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Anna Fiveash, Daniele Schön, Laure-Hélène Canette, Benjamin Morillon, Nathalie Bedoin, et al.. A stimulus-brain coupling analysis of regular and irregular rhythms in adults with dyslexia and controls. *Brain and Cognition*, 2020, 140, pp.105531. 10.1016/j.bandc.2020.105531 . hal-02461371

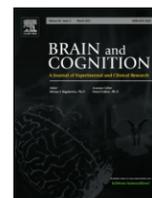
HAL Id: hal-02461371

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Submitted on 30 Jan 2020

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A stimulus-brain coupling analysis of regular and irregular rhythms in adults with dyslexia and controls

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ARTICLE INFO

Keywords

Rhythm
Music
Temporal attention
Neural oscillations
Dyslexia

ABSTRACT

When listening to temporally regular rhythms, most people are able to extract the beat. Evidence suggests that the neural mechanism underlying this ability is the phase alignment of endogenous oscillations to the external stimulus, allowing for the prediction of upcoming events (i.e., dynamic attending). Relatedly, individuals with dyslexia may have deficits in the entrainment of neural oscillations to external stimuli, especially at low frequencies. The current experiment investigated rhythmic processing in adults with dyslexia and matched controls. Regular and irregular rhythms were presented to participants while electroencephalography was recorded. Regular rhythms contained the beat at 2 Hz; while acoustic energy was maximal at 4 Hz and 8 Hz. These stimuli allowed us to investigate whether the brain responds non-linearly to the beat-level of a rhythmic stimulus, and whether beat-based processing differs between dyslexic and control participants. Both groups showed enhanced stimulus-brain coherence for regular compared to irregular rhythms at the frequencies of interest, with an over-representation of the beat-level in the brain compared to the acoustic signal. In addition, we found evidence that controls extracted subtle temporal regularities from irregular stimuli, whereas dyslexics did not. Findings are discussed in relation to dynamic attending theory and rhythmic processing deficits in dyslexia.

1. Introduction

Accumulating empirical evidence suggests that when presented with an external rhythmic stimulus, neural oscillations in the brain align at multiple frequency levels to this stimulus (Doelling & Poeppel, 2015; Fujioka, Zendel, & Ross, 2010; Giraud & Poeppel, 2012; Harding, Sammler, Henry, Large, & Kotz, 2019; Nozaradan, 2014; Nozaradan, Peretz, Missal, & Mouraux, 2011; Stupacher, Wood, & Witte, 2017; Tierney & Kraus, 2014). However, the underlying cognitive and neural basis of the *entrainment* of endogenous neural oscillations to exogenous rhythms is still debated (Haegens & Zion Golumbic, 2018; Novembre & Iannetti, 2018; Rimmele, Morillon, Poeppel, & Arnal, 2018; Zoefel, ten Oever, & Sack, 2018). Although theoretical frameworks of neural entrainment predict that endogenous neural oscillations are actively tracking and predicting external stimuli (e.g., Jones, 2016; Large, 2008; Large & Jones, 1999

), and empirical findings provide evidence that neural entrainment is a mechanism of attentional selection (Barczak et al., 2018; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Morillon & Baillet, 2017; Rimmele et al., 2018), it is argued that the observed neural response might rather be the accumulation of steady-state evoked potentials (SSEPs) responding passively at frequencies present in the external input, without functional meaning (Capilla, Pazo-Alvarez, Darriba, Campo, & Gross, 2011; Keitel, Quigley, & Ruhnau, 2014; Novembre & Iannetti, 2018). Because external rhythmic stimuli often contain frequencies at the expected entrainment rate, these alternative hypotheses are difficult to tease apart. Our present stimulus-brain coupling analysis aims to disentangle these possibilities by determining whether neural entrainment is observed at a beat-level frequency that is weakly present in the stimulus, and whether this entrainment response differs in adults with dyslexia who are suggested to have impairments in neural synchronization (Goswami, 2011; Henry, Herrmann, & Grahn, 2017).

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1.1. Beyond evoked potentials

An influential theory that predicts entrainment beyond SSEPs is the dynamic attending theory (DAT; Jones, 1976, 2016, 2019; Large & Jones, 1999); see also the neural resonance theory; Large, 2008; Large & Snyder, 2009). The DAT suggests that the entrainment of neural oscillations to an external, temporally regular stimulus results in attention directed to expected points in time, leading to temporal predictions and facilitated processing for expected events. In support of the DAT, behavioral research has shown that perceptual judgements are facilitated at predictable points in time (suggesting dynamic attending) for auditory (Barnes & Jones, 2000; Jones, Johnston, & Puente, 2006; Large & Jones, 1999; McAuley & Kidd, 1998; Morillon, Schroeder, Wyart, & Arnal, 2016; Sidiras, Iliadou, Nimatoudis, Reichenbach, & Bamiou, 2017) and visual (Bolger, Trost, & Schön, 2013; Escoffier, Sheng, & Schirmer, 2010; Trapp, Havlicek, Schirmer, & Keller, 2018) stimuli. The continuation of rhythmic prediction after the cessation of the external stimulus suggests an internal oscillator that continues to oscillate, rather than groups of neurons firing only to the regularities in the external stimulus (Doelling, Assaneo, Bevilacqua, Pesaran, & Poeppel, 2019).

Strong evidence for neural oscillations reflecting more than steady-state responses would be the observation of neural oscillations that respond to a cognitive element of the stimulus (i.e., abstracted metrical regularities) at a frequency that is not present or is weakly present in the signal. To investigate whether such oscillations could be observed, Nozaradan et al. (2011) presented participants with a rhythmic stimulus containing a 2.4 Hz beat frequency while participants imagined either a binary (march, 1.2 Hz) or ternary (waltz, 0.8 Hz) meter. The beat frequency and the specific imagined meter frequencies (march or waltz) were represented in the oscillatory brain activity, showing that the neural oscillations were tracking both the physically present beat frequency, and the frequency of a meter that was not physically present in the stimulus but was being imagined by the participants (see similar results in Okawa, Suefusa, & Tanaka, 2017). However, such methods have been questioned as proof of neural entrainment, as the act of directing attention toward an imagined meter or beat may also enhance evoked potentials, and could therefore be misinterpreted as entrainment (e.g., Novembre & Iannetti, 2018).

To reject this interpretation, Tal et al. (2017) manipulated complex auditory rhythmic stimuli so that they contained no acoustic energy at the beat or pulse level. The authors observed oscillatory activity at the beat frequency and phase-locking to the *missing pulse*, suggesting that the neural oscillations were linked to the internally generated beat, and were not just a reflection of the frequency present in the signal (see also Large, Herrera, & Velasco, 2015; Nozaradan, Peretz, & Mouraux, 2012 for converging evidence). These studies, as well as others reported in recent reviews (Haegens & Zion Golumbic, 2018; Zoefel et al., 2018; see also Notbohm, Kurths, & Herrmann, 2016 for evidence in the visual domain), suggest that neural oscillations reflect the entrainment of endogenous oscillations to external stimuli in a non-linear way, i.e., the oscillatory brain response is more than a linear response to frequencies in the external stimulus, and additionally incorporates top-down expectations that play a direct role in perception (Large, 2008; Rimmele et al., 2018). However, to further support the interpretation of endogenous oscillations with functional meaning, Henry et al. (2017) suggested that neural entrainment measures should be linked to behavioral measures, and should be assessed in participant groups expected to respond differently to the stimulus being measured. In the present study, we measured rhythmic production and perception skills in all participants, and addressed this issue in adults with developmental dyslexia.

