



The relationship between entrainment dynamics and reading fluency assessed by sensorimotor perturbation

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Abstract

A consistent relationship has been found between rhythmic processing and reading skills. Impairment of the ability to entrain movements to an auditory rhythm in clinical populations with language-related deficits, such as children with developmental dyslexia, has been found in both behavioral and neural studies. In this study, we explored the relationship between rhythmic entrainment, behavioral synchronization, reading fluency, and reading comprehension in neurotypical English- and Mandarin-speaking adults. First, we examined entrainment stability by asking participants to coordinate taps with an auditory metronome in which unpredictable perturbations were introduced to disrupt entrainment. Next, we assessed behavioral synchronization by asking participants to coordinate taps with the syllables they produced while reading sentences as naturally as possible (tap to syllable task). Finally, we measured reading fluency and reading comprehension for native English and native Mandarin speakers. Stability of entrainment correlated strongly with tap to syllable task performance and with reading fluency, and both findings generalized across English and Mandarin speakers.

Keywords Entrainment · Synchronization · Dynamical system · Auditory cognition · Reading

Introduction

A number of studies have found a relation between musical rhythm processing and reading skills (see reviews: Ladányi et al. 2020; Nayak et al. 2021; Ozernov-Palchik and Patel 2018), which is thought to reflect the rhythmic nature of both music and language. The link between reading and rhythm has often been attributed to a common need for precise timing (e.g., Goswami et al. 2002; Huss et al. 2011; Tierney

and Kraus 2013b, 2014; Wolff 2002; Woodruff Carr et al. 2016). In the present work, we consider this idea in terms of the ability to maintain a stable oscillation and to flexibly adapt to changes in exogenous rhythms, as may be important when tracking acoustic features critical to developing robust phonological representations. The current study uses a perturbation paradigm, internal and external entrainment tasks, and standardized reading assessments in neurotypical adults to measure the relationship between behavioral entrainment, synchronization, and reading skills. This perturbation paradigm, with its relevance to theoretical and modeling work, provides a more rigorous characterization of the role of timing mechanisms in reading.

Rhythm entrainment and reading ability

Entrainment has been defined as the response of one or more oscillations to an external rhythm, bringing the oscillation(s) into synchrony with the external rhythm (Lakatos et al. 2019; Pikovsky et al. 2001). In behavioral entrainment, individuals coordinate movements with rhythmic stimuli, such as isochronous rhythms (DeGuzman and Kelso 1991; Repp 2005), music (Large 2000), and speech (Fridriksson et al. 2012; Lacrois et al. 2019). Neuronal entrainment (Lakatos et al.

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2019) is a critical factor in behavioral entrainment (Large et al. 2015; Nozaradan et al. 2015; Tal et al. 2017), and it is important in the perception of music and rhythm (Nozaradan et al. 2011; Repp et al. 2008; Tal et al. 2017), and in the perception and intelligibility of speech (Giraud and Poeppel 2012; Mai et al. 2016; Meyer 2018; Peelle and Davis 2012). Entrainment is closely related to synchronization, the bidirectional coupling of oscillators exerting a mutual influence on one another (Lakatos et al. 2019; Pikovsky et al. 2001). Behavioral synchronization can be observed in the coordination of limbs (Haken et al. 1985; Treffner and Turvey 1993), individuals (Goodman et al. 2005; Konvalinka et al. 2010), and in the coordination between hand movements and syllables (Stahl et al. 2011). Neuronal synchronization of anatomically distributed networks is necessary for behavioral synchronization (Jantzen et al. 2018; Mayville et al. 1999; Palva and Palva 2018) and more generally is thought to underlie large-scale functional integration during complex activities (Buzsáki et al. 2013; Buzsáki and Draguhn 2004; Varela et al. 2016) such as speaking or reading (Meyer 2018).

The ability to entrain behaviorally and neurally in non-linguistic rhythm perception and production tasks has been linked to pre-literacy and literacy skills across the lifespan. Behaviorally, rhythm performance or degree of entrainment is most often measured as variability in inter-tap intervals when producing rapid or paced motor sequences. From preschool, poorer entrainment has been related to poorer pre-literacy skills and less precise neural encoding of the speech syllable envelope (Woodruff Carr et al. 2014). Similar relationships have been found in neural and behavioral entrainment and word reading and decoding skills in neurotypical children (Bonacina et al. 2018), adolescents (Tierney and Kraus 2013a, b; Woodruff Carr et al. 2017), and young adults (Carello et al. 2002). Longitudinal studies have also shown a link between children's entrainment performance in grade one and later word reading and decoding skills through grade five (David et al. 2007). Similar findings were reported by Moritz et al. (2013), also on English speaking children, and by Dellatolas et al. (2009) on French speaking children. Deficits in rhythmic skills have also been observed in populations with different types of reading deficits across different languages (Alcock et al. 2000a, b). Further studies have shown a consistent positive relationship between the deficits in clinical populations' reading ability and the deficits in their rhythmic ability (Corriveau and Goswami 2009; Goswami et al. 2002; Wolff 2002). For example, Alcock et al. (2000a, b) found that members of the KE family, in which a developmental disorder of speech and language is inherited, performed worse in rhythm perception/production tasks, but not in pitch and melody perception/production task, compared to the control group. There is also evidence that poor rhythm entrainment and poor reading ability co-segregate in

families (Gooch et al. 2014; Viholainen et al. 2002, 2006; Wolff 1999). Family and twin-based methods have found moderate heritability of musicality and language, with some recent evidence showing certain musicality is genetically associated with certain language skills (Gustavson et al. 2021; see Nayak et al. 2021 for a review; Wesseldijk et al. 2021), suggesting the connection between entrainment and reading may have a common biological basis driven in part by a common genetic factor (Sodini et al. 2018).

