przybylski et al., 2013) to  
5 the investigation of its underlying electrophysiological correlates for syntax processing in  
6 dyslexic adults and their matched controls. The results showed that the syntax violations in  
7 the ungrammatical sentences evoked a P600 component (in comparison to the grammatical  
8 sentences), which followed a centro-posterior distribution in both participant groups  
9 (Friederici, 2002; Osterhout & Holcomb, 1992). Most importantly, the P600 was enhanced in  
10 both groups when the sentences followed a rhythmic prime that had a regular rhythmic  
11 structure in comparison to an irregular structure. The priming effect was observed for the  
12 mean amplitude in the P600 over the time windows of interest, as well as for the peak  
13 amplitude analyses, with the peak of the difference wave being of larger amplitude after  
14 regular primes than irregular primes.

15         The enhanced P600 following the regular prime is in agreement with previous findings  
16 reported by Kotz et al. (2005) for basal ganglia patients. While these patients did not show the  
17 P600 component related to syntax violations (Kotz et al., 2003), listening to a regular  
18 rhythmic prime has been reported to restore the P600 for sentences presented thereafter (Kotz  
19 et al., 2005). The comparison between the two findings in basal ganglia patients (Kotz et al.,  
20 2003; 2005) suggests potential compensation of impaired syntax processing with rhythmic  
21 stimulation. Our findings extend the rhythmic stimulation effect (i.e., the beneficial effect of

1 regular rhythmic primes) on the P600 from basal ganglia patients to dyslexic adults and their  
2 matched controls. Importantly, this benefit was shown within the same participants  
3 (comparison of irregular to regular prime conditions). These priming effects can be  
4 interpreted within the framework of Dynamic Attending Theory (e.g., Jones, 1976; Large &  
5 Jones, 1999), notably in terms of entrainment that modulates attentional resources and  
6 influences the P600 (e.g., Schmidt-Kassow & Kotz, 2008). The idea is that entrainment to a  
7 regular prime, with its influence on temporal attention and predictive timing, might persist  
8 subsequently via sustained oscillations (e.g., Jones, 1976; Large & Jones, 1999) and facilitate  
9 entrainment to the less regular speech signal. The sustained oscillations may then benefit  
10 sentence processing by facilitating segmentation and sequencing of the speech signal and the  
11 processing of its syntactic structures. Following the entrainment and the rhythmic allocation  
12 of attentional resources over time, the syntactic violation would be perceived as more salient,  
13 leading to the increased P600 observed here (e.g., Jones, 2019; Schmidt-Kassow & Kotz,  
14 2008, 2009). Future research now needs to further investigate the strengths and limits of the  
15 rhythmic priming effect, notably by testing how long the effect of the sustained oscillations  
16 might last over time (e.g., for how many sentences and/or for what duration), how long a  
17 musical prime needs to be to trigger the potential oscillator contribution (see Fiveash et al.,  
18 submitted, for a first attempt) and also whether the effect might extend to other linguistic  
19 processing tasks that require sequencing and segmentation (see Bedoin et al., in preparation,  
20 for a reading task).

21 In the current study, sentences were presented as naturally spoken speech. The  
22 influence of the temporal structure of the musical prime on the naturally spoken speech  
23 signal, which was presented afterwards, extends previous findings that have manipulated the  
24 temporal structure of the speech signal itself. For example, Schmidt-Kassow and Kotz (2008)  
25 manipulated the metrical structure of sentences (regular, irregular) in conjunction with

1 syntactically correct or incorrect sentences. They reported that metrical and syntactic  
2 structures interact in the processes underlying the P600. The regular metric structure of the  
3 incoming continuous speech stream, which allows for predictive timing and coding,  
4 influences syntactic processing, which requires some form of segmentation and sequencing as  
5 well as the prediction of future events. Considering that the P600 is thought to reflect  
6 controlled processes of structural reanalysis and repair (e.g., Hahne & Friederici, 2002), these  
7 and the current findings support the link to Dynamic Attending Theory, suggesting the  
8 involvement of attentional resources distributed over time. Here we show that grammatical  
9 processing is also sensitive to the presence of temporal regularity of a previously presented  
10 musical prime, and not restricted to regularities implemented in the speech signal itself, as  
11 shown previously, thus supporting the interpretation of prime entrainment providing a benefit  
12 to subsequent speech signal analyses.