1.2. Neural oscillations in dyslexia

Individuals with dyslexia primarily have difficulties with reading and spelling, despite normal IQ, intact hearing, and adequate learning environments (Goswami, 2011; Lyon, Shaywitz, & Shaywitz, 2003; Vellutino, Fletcher, Snowling, & Scanlon, 2004). For at least two subtypes of dyslexia (phonological and mixed), a common underlying phonological impairment has been observed (Goswami et al., 2010; Ramus, Marshall, Rosen, & van der Lely, 2013; Ziegler & Goswami, 2005). To explain this phonological deficit, Goswami (2011) proposed the temporal sampling framework of developmental dyslexia (TSF), suggesting that observed deficits in dyslexia are based upon impaired sampling of the speech envelope by neural oscillations. The TSF proposes that impaired neural tracking of slow modulations in the delta (1.5–4 Hz) and theta (4–10 Hz) ranges affects the processing of stressed (~2 Hz) and unstressed (~5 Hz) syllables in dyslexia (Goswami, 2018).

For dyslexic children in particular, impairments have been observed for beat synchronization, musical meter perception, and rhythm production and perception, even in non-linguistic, musical materials (Colling et al., 2017; Flaugnacco et al., 2014; Forgeard et al., 2008; Huss, Verney, Fosker, Mead, & Goswami, 2011; Overy, Nicolson, Fawcett, & Clarke, 2003; Thomson & Goswami, 2008). Based on this evidence, it has been suggested that children with dyslexia may not have a reliable internal representation of the beat in music (Huss et al., 2011). Considering that adults with dyslexia are often reported to have rhythmic processing deficits similar to dyslexic children (Pasquini, Corriveau, & Goswami, 2007; Thomson, Fryer, Maltby, & Goswami, 2006), the internal beat representation might also be impaired in dyslexic adults. However, data for dyslexic adults have shown inconsistent results. For example, Leong and Goswami (2014) found no differences in inter-tap-intervals or p-center alignment between dyslexic and control participants when tapping along to rhythmic sentences, and mixed results in the phase of tapping for dyslexics: depending on the stress pattern of the sentence they were tapping to, the dyslexic group entrained to an earlier phase than controls. Dyslexic adults (often recruited from Universities) may be an even more heterogeneous group than dyslexic children (who are already considered quite heterogeneous; Protopapas, 2014), as they may use different compensation approaches for their dyslexia. One possible compensation strategy is suggested by Cavalli, Duncan, Elbro, El Ahmadi, and Colé (2017), who reported that University students with dyslexia showed persistent phonological impairment, but intact morphological skills compared to controls. The authors suggest that morphological skills may be used to compensate for impaired phonological skills, a suggestion supported by a correlation between reading level and the difference between phonological and morphological skills in the dyslexic students.

As differences in behavioral measures might be masked by compensation strategies, electrophysiological measurements are therefore key to investigate whether dyslexic adults process rhythmic stimuli differently to control participants. When listening to amplitude modulated white noise at different frequencies, dyslexic adults showed impaired inter-trial phase-locking at 2 Hz (but not 4, 10, or 20 Hz) in the right auditory cortex (Hämäläinen, Rupp, Soltész, Szücs, & Goswami, 2012). Converging evidence was obtained with rhythmic tones presented at 2 Hz and 1.5 Hz: while dyslexic adults entrained to the tones at both tempi, inter-trial phase coherence at 2 Hz was significantly reduced in dyslexics compared to controls, and there was evidence that dyslexics also prepared less successfully for upcoming events (Soltész, Szücs, Leong, White, & Goswami, 2013). This evidence converges with previous findings that adult dyslexic participants were less sensitive than controls to auditory stimuli presented at 2 Hz (Witton et

al., 1998). These studies provide preliminary evidence that the entrainment of neural oscillations to slow frequencies may be abnormal in adults and children with dyslexia (supporting the temporal sampling framework, Goswami, 2011, 2018). However, neural entrainment was only measured to isochronous material, and more complex rhythmic stimuli has not been assessed in this population.

1.3. The current study

The current electroencephalography (EEG) analysis investigated beat-based processing of acoustically complex rhythms (regular and irregular) in adults with dyslexia and control participants. The regular rhythms contained the majority of their acoustic energy at 4 Hz, and significantly less at 2 Hz, which represents the beat level in these sequences. The low acoustic energy at the beat level allows us to investigate whether the brain responds primarily to the acoustic energy in the signal, or responds to the perceived beat in a top-down manner. Irregular rhythms contained the same acoustic information as the regular rhythms, but they were randomized so that there were no regularities and therefore no clear pulse or meter. We employed the stimulus-brain coupling measure of *coherence* and predicted that the neural response to the 2 Hz beat level in the regular rhythms should be observed for both groups (suggesting top-down, beat based processing), but may be reduced for dyslexics, based on evidence suggesting impaired beat synchronization and abnormal neural processing at 2 Hz in dyslexia (Colling et al., 2017; Hämäläinen et al., 2012; Soltész et al., 2013).

The current analysis focuses on the musical material (i.e., regular and irregular rhythmic sequences) that were presented interleaved with auditory sentences in a rhythmic priming paradigm. Building on behavioral data showing improved grammaticality judgements after having listened to regular primes in comparison to irregular primes in dyslexic children (Przybylski et al., 2013), Canette et al. (2019) showed that the electrophysiological marker of syntax violation detection, the P600, was enhanced after regular compared to irregular primes in dyslexic adults and matched controls. Canette et al. (2019) only analyzed the ERPs for the sentences presented after the primes. Here, we analyzed the EEG responses to the regular and irregular rhythmic primes in the two populations. We were particularly interested to investigate the brain response to complex rhythmic music in dyslexic adults, as previous research has only used very simple stimuli, such as notably isochronous sequences. This is the first EEG experiment to investigate the brain response of adult dyslexic participants to more complex musical stimuli, which are more ecologically valid.

2. Method

2.1. Participants

Thirteen adults with developmental dyslexia and 13 matched controls participated in the current study. One control participant was removed due to poor data quality (removal was determined prior to analysis based on visual inspection of the data), leaving 13 dyslexic participants (seven women, 10 right-handed, three left-handed; $M_{\text{age}} = 23.2$ years, $SD = 2.95$ years) and 12 control participants (seven women, nine right-handed, three left-handed; $M_{\text{age}} = 22.42$ years, $SD = 2.15$ years) who all reported French as their native language. There was no difference between dyslexics and controls for the number of years of private music lessons (dyslexics: $M = 2.00$ years, $SD = 2.16$, range = 0–7; controls: $M = 1.67$ years, $SD = 2.23$, range = 0–7 years, $p = .72$), years of education (dyslexics: $M = 15.31$, $SD = 0.95$; controls: $M = 14.75$, $SD = 1.55$, $p = .27$), or age ($p = .44$). No participants reported any auditory deficits.