Dynamics of entrainment

The link between reading and rhythm has broadly been attributed to a common need for precise timing (e.g., Goswami et al. 2002; Huss et al. 2011; Tierney and Kraus 2013b, 2014; Wolff 2002; Woodruff Carr et al. 2016). In the present work, we consider this idea in terms of the ability to maintain a stable oscillation and to flexibly adapt to changes in exogenous rhythms, as may be important when tracking acoustic features critical to developing robust phonological representations. The ability of any oscillatory system to maintain an entrained or synchronized state is called stability. The most direct way to measure stability of entrainment is to bring the system into steady state (i.e., an attractor state), deliver a phase or frequency perturbation, and observe the system's relaxation back to steady state (e.g., Pikovsky et al. 2001). Greater stability means the system can recover smoothly from larger perturbations, it can relax back to the attractor more quickly after a perturbation and, in the presence of noise, a more stable state exhibits less variability (Pikovsky et al. 2003). Empirical perturbation methodologies have successfully been used to characterize stability of entrainment in healthy young adults (Large et al. 2002; Repp 2005), adults with rhythmic deficits (Palmer et al. 2014), and animals known to synchronize to the beat of music (Rouse et al. 2016). As discussed above, several studies have found atypical sensorimotor synchronization in children with reading deficits and in relation to reading skills in neurotypical populations, usually operationalized as variability in inter-tap intervals. This variability may arise from multiple sources. Although the past literature has not approached this finding from a dynamical systems perspective, inter-tap variability can be considered as measuring the variability of an entrained system, which may reflect noise-induced perturbations of the system (i.e., from unspecified endogenous brain activity) or that the system has chaotic dynamics (e.g., the van der Pol oscillator). Although variability provides an empirical metric for evaluating a model of behavior, it does not directly help us characterize the parameters of the model. A perturbation paradigm, on the other hand, allows us to measure how quickly a system can return to a stable, entrained state in response to a controlled

perturbation. This measurement provides a useful parameter that constrains possible models of brain and behavior.

Wolff (2002) showed that, when tapping to an isochronous metronome, children with dyslexia showed larger negative mean asynchrony (NMA) than their control group, and when tapping to a metronome with tempo change, children with dyslexia showed longer recovery time compared to their age-matched control group. In the present work, we examine the dynamics of recovering synchronization, i.e., entrainment stability, to a perturbed rhythm, under various types of perturbations and in an adult neurotypical population. Using a tap to syllable task, in which participants tap to the syllable onset time of their own speech, as an index of behavioral synchronization, we also examine the relationship between entrainment stability and behavioral synchronization. Finally, we test the relationship with oral reading fluency and comprehension in both native English and native Mandarin speakers.

Methods

Participants

Thirty-four neurotypical participants were recruited from the University of Connecticut community (22 females; age range 18–67 years, mean = 27, *sd* = 9). All participants were right-handed and either native English (*n* = 17), or native Mandarin speakers (*n* = 17). All Mandarin speakers were international university students at UConn. Their English skills were not tested during this study, but all met a University criterion for spoken and written English language proficiency, e.g., achieving a score > 22/30 ('high-intermediate' or 'advanced') on each section of the Test of English as a Foreign Language. Some participants had experience playing musical instruments including string, keyboard, and wind instruments. Years of playing ranged from 0 to 25 years (mean = 5, *sd* = 5.7), and years of music theory training ranged from 0 to 17 years (mean = 1.6, *sd* = 3.1).

Tasks

Behavioral entrainment

Isochronous rhythms with unpredictable phase and tempo perturbations were generated in MATLAB at different base tempi with different perturbation types, sizes, and directions. There were three base tempi: 2 Hz, 2.5 Hz, and 3 Hz. All rhythms started with at least 4 tones at isochronous intervals, and the perturbation occurred at a pseudorandomized place within the following 8 tones. There were always 15 tones after the perturbation. For phase perturbations, only one inter-onset interval (IOI) at the perturbation site was

changed, with the rest of the IOIs staying the same as the IOIs before the perturbation. For tempo perturbations, all IOIs after the perturbation were changed, creating a new tempo. Thus phase perturbations briefly accelerate the system, while tempo, or step, perturbations require adaptation to a new stable frequency. The IOI change had three different sizes: 8%, 15%, and 25% of the original IOI, and two directions: positive (slowing down) and negative (speeding up). This created 36 conditions in all: 3 tempi × 2 types × 3 sizes × 2 directions. Participants were instructed to synchronize their taps to every tone in the stimuli as accurately as they can.

Metric test

Participants completed the Metric Test from The Montreal Battery of Evaluation of Amusia (Peretz et al. 2003). In the Metric Test, 30 short melodic sequences were presented to participants one at a time in a pseudorandomized order. Half of the sequences are written in duple meter and half in triple meter. Participants were asked to judge whether what they heard was a march or a waltz, and then to press a key to make their decision as soon as they were confident about their choice. This task has been used to identify beat-deaf individuals, who have a less than 70% accuracy on this task (Palmer et al. 2014).

Tap to syllable task

This task was adapted from the melodic intonation therapy technique, which is a widely known method of improving speech fluency. The original technique involves 1) "singing" or intoning the to-be-produced speech, and 2) synchronizing hand movements with the syllables as they are produced (Hurkmans et al. 2012; Schlaug et al. 2008; Van Der Meulen et al. 2016; Wan et al. 2014; Zumbansen et al. 2014a, b). However, there was no intonation aspect of this task in the current study. First, participants saw a sentence on the screen and were asked to familiarize themselves with it by reading the sentence aloud. Then, participants were asked to produce the sentence as naturally as possible (the text remained on the screen) while to synchronizing taps with the onset of every syllable.

Language assessments

Language assessments were different for English speakers and Mandarin speakers. The English speakers completed tests of word reading fluency and passage reading fluency and comprehension. Word reading fluency was assessed using the Word-Letter ID and Word Attack subtests from WJIII (Woodcock et al. 2001). In the Word-Letter ID and Word Attack subtests, participants read a list of words and

nonwords out loud, respectively, with no time constraints. Passage reading fluency and comprehension were assessed using the Gray Oral Reading Test (GORT, Wiederholt and Bryant 2012). The GORT is a timed task in which participants read aloud passages at different difficulty levels. Participants then answer comprehension questions. The GORT is scored on fluency and comprehension. The fluency score takes into account the time to finish reading the passage and the number of errors made during reading. The comprehension score is based on the number of correct answers on the comprehension questions.

For Mandarin speakers, tests of word reading fluency and sentence comprehension were administered. The word reading fluency test consisted of 100 two-character words, and participants were required to read every word from the beginning to the end as quickly and as accurately as possible. Fluency was assessed as the time to finish reading and the number of mistakes made (Li et al. 2017). For the sentence comprehension test, participants silently read a list of sentences. After reading each sentence, they made a judgment about the truth value of the sentence. Participants had 3 min in total to finish judging as many sentences as possible. Comprehension was assessed as the number of correct judgements (Song et al. 2015).