13         The enhanced P600 (for average amplitude and peak amplitude) after the regular  
14 primes was observed for control participants and dyslexic participants. Both participant  
15 groups benefitted from the regular prime in comparison to the irregular one. The only  
16 amplitude difference that emerged between participant groups in interaction with the prime  
17 was observed in the second half of the time window and related to topography (see  
18 Supplementary materials). For the control participants, the effect of regular compared to  
19 irregular primes on P600 was mainly observed in centro-posterior regions, whereas for  
20 dyslexic participants, it also extended to frontal areas. This activation might reflect extended  
21 recruitment of cerebral networks in pathology, notably to compensate for deficits in syntax  
22 processing and/or temporal processing.

23         The participant groups also differed regarding the latency of the peak of the P600,  
24 with a later peak for dyslexic than for control participants. This finding is in agreement with  
25 previously shown delayed P600 peaks for dyslexic adults in response to morpho-syntactic

1 violations (i.e., subject-verb agreement; Cantiani et al., 2013; Rispens et al., 2006), as used  
2 here. Interestingly, the P600 latency was not influenced by rhythmic prime type for either  
3 group, in contrast to the amplitude-related measures as presented above for both groups.

4       Regarding the P600, Gouvea, Philips, Kazanina & Poeppel (2010) proposed that  
5 latency versus amplitude and duration of the P600 reflect different aspects of processing. In  
6 particular, latency might reflect the time needed to retrieve information related to structural  
7 relations while amplitude and duration of the P600 might reflect the construction and repair of  
8 syntactic relations. While latency of the P600 was delayed in the dyslexic group, latency was  
9 not sensitive to regular versus irregular primes, suggesting that a regular prime does not  
10 appear to facilitate an impaired processing step, that is, reduce the time needed to retrieve  
11 syntactic information in dyslexia. However, the amplitude of the P600 peak as well as its  
12 mean amplitude over the time window (i.e., related to P600 duration) were influenced by the  
13 rhythmic prime for both dyslexic and control participants. This finding is in agreement with  
14 the hypothesized effect of rhythmic primes on cognitive sequencing involving segmentation  
15 and structural processing as well as temporal attention and prediction (e.g., Przybylski et al.,  
16 2013).

17       The enhanced P600 following regular primes was observed for both participant  
18 groups, suggesting that dyslexic individuals can also benefit from regular primes despite  
19 previously reported temporal processing deficits (e.g., Leong & Goswami, 2014; Wolff, 2002  
20 in dyslexic adults; and Muneaux et al., 2004, in dyslexic children). This observation echoes  
21 the findings by Kotz et al. (2005) who reported beneficial effects of a regular musical  
22 stimulus (a marching rhythm) on syntax processing in patients with basal ganglia lesions,  
23 even though deficits in temporal processing have also been reported for this population  
24 (Schwartz, Keller, Patel & Kotz, 2011). For both pathological populations, temporal  
25 processing thus seems to be impaired, but not fully abolished. The decreased functionality



1 may particularly affect language processing as rhythmic structures and regularities are more  
2 subtle and variable than in music, for example. The impaired system might be activated by the  
3 musical prime with its clear metrical structure, providing predictable cues to boost and entrain  
4 internal oscillators, which then also benefit sequencing and temporal segmentation at the  
5 sentence level, enhancing syntax processing (Przybylski et al., 2013). The benefit of a clear  
6 metrical structure (also referred to as “high-groove music” together with other features) in  
7 comparison to low-groove music has been observed also for motor-cueing (Leow, Parrott &  
8 Grahn, 2014).