Dyslexic participants were part of a larger group of dyslexic University students involved in previous research (Abadie & Bedoin,

2016; Mazur-Palandre, Abadie, & Bedoin, 2016), who were recruited to assess the persistence of reading difficulties and cognitive and linguistic deficits through a neuropsychological and speech therapy investigation. All dyslexic participants reported that they had been diagnosed as dyslexic and had seen a speech therapist for at least two years during childhood¹. No participants were involved in speech therapy at the time of testing. A neuropsychologist verified that the dyslexic participants had no auditory or visual deficits, no known psychiatric disease or neurological trouble such as epilepsy, head injury, meningitis, or brain tumours, and had no other neurodevelopmental disorder (i.e., developmental language disorder, dyspraxia, dyscalculia, dysgraphia, attention deficit hyperactivity disorder, autism spectrum disorder). Consistent with the diagnosis of dyslexia, all dyslexic participants scored normally on the Raven's matrices test and for reading comprehension (see Supplementary Table 1). The persistence of dyslexia for each participant was confirmed with ECLA16+ (Gola-Asmussen, Lequette, Pouget, Rouyer, & Zorman, 2010), a French battery investigating written language abilities for over 16-year-olds (reading of words, pseudo-words and text; dictation of words and pseudo-words). Pathological scores for orthographic skills and/or reading of irregular words and/or pseudo-words was observed for eleven dyslexic participants. The other two dyslexic participants showed deficits in phonological awareness (usually underlying phonological and mixed dyslexia) and/or a visual-attention deficit (often observed in surface dyslexia). Because of compensatory mechanisms, it is challenging to fully specify the type of dyslexia, especially for University students. However, the dyslexic students in the current study largely had difficulties with phonology, which can be considered to be phonological or mixed forms of dyslexia, as commonly observed within the dyslexia pathology. See Canette et al. (2019) and Supplementary Table 1 for more information.

2.2. Design

The experiment was a 2 (rhythm: regular, irregular) by 2 (sentence: grammatical, ungrammatical) by 2 (group: dyslexics, controls) mixed design. There were 48 experimental blocks, with each block consisting of one rhythm (regular or irregular) followed by six sentences. Rhythms were pseudo-randomized across participants, such that four of the same type of rhythm (regular or irregular) were presented in a row. Initial rhythm order (regular first, irregular first) was counterbalanced across participants. All rhythms were repeated twice across the experimental session, and two of the rhythms were randomly selected to be presented a third time to reach the number of necessary blocks for each participant.

2.3. Stimuli

Rhythms consisted of 11 regular and 11 irregular 34-second audio files. One regular and one irregular rhythm were taken from Przybylski et al. (2013), and the other twenty rhythms were composed by a musicologist using various percussion instruments to create acoustically complex stimuli. All regular rhythms were 120 beats per minute (bpm) and composed to induce a strong beat percept at 2 Hz, corresponding to a 500 ms (ms) inter-beat-interval. Irregular rhythms consisted of the same acoustic events rearranged across time so that there were no regularly recurring elements. Sentences contained five words and were spoken by a native French speaker at a natural production rate. Participants heard 288 unique sentences in total (half grammatical, half un-

¹ No control participants reported seeing a speech therapist, except for one who saw a speech therapist for the correction of tongue position. No controls reported any history of written or spoken disorders of language.

grammatical). For a more detailed presentation of the sentence material, see Canette et al. (2019).

2.4. Procedure

Participants listened to the stimuli through headphones (Pioneer, HDJ-500) in a sound-attenuated booth while concentrating on a fixation cross on the computer screen. They were asked to listen attentively to the music, and then to judge whether each sentence was grammatically correct or incorrect. The experiment lasted for approximately 50 min, and participants had a break every 12 blocks. The temporal processing tests were completed in a second testing session.

2.5. Temporal processing tests

Rhythm perception and production skills were measured using an adaptation of the complex beat alignment test (cBAT, Einarson & Trainor, 2016) and a synchronization task. The cBAT measured perception and production using nine musical excerpts (with inter-beat-intervals ranging from 366 ms to 692 ms). For the perception task of the cBAT, participants were asked to judge whether an isochronous sequence superimposed to the musical excerpt was on-beat or off-beat. For the production task of the cBAT, participants were asked to tap along with the musical excerpt using a drum stick tapping on a drum pad (Roland, V-Drums). For the synchronization task, participants were asked to synchronize with isochronous sequences at three different tempi with inter-onset-intervals (IOIs) of 400 ms, 550 ms, and 700 ms, using the drum pad. Rhythm production for both measures was analyzed with circular statistics (Berens, 2009; Dalla Bella & Sowiński, 2015), resulting in measures of angle (re-transformed into ms) as a measure of precision (e.g., how accurate they were at predicting the beat), and R as a measure of consistency (e.g., how consistently were they close to the beat), with values from 0 to 1 (1 being the most consistent). Full results are reported in Canette et al. (2019). For the current analysis, we focused on tapping at the 550 IOI tempo, as this is the closest to the beat rate of the regular rhythms. Rhythm perception was analyzed with d' and mean confidence judgements. Stimuli were presented via headphones using Presentation software (Neurobehavioral Systems).

2.6. Acoustic analysis of stimuli

Power spectral density (PSD) of the regular and irregular rhythms was calculated with a custom-made program from Falk, Lanzilotti, and Schön (2017) using Matlab (version R2016b, Mathworks) (Fig. 1). Stimulus envelopes were extracted using the Hilbert transform on a zero-padded and spectrally filtered (6th order Butterworth filter, 50-10e4 Hz) acoustic signal, and were used for both the coherence analysis and the PSD calculation. For the stimulus-phase coherence analysis, the acoustic envelopes were downsampled to 250 Hz to match the EEG signal. For the PSD calculation, the acoustic envelopes were transformed into the frequency domain with a frequency resolution of 0.0026 Hz (*pwelch* function with a non-overlapping hanning window).

As shown in Fig. 1, the regular rhythms had high energy at 4 Hz, and less energy at the 2 Hz beat level. To test whether this difference between 4 Hz and 2 Hz was present across all regular stimuli ($N = 11$), the three frequency bins around the peaks of interest were averaged (e.g., the 2 Hz peak was the average of the bins at 1.9977, 2.0003, and 2.0030 Hz) and compared using a paired-samples t -test. The PSD of the regular rhythms was significantly higher at 4 Hz ($M = 52.33$, $SD = 30.23$) compared to 2 Hz ($M = 13.08$, $SD = 18.73$), $t(10) = 3.83$, $p' = 0.009$, $d = 1.16$, supporting the visual interpretation. In addition, because the PSD at 2 Hz was visually similar to the PSD at 1.5 Hz and 3 Hz (neighbouring frequencies unrelated to