Procedure

The experiment was completed on 2 separate days. Across the 2 days, participants completed (1) the metric test, (2) the behavioral entrainment task (four blocks), (3) tap to syllable task (two blocks), and (4) the language assessments. For English speakers, the language assessments included word reading fluency, and passage reading fluency and comprehension. For Mandarin speakers, the language assessments included word reading fluency and sentence reading comprehension. All participants completed all the tasks in the same order. All methods and procedures were approved by the IRB at the University of Connecticut.

Analysis

Behavioral entrainment

The phase of each tap relative to the nearest stimulus tone (Large et al. 2002) was computed according to the formula

$$\varphi_n = \frac{T_n - S_n}{S_{n+1} - S_n} \pmod{0.5, 0.5, 1}, \quad (1)$$

in which T_n is the time of tap n and S_n is the time of the stimulus event closest to the tap n .

Relative phase was then averaged for each participant across the four trials in each condition (four trials for each

of 36 conditions). Relative phases were analyzed in three different time windows: (1) pre-perturbation (N = number of taps before the perturbation point), (2) perturbation/relaxation (N = 8), and (3) post-perturbation (N = 8).

Relaxation time is a good index of entrainment stability (Large et al. 2002; Pikovsky et al. 2001). We used the synchronization coefficient (SC) during the relaxation window as a sensitive measure of relaxation time, to compare entrainment stability with performance on the other tasks. SC was computed according to the formula

$$SC = \frac{1}{N} \left| \sum_{n=1}^N e^{i(\varphi_n)} \right|, \quad (2)$$

in which N is the number of taps during the relaxation window.

Stability of entrainment

Stability of entrainment was defined as the SC during the perturbation/relaxation window. For each participant, we computed SC (1) first, across all conditions, and then for each perturbation condition separately: (2) tempo, (3) type, (4) size, and (5) direction. Thus, an SC was computed for the 8 relative phases in the relaxation window in each trial (1) for all conditions, and separately (2–5) for each different condition, for each participant. The effect of perturbation on SC within the relaxation window was modeled using a series of hierarchical linear mixed-effects regression models, implemented in the lme4 package (Bates et al. 2015) in R. A base model was built by adding age, language, and music experience sequentially as fixed effects, while keeping participants as a random effect. The base model is summarized in Table 1. Comparisons between the base model and each of the perturbation models are summarized in Table 2 and described in more detail in the results section. Kruskal–Wallis or Wilcoxon tests were conducted for main effects due to the non-normal nature of the entrainment data distribution [see Fig. 2 (ggpubr package in R, Kassambara and Kassambara 2020)]. Wilcoxon tests were conducted for post hoc pairwise comparisons reported in the following sections. All p values for post hoc pairwise comparisons were adjusted using the Bonferroni method.

Tap to syllable task

Each syllable onset time (SOT) was manually marked using Pratt (Boersma 2001) across all sentences. First, a normalized asynchrony (NA) was calculated to measure the variability of each tap-syllable coordination using the following equation:

$$NA = \frac{SOT_n - T_n}{T_{n+1} - T_n}. \quad (3)$$

This measure is essentially similar to relative phase, but it does not assume periodicity. We then calculated the standard deviation of NA for each participant.

To test the relationship between entrainment stability (measured by SC in the behavioral entrainment task) and normalized asynchrony in the tap to syllable task, a series of hierarchical multiple regressions were conducted in R. Similarly to the stability of entrainment analysis above, age, language, musical experience, and metric test score were entered as fixed effect on the first step. Additional models were built to test the relationship between entrainment stability in different conditions and tap to syllable task performance over and above that explained by participants' age, language, and musical experience. Details of the models are described in the results section.

Language assessments

English speakers: Word reading fluency was measured by adding the raw scores from the Letter-Word ID and Word Attack subtests forming a basic reading composite score (Tierney and Kraus 2013b). Higher score indicates better performance. Passage reading fluency and comprehension were measured using raw scores of fluency and comprehension on the GORT, respectively. Higher score indicates better performance on both tests. The use of raw scores for all language assessments makes the analysis of Mandarin language measures, for which standardized scores are not available, more comparable to the English assessments. For both languages, age-related variance in reading skills is accounted for by the age predictor in the base model.

Mandarin speakers: To assess word reading fluency, we used inverse efficiency scores (IES, Vandierendonck 2017). The IES takes into account time required to finish reading all words, as well as the number of errors; thus, higher scores indicate poorer performance. Because this measure is an inverse measure of fluency, we refer to it henceforth as word reading disfluency. To assess sentence reading comprehension, we measured how many sentences the participants judged correctly within the 3 min time limit. In this case, higher scores indicate better performance.

We used a series of hierarchical multiple regression models to test whether entrainment stability explains variance in reading fluency and comprehension over and above that explained by participants' age and musical experience. Age, musical experience, and metric test score were entered as fixed effects on the first step. Then, two additional sets of models were built to test the relationship between (1) entrainment stability and English language measurements,

and (2) entrainment stability and Mandarin language measurements, with the outcomes of (1) English word reading fluency, (2) English passage reading fluency, (3) English passage reading comprehension, (4) Mandarin word reading disfluency, and (5) Mandarin sentence reading comprehension. For each set of models, entrainment stability in different conditions was modeled separately. The base models are summarized in Supplementary Tables 2A, 2C, 2E, 3A, and 3C, for each outcome measure, respectively. Figure 3 shows the raw correlation between all participants' entrainment stability and their tap to syllable task performance.

The relationship between entrainment stability and reading measurements was analyzed separately for English and Mandarin speakers due to the intrinsic differences in language and writing systems, and different sets of reading assessments used in this study. The relationship between entrainment stability and English language assessments are summarized in Table 4, and Supplementary Tables 2B, 2D, and 2F. The relationship between entrainment stability and Mandarin language assessments are summarized in Table 5, and Supplementary Tables 3B and 3D. Figure 4 shows the raw correlations between English speakers' entrainment stability and passage fluency. Figure 5 shows the raw correlations between Mandarin speakers' entrainment stability and word reading fluency.

Results

Behavioral entrainment

Figure 1 shows average relative phase for each participant (thin lines) and for all participants (thick lines). Relative phase reaches a steady state before the perturbation (negative phase means participants tapped before the tone on average). At the site of the perturbation, relative phase is positively or negatively displaced (depending on perturbation direction). During the relaxation time window, relative phase relaxes back to the attractor, reaching steady state by the post-perturbation time window (Fig. 1 shows only the largest perturbation, 25%). Because responses to phase perturbations generally include an over-correction, phase, and tempo yield similar relaxation times. These results are consistent with the previous experiments using this methodology (e.g., Large et al. 2002; Palmer et al. 2014; Rouse et al. 2016).