9         Our additional temporal processing battery testing for perception and production also  
10 revealed some deficits in temporal processing in the dyslexic adults in comparison to the  
11 matched controls. Even though dyslexic participants performed in some tasks as well as non-  
12 musician control participants, deficits were observed for rhythm production and perception.  
13 For the synchronization task with isochronous sequences, dyslexic adults’ production differed  
14 significantly from controls for the tempo of 550 ms IOI. While controls were anticipating  
15 (i.e., responding 72 seconds before the tone onset), dyslexics were not (i.e., responding 2  
16 seconds after the tone onset) – an outcome suggesting less or no entrainment for the dyslexics.  
17 As weaker tapping accuracy was not observed for the two other tempi (400 and 700 ms IOI),  
18 this impairment might be linked to previous data reporting a processing deficit for dyslexics at  
19 a 2 Hz-rate in particular (Power, Colling, Mead, Barnes & Goswami, 2016; Thomson &  
20 Goswami, 2008). The 2 Hz rate is relevant for speech decoding, as discussed by Goswami  
21 (2013; 2018), in particular for the processing of stressed syllables and speech prosody.  
22 Impaired processing of these slow-frequency modulations (i.e., delta rate) might thus be  
23 linked to dyslexics’ language deficits, as postulated in the Temporal Sampling Framework  
24 (Goswami, 2011).

25         In the present study, the beat rate of the musical primes was at 2 Hz, which might thus

1 have boosted oscillatory activity at the related delta rate, benefiting encoding of the low-  
2 frequency speech envelope of the subsequently presented sentences. Future studies need to  
3 further investigate the underlying neural correlates of our observed priming effect and its  
4 relation to the 2 Hz-processing deficit in dyslexia, notably by measuring more specifically  
5 oscillatory activity during the musical prime and subsequent speech processing (Fiveash et al.,  
6 in progress). Promising data for a potential sustained entrainment effect has been reported for  
7 sentences with strong accent structure preceded by an auditory non-verbal rhythmic cue in  
8 healthy young adults (Falk, Lanzilotti & Schön, 2017): After a regular cue with matching  
9 accent structure, phase coupling during sentence processing was stronger than after a non-  
10 matching irregular cue.

11 For the production part of the cBAT based on musical excerpts, dyslexics were less  
12 precise in their tapping (i.e., showed weaker synchronization consistency) than controls, and  
13 average performance further suggested weaker anticipation than controls (even though not  
14 significantly). For the perception part of the cBAT, dyslexics' performance was not  
15 significantly below controls, even though  $d'$  differences were in the direction of weaker  
16 performance for dyslexics. However, dyslexics were significantly less confident in their  
17 responses than controls, and tended to respond more slowly. Further, cBAT production and  
18 perception performance correlated positively with participants' performance on the  
19 grammaticality judgment task. This relation between syntax processing and beat perception  
20 and production is in agreement with previously reported findings for children and adults (e.g.,  
21 Gordon et al., 2015a, b; Woodruff Carr et al., 2014). For example, performance in rhythm  
22 discrimination tasks predicts grammar skills in children (Gordon et al., 2015b).

23 The correlation between rhythmic perception/production performance and  
24 grammaticality judgments emerged even though performance of both controls and dyslexics  
25 was close to ceiling for the syntax task during the EEG recording session. The dyslexic adults

1 processed the morpho-syntactic violations used in the experiment as successfully as the  
2 control participants. This finding is in agreement with Rispens et al. (2006) who also used  
3 subject-verb agreement violations and reported no deficit for dyslexics in the grammaticality  
4 judgments. However, our data as well as that of Rispens et al. (2006) revealed an increased  
5 latency for the P600 peak in the dyslexic participants for the processing of these syntax  
6 violations. When more subtle syntax violations were tested (as in our post-test),  
7 grammaticality judgments of the dyslexic participants were impaired in comparison to the  
8 control group. This performance correlated with the performance in the easier syntax task  
9 during the EEG recording. These data thus confirm some syntactic processing deficits in this  
10 population.