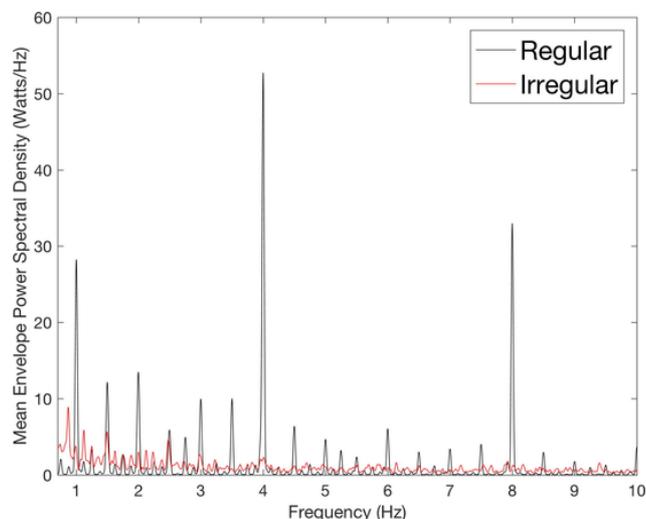


Fig. 1. Power spectral density (PSD) of the temporal envelope of regular (black) and irregular (red) rhythms. Regular rhythms show peaks at 4 Hz and 8 Hz. The beat level (2 Hz, 500 ms inter-beat-interval) is not strongly represented in the acoustic envelope for regular rhythms. The irregular rhythms show no strong peaks across the frequency spectrum, as there were no recurring elements. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

beat tracking and meter), we performed some additional comparisons: if the brain was only tracking the acoustic energy in the signal, then we would expect similar coherence at each of these frequencies. Paired-samples t -tests confirmed non-significant differences between 2 Hz and both 1.5 Hz ($M = 11.75$, $SD = 11.48$, $t(10) = 0.18$, $p' = 1.0$) and 3 Hz ($M = 9.7$, $SD = 11.48$, $t(10) = 0.50$, $p' = 1.0$). Adjusted p values (p') were reported for three multiple comparisons using the Holm-Bonferroni correction. Finally, the peak at 8 Hz in the PSD spectrum is likely to be a mixture of the first harmonic of the 4 Hz signal and the acoustic signal repeating every 125 ms, and is reported for completeness.

2.7. Data recording and analysis

2.7.1. EEG recording

EEG was recorded from 95 Ag/AgCl electrodes (ActiCAP, Brain Products GmbH), arranged according to the international 10–20 system. A BrainAmp amplifier recorded the signal at a resolution of 16 bits and a 500 Hz sampling rate, with an analog low-pass filter at 1000 Hz, and a high-pass filter at 0.016 Hz. The ground electrode was placed at AFz, there was a reference electrode on the nose, and there was an eye-movement monitoring electrode under the right eye. Electrode impedances were kept below 20 k Ω .

2.7.2. EEG pre-processing

Data were pre-processed using Matlab (version R2016b Mathworks) and EEGLAB (version 14.1.1b; Delorme & Makeig, 2004). Periods in the data without stimulus presentation were manually removed. Data were filtered between 0.5 Hz and 40 Hz and downsampled to 250 Hz. ICA was computed and components reflecting artefacts and channel noise were rejected. Data were then re-referenced to the average across all electrodes.

2.7.3. Stimulus-brain coherence

Stimulus-brain coherence provides a measurement of synchronization in the frequency domain between the EEG signal and the acoustic envelope of the stimulus. Coherence takes into account both phase and amplitude similarity between the two signals, and differs as such from phase-locking value, which only takes into account phase information (Alexandrou, Saarinen, Kujala, & Salmelin, 2018; Lepage & Vijayan, 2017; Zoefel, 2018). The current coherence measurement in-

cluding both phase and amplitude is a classic measure to calculate the correspondence between the stimulus and the brain signal (Lepage & Vijayan, 2017), as phase and amplitude are physiologically linked and reflect two aspects of a single phenomenon. Indeed, without amplitude, there can be no phase-locking. If the signal is stronger, it is logical that more phase-locking should also be observed. Taking into account both measures is therefore more reflective of the underlying brain activity than taking into account only one measure. It also improves the signal-to-noise ratio, as the model uses more information. Potential concerns that amplitude may be more influential at lower frequencies according to the $1/f$ power law (see Levitin, Chordia, & Menon, 2012) does not affect the current analysis, as (1) the same measurement is compared across groups, (2) regular and irregular primes are compared at the same frequencies, and (3) lower and higher frequencies are not directly compared in the current analysis. Stimulus-brain coherence is therefore a useful metric for measuring our current brain response of interest. Values for coherence range from 0 to 1, with 0 reflecting no synchronization between the stimulus and the brain signals, and 1 reflecting complete synchronization.

To prepare the data for the calculations, the EEG response to the rhythms was extracted and concatenated to create vectors of the EEG response to (a) all regular rhythms and (b) all irregular rhythms. The corresponding stimulus sound envelopes were concatenated in the same order. Data were then transformed into the frequency domain between 1 and 10 Hz with a 0.1 Hz resolution. Stimulus-brain coherence was calculated for each participant and condition across time (t ranging from 1 to n) according to Formula (1), following Lepage and Vijayan (2017).

$$C_{c,f} = \left| \frac{\sum_{t=1}^n A_{c,f,t}^{stim} A_{c,f,t}^{brain} e^{i(P_{c,f,t}^{stim} - P_{c,f,t}^{brain})}}{\sqrt{\sum_{t=1}^n (A_{c,f,t}^{stim})^2 \cdot \sum_{t=1}^n (A_{c,f,t}^{brain})^2}} \right| \quad (1)$$

where, $C_{c,f}$ corresponds to the estimated coherence at EEG channel c and frequency f (1 to 10 Hz), $A_{c,f,t}^{stim}$ and $P_{c,f,t}^{stim}$ refer to the amplitude and phase angle of the acoustic signal respectively, and $A_{c,f,t}^{brain}$ and $P_{c,f,t}^{brain}$ refer to the amplitude and phase angle of the EEG signal respectively.

2.7.4. Analysis

First, to compare the stimulus-brain coherence to regular and irregular rhythms, a two-tailed paired-samples permutation t -test using the Monte-Carlo estimate was run on the regular *minus* irregular contrast across all frequencies ($n = 91$, corresponding to the frequencies 1:10 Hz at a frequency resolution of 0.1 Hz) and all electrodes ($n = 95$ in Brainstorm (version 3.4; Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011) for each participant group. Multiple comparisons were controlled using the false discovery rate (FDR), and 10,000 permutations were run to ensure a reliable result (Maris & Oostenveld, 2007). Permutation t -tests permute the data a number of times (here 10000) to assess the likelihood that the difference between two conditions could have occurred by chance. Such non-parametric tests are suggested to be especially appropriate for EEG and MEG data that often require multiple comparisons across multiple electrodes and time or frequency points (Maris & Oostenveld, 2007). An unpaired permutation t -test was also run with the same parameters to investigate whether there was a difference in coherence (regular *minus* irregular) between participant groups. Activations at the frequencies of interest (2 Hz, 4 Hz, 8 Hz) were compared to the neighboring frequencies not involved in beat processing (1.5 Hz, 3 Hz). Results are reported with a threshold of $p < .05$ after FDR correction.