Stability of entrainment

Base tempo, perturbation size, and perturbation direction, but not perturbation type, were important determinants of the stability of behavioral entrainment, each significantly

improving model fit over a base model accounting for the effects of age, music experience, and native language on synchronization coefficient (SC). Compared to the base model (Table 1), the addition of base tempo significantly improved predictions of SC in the relaxation time window ($\chi^2 = 9.5465, p < 0.001$) (Model 1, Table 2). A Kruskal–Wallis test showed a significant main effect of base tempo ($p = 0.0045$), and pairwise analysis showed that SC is significantly lower in the 3 Hz base condition than 2 Hz ($z = -5.45, p < 0.001$) and 2.5 Hz ($z = -6.54, p < 0.001$). SC did not differ in the 2.5 Hz and 2 Hz conditions ($z = -0.59, p = 0.55$) (Fig. 2a).

Table 1 Base model for entrainment stability analysis. Participants’ age, language, and musical experience did not show significant effects in predicting SC (entrainment stability) during the relaxation time window

	Estimate	Std. error	T value	Pr(> t)
(Intercept)	8.738e-01	1.258e-02	69.465	< 2e-16***
Age	2.832e-04	4.573e-04	0.619	0.540
Experience	5.971e-05	7.718e-04	0.077	0.939
Language (English)	1.017e-02	7.782e-03	1.306	0.200

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2 The results of linear mixed-effects models for analyzing the predictive values of different perturbation conditions on entrainment stability

	Added predictors (fixed effects)	χ^2
Base model	Age + experience + language	
Model 1	Age + experience + language + base tempo	9.5465**
Model 2	Age + experience + language + perturbation type	2.5004
Model 3	Age + experience + language + perturbation size	719.03***
Model 4	Age + experience + language + perturbation direction	51.669***

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

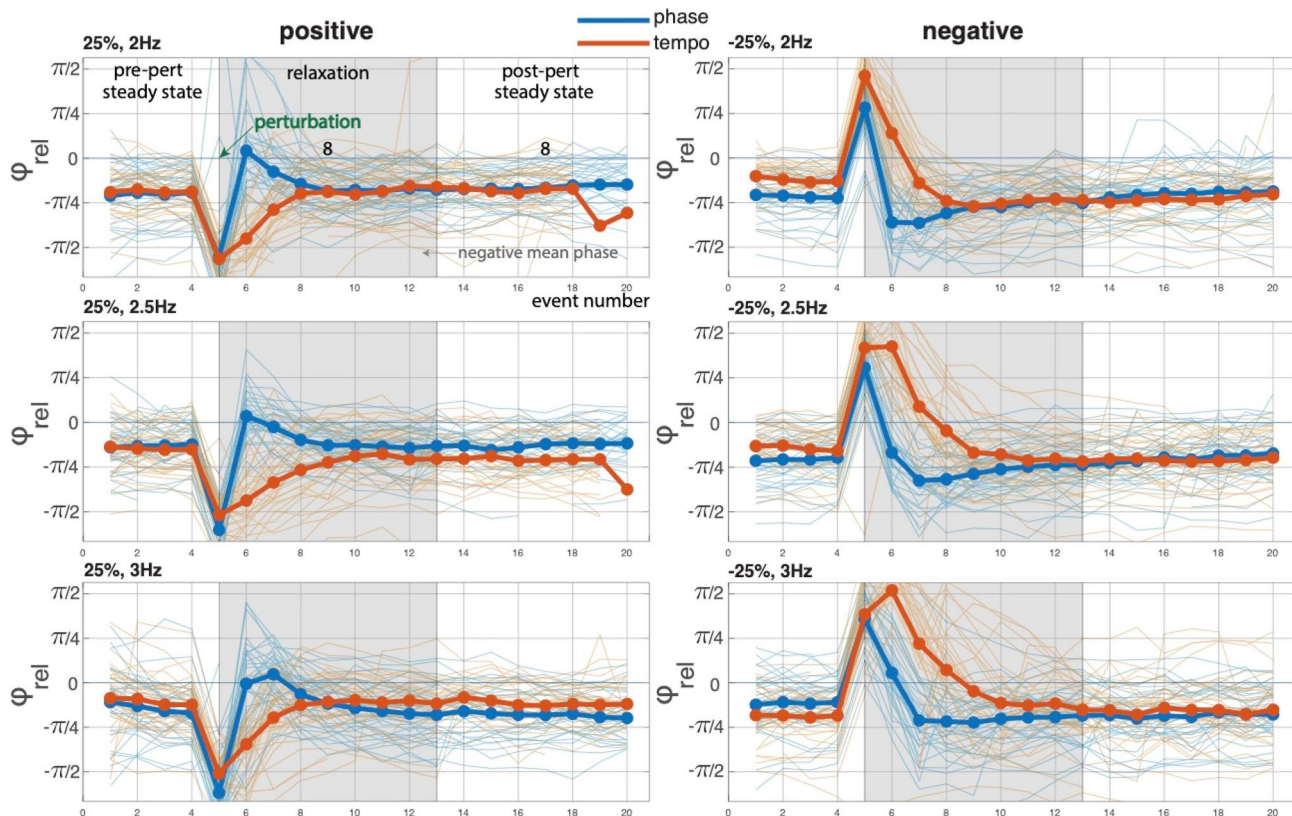


Fig. 1 Average relative phase for each participant (thin lines) and across all participants (thick lines) at each tap at 25% perturbation size condition. The eight taps during the relaxation window (gray area) were used to calculate the synchronization coefficients (SC)