11         The syntax task during the EEG recording session might have been relatively easy  
12 because, as we aimed for reliable EEG recordings, we only used one type of morpho-syntactic  
13 error for the target sentences (time-locking the ERP to the same phoneme), even though these  
14 experimental sentences were combined with gender agreement errors of the filler sentences.  
15 With the ceiling performance for the syntax task during the EEG recording, we did not  
16 observe the beneficial effect of the regular rhythmic prime (over the irregular prime) for the  
17 grammaticality judgments, as previously reported in children (e.g., Przybylski et al., 2013;  
18 Chern et al., 2018; Canette et al., 2020). As the task was somewhat easy for all adults, the  
19 rhythmic prime effect was observed at the electrophysiological level, reflected in the P600  
20 component, but was not observed behaviorally. In a recent study, we have used the more  
21 subtle syntax violations of our post-test in a priming paradigm with healthy adults and have  
22 observed enhanced grammaticality judgments after regular musical primes compared to  
23 irregular primes (Canette et al., in revision). Future research could now apply this refined  
24 syntax material with electrophysiological recordings to dyslexic adults.

25         One caveat to be considered here is that in the present study, we compared regular

1 musical primes to irregular primes, thus leading to the observation of “relative facilitation”, as  
2 previously shown in Przybylski et al. (2013) for children and behavioral measurements. For  
3 behavioral data, subsequent studies have shown better performance after regular primes in  
4 comparison to various baseline conditions, notably environmental sound scenes (Bedoin et al.,  
5 2016) and musical textures without rhythm or silence (Canette et al., under revision). These  
6 findings confirmed that the “relative facilitation” was not solely due to a cost of the irregular  
7 prime, but included also a benefit of the regular prime. Up to now, for the  
8 electrophysiological correlates, we can only refer to “relative facilitation” comparing regular  
9 to irregular primes, and future research is needed to measure neural correlates by including  
10 additional baseline conditions.

11

## 12 **Conclusion**

13 The present study examined the influence of a rhythmic musical prime on the late  
14 P600 evoked-potential associated with grammatical error detection, for dyslexic adults and  
15 matched controls. Our findings revealed an enhanced P600 after regular primes in comparison  
16 to irregular primes for both participant groups. These findings are in agreement with previous  
17 data for basal ganglia patients within a priming-like paradigm (Kotz et al., 2005) and for  
18 healthy controls within metrically manipulated speech (Schmidt-Kassow & Kotz, 2008,  
19 2009). The P600, in particular regarding amplitude and duration (see Gouvea et al., 2010), has  
20 been interpreted as a marker of syntactic integration difficulty (Cantiani et al., 2013), being  
21 involved in syntactic repair (Rispens et al., 2006) and requiring controlled, attentional  
22 processes of structural reanalysis and revision (Hahne & Friederici, 2002). Based on our  
23 observed musical priming effect on the P600, together with the Dynamic Attending Theory  
24 (Jones, 1976), our findings suggest that a regular rhythmic prime benefits temporal attention,  
25 sequencing and structural integration, not only for the processing of the musical prime itself,

1 but also extending to subsequently presented speech material that requires segmentation and  
2 other sequencing steps to process its syntax structures. In line with Kotz et al. (2005) and  
3 Goswami (2011), our findings are promising for the potential benefits of therapeutic  
4 interventions or educational practices based on rhythm and music to boost impaired  
5 oscillatory processes (as in dyslexia, for example) and stimulate language-related processes.  
6 This is consistent with reports that rhythm-based musical training programs can lead to  
7 benefits in phonological processing or reading in dyslexic children (e.g., Overy, 2000;  
8 Flaugnacco et al., 2015) and – more closely related to the paradigm used here – that the  
9 addition of regular musical primes within speech-therapy sessions on syntax processing can  
10 lead to enhanced training benefits, as shown for children with cochlear implants (Bedoin et  
11 al., 2017).

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## Supplementary material

In addition to the reported main analyses over the entire P600 time window [300-900 ms], we ran ANOVAs (for both ROIs and midline electrodes) separately for the early and late parts of the time window, specifically, 300-600 ms and 600-900 ms. This separation was motivated by previous findings showing delayed P600 responses for dyslexic adults in response to morpho-syntactic violations (i.e., subject-verb agreement; Rispens et al., 2006; Cantiani et al., 2013), as used here.