Second, a region of interest (ROI) analysis was conducted to investigate the predicted frequencies of interest (2 Hz, 4 Hz, 8 Hz). The ROI was selected based on the electrodes exhibiting the highest difference in coherence for the regular *minus* irregular contrast at the 2 Hz beat level averaged across all participants (shown in Fig. 2: FFC1h, FFC2h, Fz).

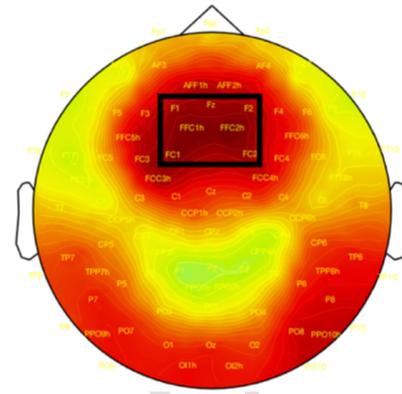


Fig. 2. Region of interest used in the coherence analyses (electrodes FFC1h, FFC2h, F1, F2, Fc1, Fc2, Fz).

FFC2h, F1, F2, Fc1, Fc2, Fz). A mixed ANOVA was conducted with the within-subject factors of frequency (2 Hz, 4 Hz, 8 Hz) and rhythm (regular, irregular), and the between-subjects factor of group (controls, dyslexics). The Greenhouse-Geisser correction was reported in cases where the assumption of sphericity was violated, and two-tailed paired-samples t -tests were controlled for multiple comparisons using the Holm-Bonferroni correction (adjusted p -values reported as p' ; Abdi, 2010). Reported Cohen's d effect sizes are based on the mean difference between conditions divided by the mean standard deviation, with correlation taken into account for paired-samples t -tests (Lakens, 2013).

Third, to investigate potential group differences in coherence for regular and irregular rhythms considered separately, independent-samples permutation t -tests (two-tailed, 10,000 permutations, Monte-Carlo estimate) were run on the ROI across the 91 frequencies (1–10 Hz, resolution of 0.1 Hz) for regular and irregular rhythms respectively. The FDR correction was applied for multiple comparisons at a corrected threshold of $p = 0.05$.

Finally, to investigate potential links between stimulus-brain coherence and rhythm production and perception performance, bivariate correlations (across both groups) were run to investigate whether there were correlations between (a) regular coherence at 2 Hz (beat extraction level), (b) regular coherence at 4 Hz (acoustic level), and (c) irregular coherence at 2.4 Hz (see Section 3.3) with the beat production scores (*angle* and *R*) of the cBAT, the isochronous synchronization task (*angle* and *R*; 550 ms IOI), beat perception accuracy of the cBAT, and mean confidence judgements. Significant correlations were visually checked for outliers. The deletion of outliers in correlation analyses is not advised as it changes the standard error calculation, which can affect the result (Pernet, Wilcox, & Rousselet, 2013). Therefore, significant correlations were re-run with skipped correlation analyses using the robust correlation toolbox (Pernet et al., 2013). This toolbox identifies bivariate outliers and calculates the robust center of the data to avoid the influence of these outliers (Rousseeuw, 1984; Rousseeuw & Driessen, 1999). Skipped correlation analyses are therefore useful to determine the robustness of the correlation, as both Pearson's r and Spearman's r are heavily influenced by outliers (Pernet et al., 2013).

3. Results

3.1. Regular *minus* irregular contrast

Controls and dyslexics showed significantly greater coherence for regular rhythms than for irregular rhythms at the frequencies of interest (2 Hz, 4 Hz, 8 Hz). See Fig. 3 for topographical maps and Fig. 4 for t -values across frequencies. These results suggest that both controls and dyslexics responded to the acoustic energy at 4 Hz and 8 Hz in the stimulus. In addition, both groups showed enhanced coherence to

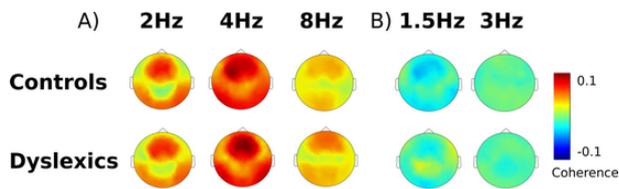


Fig. 3. (A) Topographical maps of coherence for the regular minus irregular contrast at the frequencies of interest—2 Hz (beat level), 4 Hz (acoustic level), 8 Hz (acoustic level). (B) Comparisons at 1.5 Hz and 3 Hz.

the 2 Hz beat level of the regular rhythms, even with reduced acoustic energy at this frequency rate compared to the 4 Hz peak. For controls and dyslexics, differences between regular and irregular stimuli were confined to the three predicted frequencies, and did not extend to 1.5 Hz or 3 Hz, as might be expected with the brain tracking only the acoustic signal. The independent-samples permutation t -test showed no significant differences between controls and dyslexics in coherence across any of the frequencies for the regular *minus* irregular contrast when the FDR correction was applied.

3.2. Region of interest analysis

The coherence values plotted in Fig. 5 show large peaks around the frequencies of interest (2 Hz, 4 Hz, 8 Hz) for regular rhythms, as expected. The ANOVA on the peaks confirmed a main effect of rhythm, $F(1, 23) = 229.00$, $p < .001$, $\eta_p^2 = 0.91$ and a rhythm by frequency interaction, $F(1.39, 31.99) = 10.55$, $p = .001$, $\eta_p^2 = 0.31$. Paired-samples t -tests revealed that the regular rhythm resulted in stronger coherence than the irregular rhythm at 2 Hz ($M_{reg} = 0.15$, $SD_{reg} = 0.05$; $M_{irreg} = 0.07$, $SD_{irreg} = 0.03$), $t(24) = 11.20$, $p < .001$, $d = 2.44$, 4 Hz ($M_{reg} = 0.17$, $SD_{reg} = 0.08$; $M_{irreg} = 0.06$, $SD_{irreg} = 0.03$), $t(24) = 8.93$, $p < .001$, $d = 2.82$, and 8 Hz ($M_{reg} = 0.12$, $SD_{reg} = 0.04$; $M_{irreg} = 0.06$, $SD_{irreg} = 0.03$), $t(24) = 8.56$, $p < .001$, $d = 1.90$. The main effect of group and its interactions were not significant (all p -values > 0.54), suggesting that controls and dyslexics showed similar stimulus-brain coupling across the frequencies of interest. There was no significant main effect of frequency, $F(2, 46) = 2.84$, $p = .07$.

3.3. Individual analyses of regular and irregular rhythms

For the regular rhythms, the independent samples permutation t -test on the ROI coherence values across 1–10 Hz (frequency resolution of 0.1 Hz) showed no differences between controls and dyslexics. For the irregular rhythms, the same analysis showed significantly more coherence to irregular rhythms at 2.3 Hz, 2.4 Hz, and 2.5 Hz for controls than for dyslexics (FDR corrected, adjusted $p = .0016$). The enhanced coherence for controls for irregular rhythms can be seen in the clear peak in Fig. 5 between 2 and 3 Hz, with a visual difference to the dyslexic response until approximately 4 Hz (see zoomed version in Fig. 6A). A small peak can also be observed in the PSD of the irregular stimuli near to 2.5 Hz (peaking at 2.49 Hz), see zoomed version in Fig. 6B. It is therefore possible that controls were sensitive to acoustic regularities in the irregular rhythms within this delta range. Fig. 7 shows the topographic plots of the 2.4 Hz irregular peak for both groups.