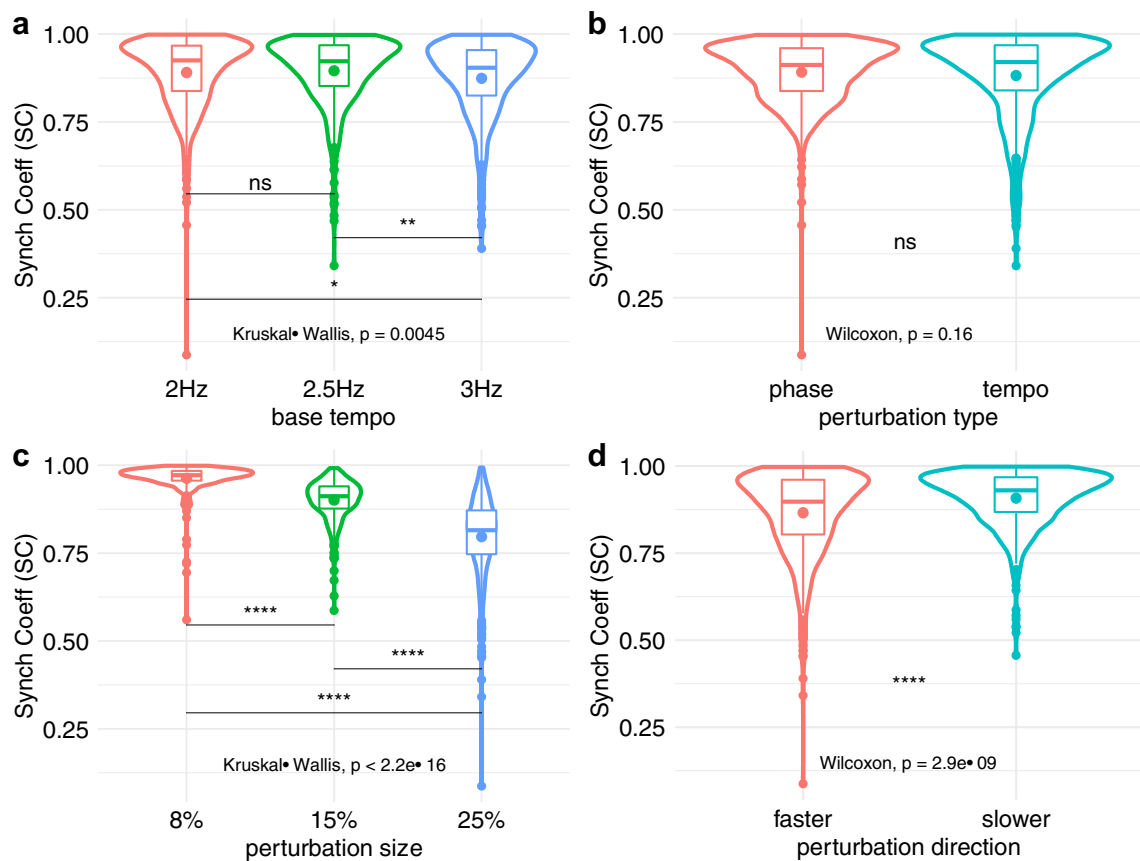


Fig. 2 Participants’ SC in the relaxation time window in **a** different base tempo conditions, **b** different perturbation type conditions, **c** different perturbation size conditions, and **d** different perturbation direc-

tion conditions. The dots in the violin plots represent group means, and the box plots depict the interquartile range and the median of the data

Compared to the base model, perturbation size (8%, 15% or 25% from the base IOI) significantly improved the prediction of SC in the relaxation time window ($\chi^2 = 719.03, p < 0.0001$) (Model 3, Table 2). A Kruskal–Wallis test showed a significant main effect of size ($p < 0.00001$), and pairwise analysis showed that SC is significantly lower in the 25% perturbation size condition than 15% perturbation condition ($z = -15.64, p < 0.0001$) and 8% perturbation condition ($z = -16.80, p < 0.0001$). Also, the 15% perturbation condition is significantly lower than in the 8% condition ($z = -15.44, p < 0.0001$) (Fig. 2c).

Compared to the base model, perturbation direction significantly improved the prediction of SC in the relaxation time window ($\chi^2 = 51.669, p < 0.0001$) (Model 4, Table 2). A Wilcoxon test showed that SC is significantly lower in the negative condition ($z = -5.24, p < 0.001$) (Fig. 2d).

The addition of perturbation type (tempo or phase) did not significantly improve the model prediction of SC in the relaxation time window over the base model ($\chi^2 = 2.5004, p < 0.114$) (Model 2, Table 2). A Wilcoxon test showed that

SC did not differ between tempo change condition and phase change condition ($z = -0.562, p = 0.57$) (Fig. 2b).

Tap to syllable task

To test the relationship between entrainment stability and the tap to syllable task performance, a series of hierarchical multiple regressions were conducted in R. Similarly to the stability of entrainment analysis above, age, language, musical experience, and metric test score were entered as fixed effect on the first step, and none of these predictors made a significant contribution (Supplementary Table 1A). Then, an additional set of models was built to test the relationship between entrainment stability in different conditions and the tap to syllable task performance. With respect to the base model, results showed that adding SC (across all conditions, Model 0, Table 3) significantly improved the model $\Delta R^2 = 0.21, p < 0.05$). Further comparisons against the base model showed significant improvements when adding SC in the 2.5 Hz or 3 Hz base

Table 3 Multiple regression model outputs for relationships between SC (entrainment stability) and all participants' tap to syllable task performance, controlling for their age, language, and musical experience

Outcome: All participants' tap to syllable task performance

	Added predictors	Compared model	R^2 change
Base model	Age + experience + metric test + language		
Model 0	Base Model + SC across all conditions	Base Model	0.2144*
Model 1.6	Base Model + 2.5 Hz	Base Model	0.1981*
Model 1.7	Base Model + 3 Hz	Base Model	0.2121*
Model 2.1	Base Model + tempo perturbation	Base Model	0.3166**
Model 3.6	Base Model + 15%	Base Model	0.1743*
Model 3.7	Base Model + 25%	Base Model	0.2353*
Model 4.1	Base Model + Negative (faster) perturbation	Base Model	0.4317***