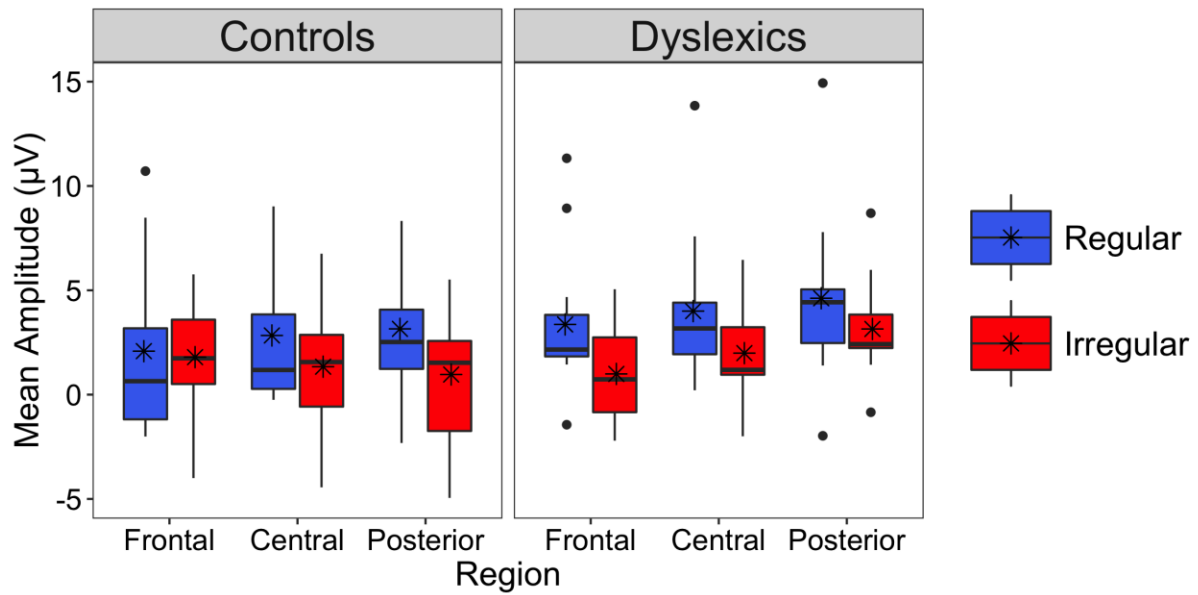
The main effect of *Grammaticality* was significant in the early part of the time window for both the ROI analysis and the midline analysis [ $F(1, 24) = 54.61, p < .001, \eta_p^2 = .69$ , and  $F(1, 24) = 56.78, p < .001, \eta_p^2 = .70$ , respectively], and also in the second part of the window [ $F(1, 24) = 39.34, p < .001, \eta_p^2 = .62$ , and  $F(1, 24) = 43.38, p < .001, \eta_p^2 = .64$ , respectively].

The main effect of *Region* was significant in the early part of the window for both the ROI analysis and the midline analysis [ $F(1.27, 30.43) = 36.15, p < .001, \eta_p^2 = .60$ , and  $F(1.37, 32.80) = 19.75, p < .001, \eta_p^2 = .45$ ] as well as in the second part of the window for the ROI analysis [ $F(1.21, 29.05) = 5.86, p = .017, \eta_p^2 = .20$ ], but not for the midline analysis, although there was a trend in that direction,  $F(1.31, 31.34) = 2.43, p = .122, \eta_p^2 = .09$ .

The factor *Grammaticality* interacted with the factor *Region* in the early part of the window for both the ROI analysis,  $F(1.21, 29.02) = 19.79, p < .001, \eta_p^2 = .45$ , and the midline analysis,  $F(1.36, 32.76) = 16.41, p < .001, \eta_p^2 = .41$ , and the later part of the window, for both the ROI analysis,  $F(1.16, 27.94) = 5.64, p = .021, \eta_p^2 = .19$ , and the midline analysis  $F(1.59, 38.09) = 12.01, p < .001, \eta_p^2 = .33$ .