3.4. Correlations with behavior

Bivariate correlations for coherence to regular rhythms at 2 Hz and 4 Hz and the measures of beat production and perception revealed only one significant correlation at 2 Hz: the coherence for regular rhythms correlated negatively with the angle measure of the 550 ms IOI isochronous synchronization tapping score ($r(23) = -0.48$, $p = .02$). This correlation suggests that the more predictive participants were in tapping at a 550 ms IOI, the higher coherence they had at the beat level. However, it appeared that the correlation between regular 2 Hz coherence and the isochronous synchronization angle score was driven by two extreme production angle values, which were greater than two standard deviations from the mean ($M = -36.48$, $SD = 95.04$). The skipped correlation analysis identified these two bivariate outliers (one control participant tapping early and one dyslexic participant tapping late), and when these were taken into account the correlation was no longer significant ($r = 0.15$, 95% confidence interval [CI] = $-0.25, 0.54$). We therefore did not find a connection between stimulus-brain coherence for regular rhythms and measures of beat production or perception in the current participant groups.

To investigate the 2.4 Hz peak in the irregular condition shown by controls, bivariate correlations were also run between the beat produc-

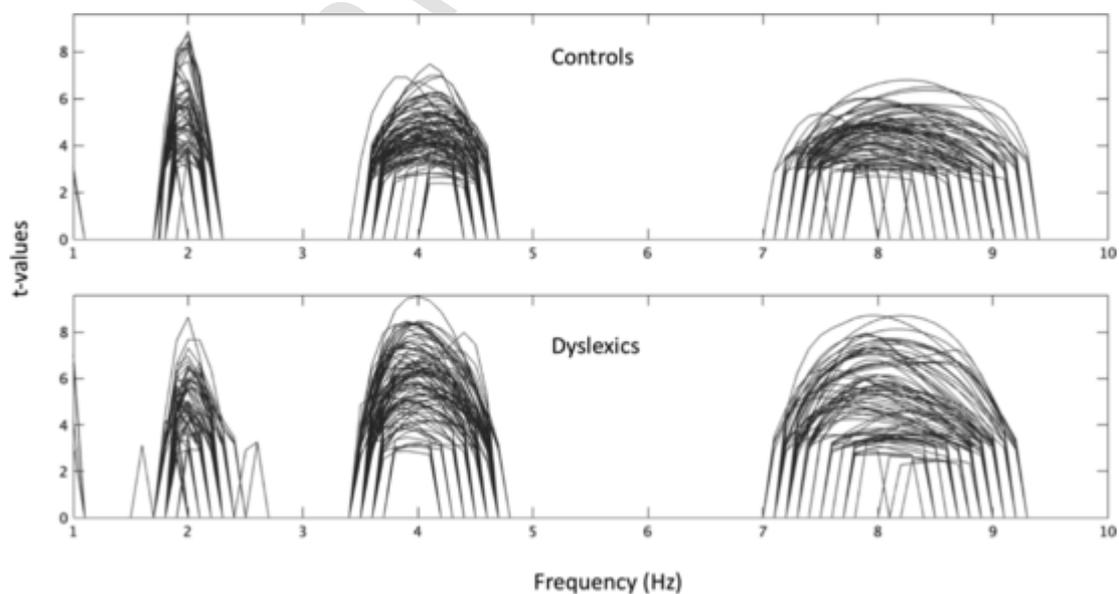


Fig. 4. Significant t -values from the regular $>$ irregular permutation paired-samples t -tests presented as a function of frequency (Hz) for control (top) and dyslexic (bottom) participants. Individual lines reflect individual electrodes. Only t -values where regular $>$ irregular are shown, FDR correction applied across frequencies ($n = 91$) and electrodes ($n = 95$).

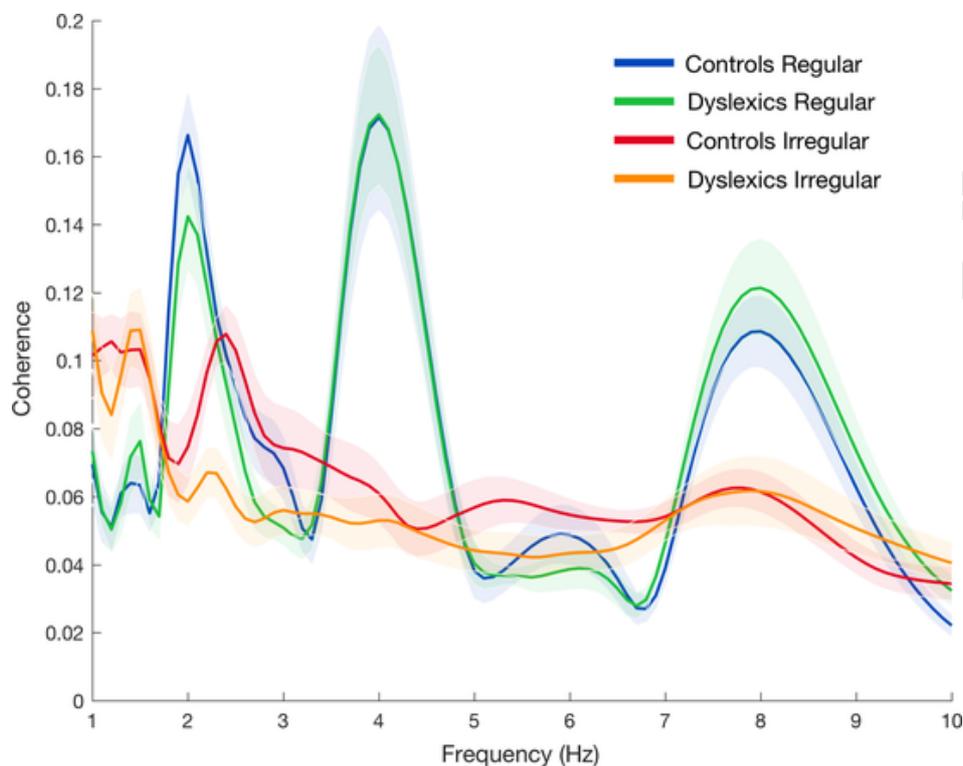


Fig. 5. Stimulus-brain coherence of regular and irregular rhythms presented as a function of frequency (Hz) for control and dyslexic participants. Values based on the region of interest defined in Section 2.7.4. Shaded error bars represent one standard error either side of the mean.