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

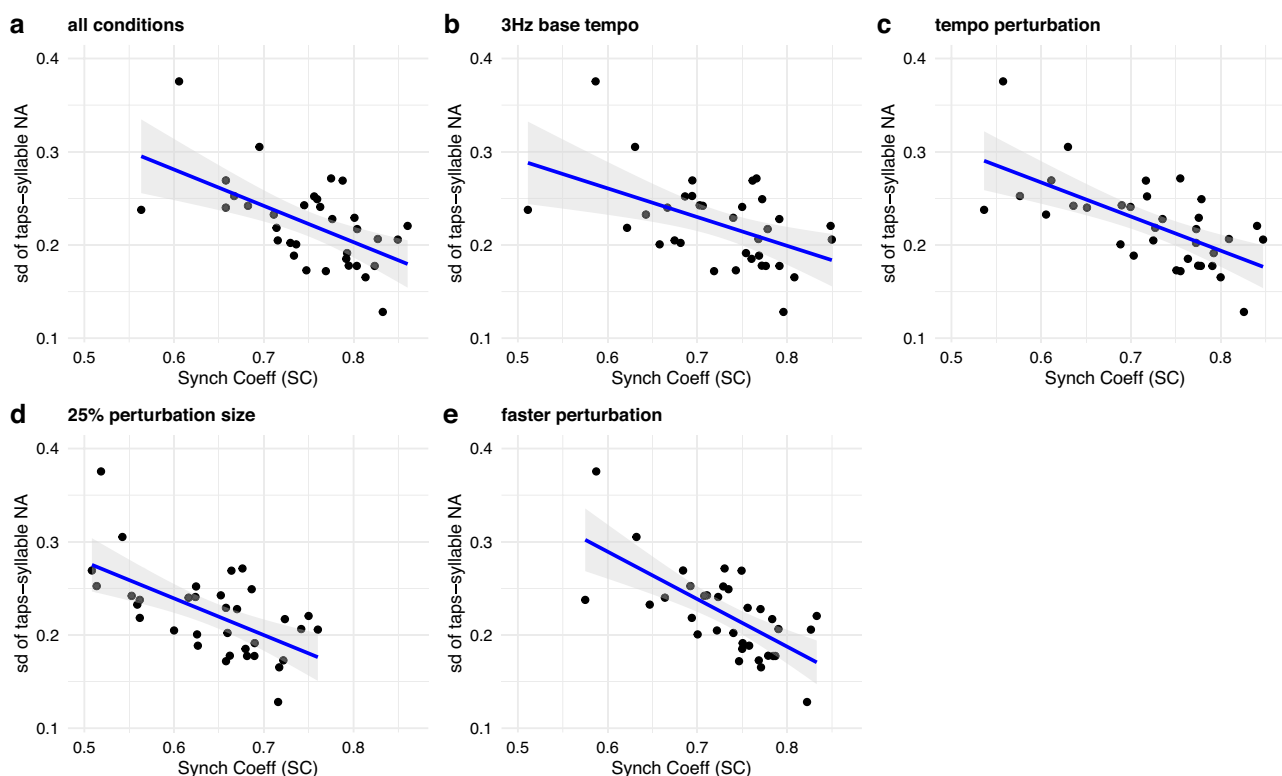


Fig. 3 Raw correlations between all participants' tap to syllable task performance and SC in the **a** relaxation window across all conditions (Model 0, $p < 0.05$, Table 3), **b** across 3 Hz base tempo condition (Model 1.7, $p < 0.05$), **c** across tempo perturbation condition (Model

2.1, $p < 0.01$), **d** across 25% perturbation size condition (Model 3.7, $p < 0.05$), and **e** across negative (faster) perturbation direction condition (Model 4.1, $p < 0.001$). Gray area represents 95% confidence interval

tempo condition ($\Delta R^2 = 0.20$, $p < 0.05$, Model 1.6; $\Delta R^2 = 0.21$, $p < 0.05$, Model 1.7), in the tempo perturbation condition ($\Delta R^2 = 0.32$, $p < 0.01$, Model 2.1), for perturbation sizes of 15% and 25% ($\Delta R^2 = 0.17$, $p < 0.5$, Model 3.6; $\Delta R^2 = 0.24$, $p < 0.05$, Model 3.7), as well as adding SC for negative perturbations ($\Delta R^2 = 0.43$, $p < 0.001$, Model 4.1). (See Supplementary Table 1B for all model comparisons). Figure 3 shows the raw correlations between entrainment

stability and tap to syllable task performance for speakers of both languages.

English word reading fluency

We used hierarchical multiple regression models to test whether entrainment stability explains variance in English word reading fluency over and above that explained by

participants’ age and musical experience. Age, musical experience, and metric test score were entered as fixed effects in the base model, none of which made significant contributions (Supplementary Table 2A). We then added entrainment stability in each condition into the model independently. Results showed that SC across all the conditions did not predict word reading fluency scores after controlling for the predictors in the base model. The only predictor that significantly improved the model is the perturbation size = 8% condition ($R^2 = 0.32, p < 0.05$) (See Supplementary Table 2B for full model comparison).

English passage reading fluency scores (GORT fluency)

We used the same hierarchical multiple regression model method with the outcome being English passage reading fluency scores. Age, musical experience, and metric test score were entered as fixed effects on the first step, and none of the base model predictors made significant contributions (Supplementary Table 2C). We then added entrainment stability in different conditions into the model independently. Results showed that adding entrainment SC as a predictor (across all conditions) significantly improved the base model ($R^2 = 0.41, p < 0.05$, Model 0, Table 4). Furthermore, independently adding SC for base tempo 2 Hz or 2.5 Hz significantly improved the base model ($R^2 = 0.30, p < 0.05$, Model 1.1; $R^2 = 0.44, p < 0.01$, Model 1.6). Independently adding SC for tempo perturbations significantly improved the base model ($R^2 = 0.47, p < 0.01$, Model 2.1). Also, adding SC for perturbation sizes 8%, 15%, and 25% significantly improved the model ($R^2 = 0.41, p < 0.01$, Model 3.1; $R^2 = 0.36, p < 0.05$, Model 3.6; $R^2 = 0.35, p < 0.05$, Model 3.7). Finally, independently adding SC for both negative and positive perturbation directions significantly improved the base model ($R^2 = 0.28, p < 0.05$, Model 4.1; $R^2 = 0.33, p < 0.05$, Model 4.3) (See Supplementary Table 2D for full

model comparison). Figure 4 shows the raw correlations between English speakers’ entrainment stability and passage fluency scores. Thus, performance over all perturbation conditions, and in almost every individual perturbation condition, predicted English passage reading fluency.

English passage reading comprehension scores (GORT comprehension)

As above, hierarchical multiple regression models were used to investigate the relationship between SC and our outcome variable, in this case English passage reading comprehension scores. Age, musical experience, and metric test score were entered as fixed effects on the first step, and none of the base model predictors made significant contributions (Supplementary Table 2E). We then added entrainment stability in different conditions into the model independently. Our results showed that entrainment SC across all conditions did not predict passage reading comprehension scores after controlling for the predictors in the base model. Similarly, none of the individual conditions predicted passage reading comprehension scores after controlling for the predictors in the base model (see Supplementary Table 2F for full model comparison). Thus, no aspect of entrainment stability predicted English passage reading comprehension.