For the midline analysis, the factor *Rhythmic Prime* interacted with the factor *Grammaticality* significantly for the second part of the time window,  $F(1, 24) = 5.00, p = .034, \eta_p^2 = .17$ , but only marginally significantly for the first part of the time window  $F(1, 24) = 3.68, p = .067, \eta_p^2 = .13$ . For the ROI analysis, the same pattern was observed, but less strongly: the interaction was marginally significant for the second part of the window,  $F(1, 24) = 3.59, p = .070, \eta_p^2 = .13$ , but not for the first part of the window,  $F(1, 24) = 2.73, p = .112$ .

The interaction between *Group*, *Grammaticality* and *Region* was significant for the ROI analysis for the second part of the time window,  $F(1.16, 27.94) = 4.30, p = .042, \eta_p^2 = .15$ , and further interacted with *Rhythmic Prime*, leading to a significant interaction between *Rhythmic Prime*, *Group*, *Grammaticality* and *Region*,  $F(1.58, 38.01) = 6.09, p = .008, \eta_p^2 = .20$ . To further investigate this interaction, we calculated the difference scores between grammatical and ungrammatical conditions (see Figure S1) and ran an ANOVA with *Rhythmic Prime*, *Region* and *Hemisphere* as within-participant factors, and *Group* as a between-participant factor. Based on the interaction between *Rhythmic Prime*, *Group*, and *Region*, we focused on each participant group separately and observed a significant interaction between *Rhythmic Prime* and *Region* in the control group,  $F(1.88, 22.58) = 6.67, p = .006, \eta_p^2 = .36$ , but not in the dyslexic group,  $F(1.16, 13.88) = 1.11, p = .321$ . While the difference between regular and irregular primes was observed for all sites in the dyslexic group, it did not extend to the frontal regions in the control group. Note that these interactions between *Group*, *Grammaticality* and *Region* as well as *Rhythmic Prime*, *Group*, *Grammaticality* and *Region* were also present for midline electrodes, but fell short of significance,  $F(1.59, 38.09) = 2.70, p = .091, \eta_p^2 = .10$  and  $F(1.35, 32.46) = 3.55, p = .057, \eta_p^2 = .13$ , respectively.



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**Figure S1.** Mean amplitude ( $\mu\text{V}$ ) for the difference between grammatical and ungrammatical conditions, for each Group (control, dyslexic), depending on Rhythmic Prime (regular, irregular) and Region (frontal, central, posterior), in the late window (600-900 ms), for ROIs. Boxplots represent the interquartile range of the data (the 25<sup>th</sup> percentile to the 75<sup>th</sup> percentile). The black line represents the median, and the asterix represents the mean. The whiskers of the boxplot represent the largest value that lies within 1.5 times the 75<sup>th</sup> or 25<sup>th</sup> percentile respectively. The black points represent outlying individual participant data.

In addition, for the ROI analysis, there was an interaction between *Rhythmic Prime, Region, Hemisphere and Group* for the second part of the window,  $F(1.85, 44.37) = 4.65, p = .017, \eta_p^2 = .16$ . For the control group, the amplitude was stronger in the left hemisphere than in the right hemisphere in the frontal region after the regular prime,  $p = .029$ , and in the central region after regular and irregular primes,  $p = .015$  and  $p = .013$ , respectively. In the dyslexic group, the amplitude was also stronger numerically in the left hemisphere, but not significantly in each region.

Finally, for the ROI analysis, there was a main effect of *Hemisphere* (i.e., overall larger amplitude in the left than right hemisphere) for the early and late parts of the time window,  $F(1, 24) = 5.23, p = .031, \eta_p^2 = .18$ , and  $F(1, 24) = 10.37, p = .004, \eta_p^2 = .30$ , respectively, and it interacted with *Grammaticality and Region*:  $F(1.88, 45.02) = 7.43, p = .002, \eta_p^2 = .23$  (early window);  $F(1.57, 37.69) = 3.88, p = .039, \eta_p^2 = .14$  (late window), as in the analyses for the full time window.