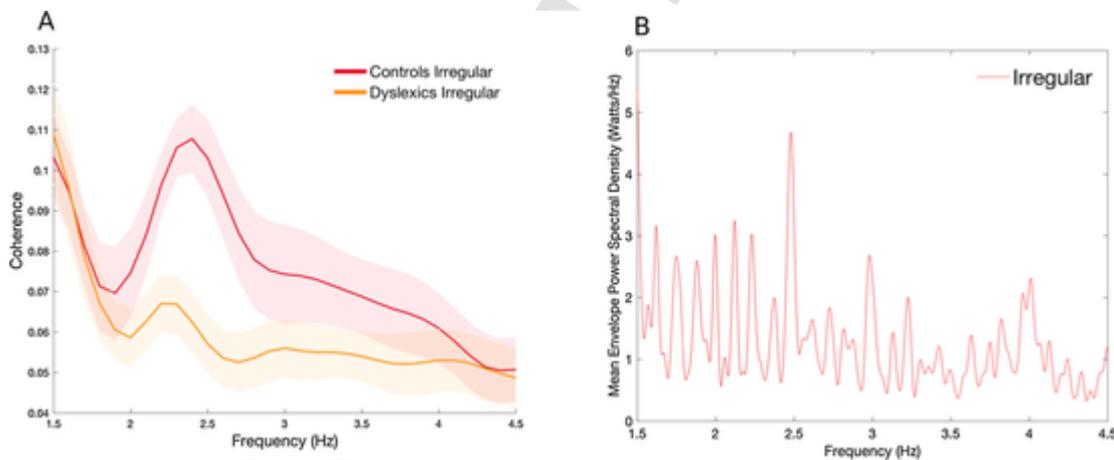


Fig. 6. (A) Stimulus-brain coherence to irregular rhythms between 1.5 and 4 Hz for control and dyslexic participants. Values based on the region of interest defined in Section 2.7.4. Shaded error bars represent one standard error either side of the mean. (B) Power spectral density (PSD) of irregular rhythmic stimuli between 1.5 and 4.5 Hz. Both figures show the irregular data from Fig. 5 and Fig. 1 respectively, zoomed between 1.5 and 4.5 Hz for illustrative purposes.

tion and perception measures and coherence to irregular rhythms at 2.4 Hz. Across participants of both groups, coherence to irregular rhythms at 2.4 Hz negatively correlated with angle in the production measure of the cBAT ($r(23) = -0.56, p = .005$), and with angle for the 550 ms IOI isochronous tapping task ($r(23) = -0.54, p = .01$). To check whether these results were robust, the skipped correlation analysis was run on these two measures as well. One bivariate outlier (a control participant tapping early) was indicated for the cBAT production angle, and the same two outliers as above were identified for the 550 ms IOI isochronous tapping angle measure. When these outliers were taken into account, both correlations remained significant: the correlation between coherence to irregular rhythms at 2.4 Hz and the cBAT production angle ($r = -0.50, CI = -0.81, -0.14$), as well as the 550 ms IOI isochronous tapping production angle ($r = -$

$0.59, CI = -0.87, -0.04$). As can be seen in Fig. 8A and 8B, controls and dyslexics showed a similar pattern, but the distributions indicate a distinction between groups for the irregular coherence response, as reflected in the group difference. These results suggest that participants who were extracting regularities from the irregular rhythms also predicted the beat more strongly, as reflected in the negative *angle* score for two separate measures of beat production.

4. Discussion

The current study investigated the neural response to regular and irregular rhythms in dyslexic adults and matched control participants. We aimed to investigate whether neural entrainment to a regular rhythmic stimulus can be observed at a 2 Hz beat level that is not strongly present in the acoustic material, and whether this response dif-

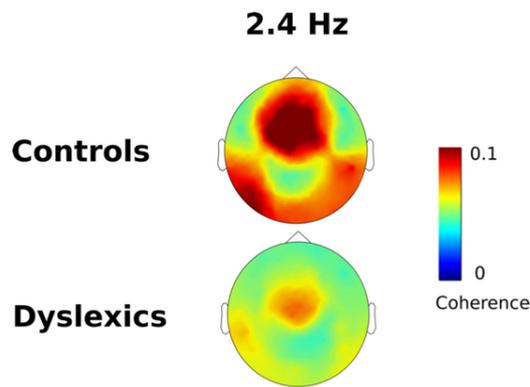


Fig. 7. Coherence for irregular rhythms at 2.4 Hz for controls and dyslexics.

ferred between a group of dyslexic adults and a group of matched controls. We observed significantly enhanced coherence to regular rhythms compared to irregular rhythms for both control and dyslexic participants at 4 Hz (acoustic level), and 8 Hz (acoustic level), as would be expected from the acoustic energy present in the stimulus. In addition, we observed enhanced coherence at 2 Hz, which was not strongly present in the acoustic signal, but corresponded to the beat level of the regular rhythms. The comparison to neighboring frequencies (1.5 Hz and 3 Hz) confirmed that the 2 Hz beat level representation for both dyslexics and controls was greater than would be expected based only on the acoustic signal. This finding suggests a top-down, beat-level construction that is greater than the response to the energy contained in the acoustic signal. Further, we found evidence that control participants were able to extract temporal regularities from the irregular rhythms, whereas dyslexics were not. These results will be discussed below, separating findings related to (1) regular rhythms, (2) irregular rhythms and (3) dyslexia.

4.1. Neural responses to regular rhythms

Our main finding was the clear representation of the 2 Hz frequency, the beat level, in the neural response to regular rhythms for controls and dyslexics, in the absence of strong acoustic energy at this frequency. These results support findings from Nozaradan et al. (2012) and Tal et al. (2017), who showed that beat-related frequencies are enhanced in the brain even with reduced or no acoustic energy at these frequencies. The regular rhythms used in this experiment were not entirely without energy at the 2 Hz level (as can be seen in the PSD analysis). However, neighboring peaks (1.5 Hz and 3 Hz) with similar energy in the signal did not engender enhanced coherence in the

brain for regular compared to irregular stimuli, suggesting that the 2 Hz beat level representation was more than a linear response to the acoustic energy in the stimuli. In contrast to previous research where participants were asked to imagine a given underlying meter (Nozaradan et al., 2011; Okawa et al., 2017), there was no task for participants when listening to the rhythms in the current experiment. Therefore, the enhancement of the 2 Hz beat level could not be because of an explicit instruction to direct attention to a certain beat or meter level.

4.2. Neural responses to irregular rhythms

An unexpected outcome of the present study was the enhanced coherence to irregular rhythms in the delta range observed in control participants but not dyslexic participants. The difference between groups was (significantly) strongest at 2.3, 2.4, and 2.5 Hz; however, the pattern appears to extend from approximately 2–4 Hz, i.e., the upper delta range. These results suggest that the control participants were sensitive to subtle temporal regularities within the irregular rhythms, as a small peak was evident around 2.5 Hz in the PSD of the irregular stimuli. Interestingly, this observation is in agreement with Falk et al. (2017) who observed a similar pattern in the irregular cues and irregular brain response for adult participants (without dyslexia). Falk et al. (2017) used a rhythmically irregular stimulus with a spectral peak around 4.3 Hz and describe a similar peak in the PSD and inter-trial coherence of the EEG data (see Figs. 3 and 6 in Falk et al., 2017). These converging results suggest that even non-musician participants are able to extract subtle temporal regularities from a stimulus that is not temporally regular. In the current experimental context (as in the experimental context in Falk et al., 2017), it is also possible that the interspersed irregular rhythms with the regular rhythms contributed to this effect, as the strong beat in the regular rhythms may have influenced participants to extract temporal regularities from the irregular rhythms. Note that we refrained from a rhythm-by-rhythm analysis of the irregular stimuli, as this would substantially reduce the number of data points for each rhythm, and the experiment was not designed to test this level of detail. However, in light of the present observation, and the converging findings from Falk et al. (2017), it would be interesting to further investigate the processing of rhythmic complexity in controls. Future studies could systematically manipulate the frequency and related amplitude within different types of irregular conditions, and could potentially provide a sensitive measure to reveal deficits in dyslexic adults when presented with temporally complex information.