Mandarin word reading fluency

We used the same hierarchical multiple regression model method with the outcome being Mandarin word reading disfluency scores. Age, musical experience, and metric test score were entered as fixed effects on the first step, and none of the base model predictors made significant contributions (Supplementary Table 3A). We then added entrainment stability in different conditions into the model independently. Our results showed that adding SC across all conditions did not significantly improve the base model ($R^2 = 0.18$,

Table 4 Multiple regression model outputs for relationships between SC (entrainment stability) and English-speaking participants’ passage reading fluency scores (measured using GORT), controlling for their age and musical experience

Outcome: English-speaking participants’ passage reading fluency scores			
	Added predictors	Compared model	R^2 change
Base model	Age + experience + metric test		
Model 0	Base model + SC across all conditions	Base Model	0.4085*
Model 1.1	Base Model + 2 Hz	Base Model	0.3034*
Model 1.6	Base Model + 2.5 Hz	Base Model	0.4352**
Model 2.1	Base Model + tempo change	Base Model	0.4687**
Model 3.1	Base Model + 8%	Base Model	0.4117**
Model 3.6	Base Model + 15%	Base Model	0.3575*
Model 3.7	Base Model + 25%	Base Model	0.3478*
Model 4.1	Base Model + Negative (faster) perturbation	Base Model	0.2844*
Model 4.3	Base Model + Positive (slower) perturbation	Base Model	0.3281*

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

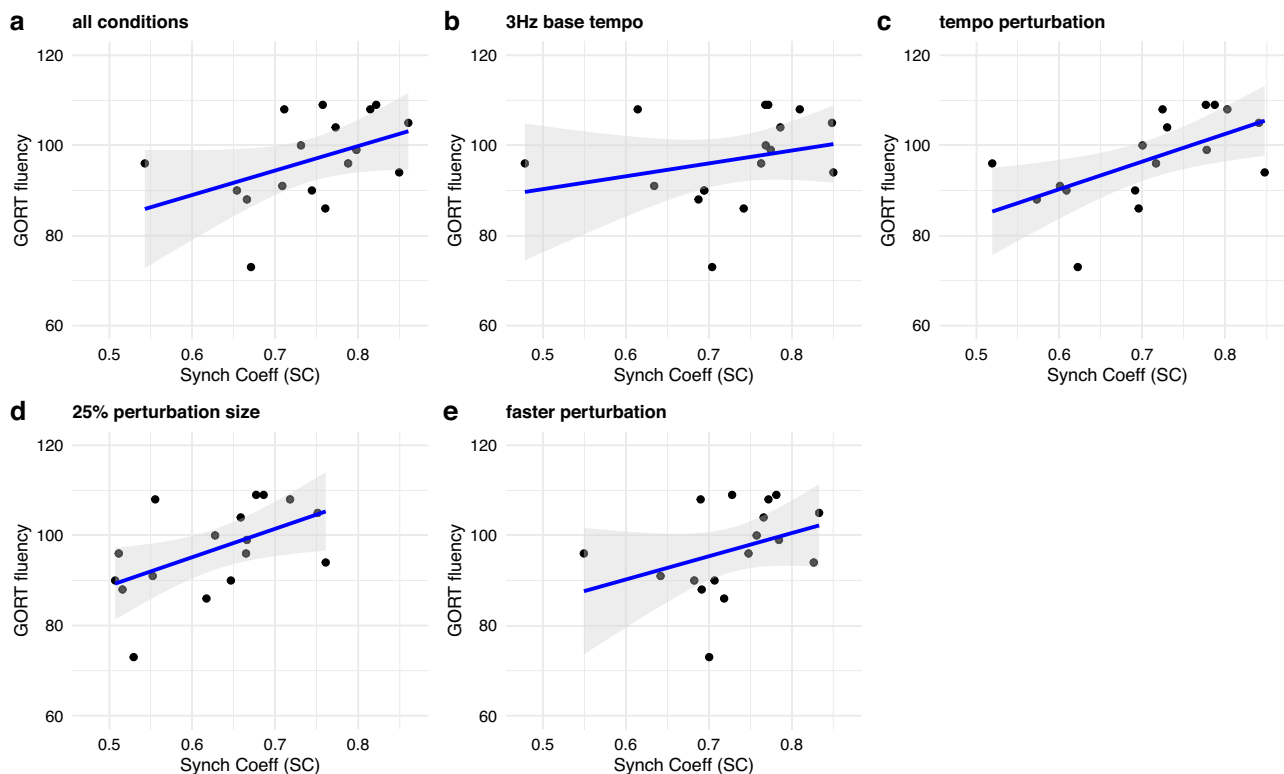


Fig. 4 Raw correlation between all English-speaking participants’ passage reading fluency and SC in the relaxation window averaged across **a** all conditions (Model 0, $p < 0.05$, Table 4), **b** across 3 Hz base tempo condition ($p = n.s.$), **c** across tempo perturbation condition (Model 2.1, $p < 0.01$), **d** across 25% perturbation size condition (Model 3.7, $p < 0.05$), and **e** across negative perturbation direction condition (Model 4.1, $p < 0.05$). Gray area represents 95% confidence interval

Table 5 Multiple regression model outputs for relationships between SC (entrainment stability) and Mandarin-speaking participants’ word reading disfluency, controlling for their age and musical experience

Outcome: Mandarin-speaking participants’ word reading disfluency scores			
	Added predictors	Compared model	R^2 change
Base model	Age + experience + metric test		
Model 1.7	Base Model + 3 Hz	Base Model	0.1952*
Model 2.1	Base Model + tempo change	Base Model	0.2926**
Model 3.7	Base Model + 25%	Base Model	0.2085*
Model 4.1	Base Model + Negative perturbation	Base Model	0.2926**

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

$p = 0.055$, Model 0, Supplementary Table 3B). However, independently adding SC for base tempo 3 Hz did significantly improve the base model ($R^2 = 0.20$, $p < 0.05$, Model 1.7, Table 5). Independently adding SC for tempo perturbations significantly improved the base model ($R^2 = 0.29$, $p < 0.01$, Model 2.1). And independently adding SC for perturbation size 25% significantly improved the base model ($R^2 = 0.21$, $p < 0.05$, Model 3.7). Moreover, independently adding SC for the negative perturbation direction significantly improved the base model ($R^2 = 0.29$, $p < 0.01$, Model 4.1, see Supplementary Table 3B for full

model comparison). Figure 5 shows the raw correlations between Mandarin speakers’ entrainment stability and word reading fluency. Thus, performance in the more difficult perturbation conditions predicted Mandarin word reading disfluency scores.