Interestingly, stimulus-brain coherence at 2.4 Hz for the irregular signal correlated with behavioral measures of beat production. The angle of the tapping performance in the production measure of the

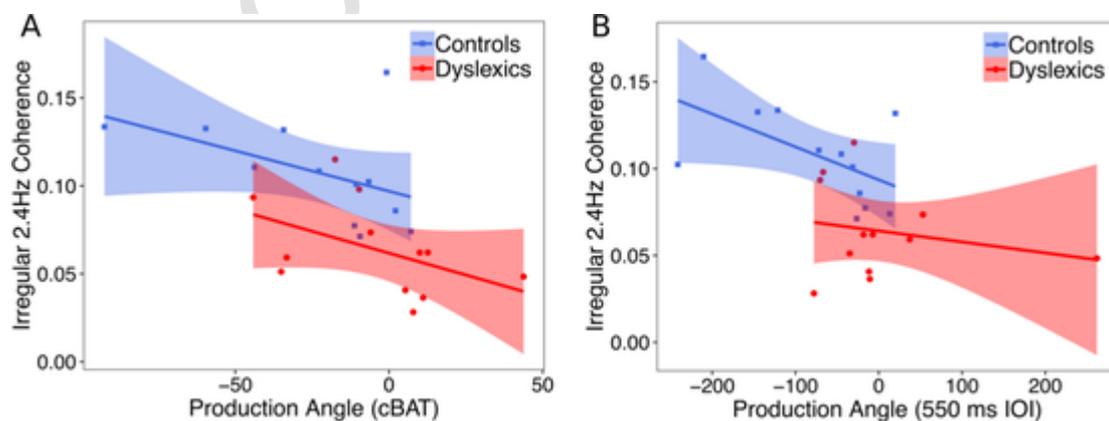


Fig. 8. Correlations between irregular 2.4 Hz coherence and (A) production angle measured by the cBAT, and (B) beat production angle at 550 ms IOI transformed into milliseconds (ms). Regression line fitted with a linear model in R for illustrative purposes, shaded error bars based on standard error of the mean.

cBAT and the angle for isochronous tapping at 550 ms IOI correlated with coherence to the irregular stimuli at 2.4 Hz across both groups, suggesting that participants who were more sensitive to temporal regularities within a complex, irregular stimulus, were also more predictive in their tapping. These correlations suggest that control participants (in particular) were sensitive to subtle acoustic regularities in the irregular rhythms, whereas this was not observed at the group level for dyslexic participants. Future research could manipulate the strength of acoustic energy at a given frequency in irregular rhythms to investigate whether control participants are more likely than dyslexic participants to extract subtle temporal regularities in complex rhythms.

4.3. Beat-Based processing in dyslexia

The current data suggest that dyslexic adults can successfully entrain to and extract the beat from a regular rhythmic stimulus containing a strong meter and complex acoustic information (i.e., multiple percussion instruments playing together), even when the beat is not supported by acoustic energy at that frequency. Although research with dyslexic adults has shown impaired rise-time discrimination (Leong, Hämäläinen, Soltész, & Goswami, 2011; Van Hirtum, Ghesquière, & Wouters, 2019), the majority of research showing impaired beat-based processing and synchronization to an external beat has been conducted with children (e.g., Colling et al., 2017; Huss et al., 2011). Further, the electrophysiological studies that have shown subtle impairments in neural tracking of regular recurring patterns for adults with dyslexia used amplitude modulated white noise in an isochronous sequence and regularly recurring rhythmic tones (Hämäläinen et al., 2012; Soltész et al., 2013), which are arguably less natural and less musical than our material, and have no clear hierarchical metrical structure.

In contrast, the stimuli used in the current experiment were played by instrumental timbres likely more familiar to participants, with a strong meter and numerous congruent cues for beat extraction. Further, the rhythms lasted for about thirty seconds, and thus provided cumulative beat extraction cues for participants, and a longer time period over which to analyze the neural response. With the more natural music stimuli perceived over a longer time frame, it appears that dyslexic participants were able to extract and follow the beat of the regular rhythmic sequences as successfully as controls. It is possible that our strongly metrical stimuli allowed dyslexic participants to overcome any subtle timing deficits, which may be observable with weakly metrical or more artificial material. Future research could therefore manipulate the strength of the metrical structure (e.g., strong, weak as defined in Povel & Essens, 1985) to investigate whether adults with dyslexia show impairments in the processing of weaker metrical structures compared to control participants.

In contrast to the regular rhythms, the two groups differed for the irregular rhythms: dyslexics were not sensitive to subtle temporal regularities in the way that controls were. Based on these findings, future research should now manipulate the strength of recurring elements within irregular sequences and investigate at what stage dyslexic adults begin to extract temporal regularities. Our results therefore suggest that adults with dyslexia were able to extract the beat from a regular rhythmic sequence, but that they were not able to extract temporal regularities in more complex rhythmic sequences without a clear underlying pulse, as is largely the case in the speech signal.

5. Conclusion

The current study investigated brain responses to regular and irregular rhythmic sequences in dyslexic adults and matched control participants. The results showed that both participant groups responded to the regular rhythms at the expected frequencies that were present in the acoustic signal. Most interestingly, strong coherence was ob-

served at the beat level, despite low acoustic energy at this frequency. These results suggest that the brain follows and extracts the beat from rhythms in a top-down manner, and that the observed neural response consists of more than steady-state evoked responses to acoustic energy in the signal. In addition, we found evidence that the control group was sensitive to temporal regularity in the irregular rhythms, whereas the dyslexic group was not. These findings support the dynamic attending theory and suggest that adult dyslexic participants are able to represent temporally regular rhythms, but appear to have difficulties extracting regularities from more complex, irregular stimuli compared to control participants.

6. Ethics statement

All participants provided written, informed consent. The experiment was conducted in accordance with the Declaration of Helsinki and was approved by the French ethics committee CPP (CPP Sud-Est II, 2007-009-3: *Processing of Music and Language*).

Acknowledgements

This research was supported by a grant from ANR to BT and NB (Grant Agreement number ANR-16-CE28-0012). The team “Auditory cognition and psychoacoustics” is part of the LabEx CeLyA (“Centre Lyonnais d’Acoustique”, ANR-10-LABX-60) and the Laboratory Dynamique Du Langage is part of the LabEx ASLAN (ANR-10-LABEX-81). BM and DS were supported by grants ANR-16-CONV-0002 (ILCB), ANR-11-LABX-0036 (BLRI) and the Excellence Initiative of Aix-Marseille University (A*MIDEX).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandc.2020.105531>.

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