Mandarin sentence reading comprehension

We used the same hierarchical multiple regression model method with the outcome being Mandarin sentence reading comprehension scores. Age, musical experience, and metric test score were entered as fixed effects on the first

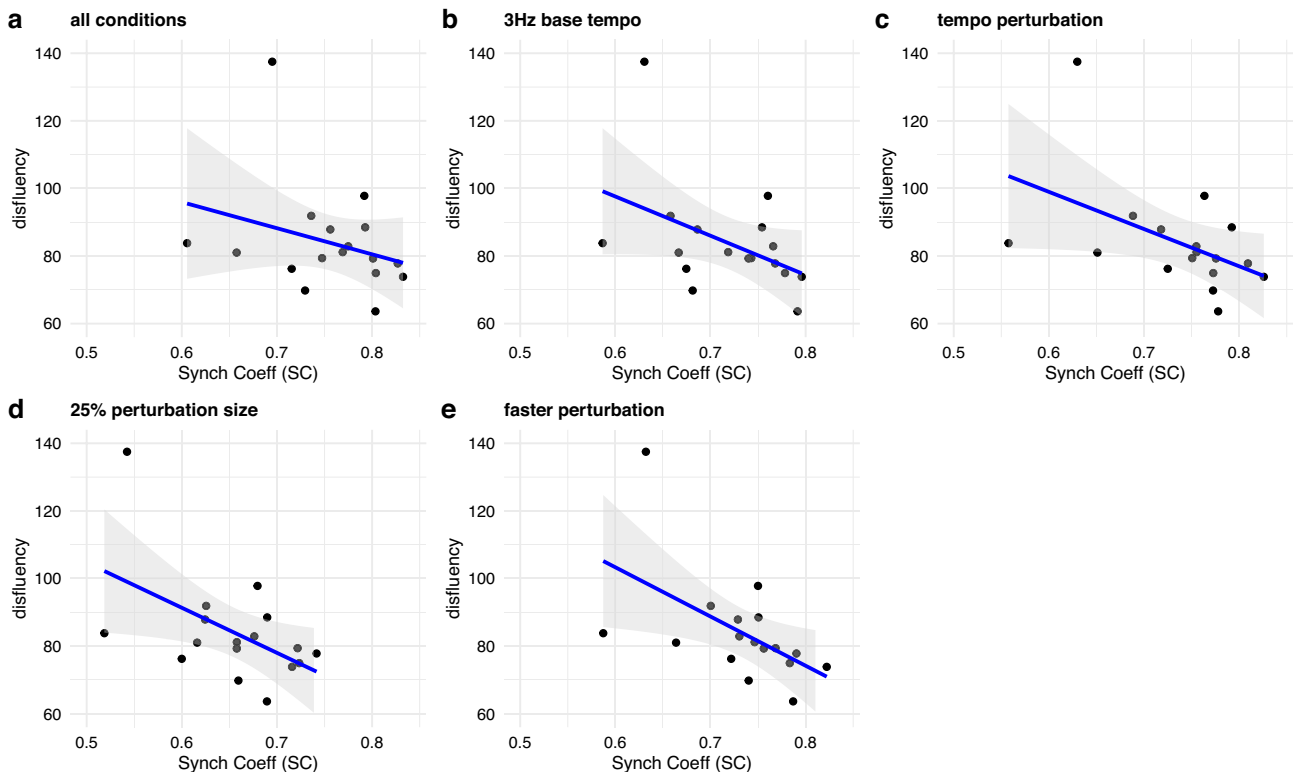


Fig. 5 Raw correlation between all Mandarin-speaking participants’ word reading disfluency and SC in the relaxation window averaged across **a** all conditions ($p=n.s$), **b** across 3 Hz base tempo condition (Model 1.7, $p<0.05$, Table 5), **c** tempo perturbation condition

(Model 2.1, $p<0.01$), **d** 25% perturbation size condition (Model 3.7, $p<0.05$), and **e** negative perturbation direction condition (Model 4.1, $p<0.01$). Gray area represents 95% confidence interval. Note that higher score indicates worse reading fluency

step, and none of the base model predictors made significant contributions (Supplementary Table 3C). We then added entrainment stability in different conditions into the model independently. Our results showed that SC across all the conditions did not predict sentence reading comprehension scores after controlling for the predictors in the base model. Similarly, SC in individual conditions did not predict sentence reading comprehension scores (see Supplementary Table 3D for full model comparison). Thus, no aspect of entrainment stability predicted Mandarin sentence reading comprehension.

Discussion

We found a strong relationship between entrainment stability, tap to syllable task performance, and reading fluency for both native English and native Mandarin speakers, but no relationship between entrainment stability and reading comprehension for either language. Specifically, after controlling for age, musical background, and meter perception ability, entrainment stability significantly predicted tap to syllable task performance for all speakers. Moreover, entrainment

stability predicted passage reading fluency for English speakers, and word reading fluency for Mandarin speakers. Some of the effects were stronger for the more difficult conditions, that is, for faster base tempo, tempo changes, larger perturbations, and negative perturbation direction (speeding up).

We used the synchronization coefficient (SC) in the perturbation window as a sensitive measure of relaxation time; low SC means longer relaxation time and lower stability. Base tempo, perturbation size, and perturbation direction were the most important predictors. SC was significantly lower for the fastest tempo (3 Hz), for the larger perturbations (15% and 25%), and for negative perturbations (speeding up). Tempo changes did not yield longer relaxation times overall, because of overcorrections in response to phase changes. These findings are consistent with the previous literature on entrainment to a changing rhythm (Large et al. 2002; Palmer et al. 2014) and with predictions of oscillator models (Kim and Large 2015; Loehr et al. 2011). Overall, some conditions were more difficult than others. These conditions, in addition to the tempo change condition, were most reflective of the abilities of individual participants.

Stability of behavioral entrainment predicted performance in the tap to syllable task across all perturbation conditions. These relationships were mainly driven by performance on the more difficult conditions, which independently predicted the tap to syllable task performance. Thus, participants whose entrainment to an external rhythm is more stable are also better at synchronizing taps (intrapersonally) with their own spoken syllables.

For native English speakers, stability of behavioral entrainment was strongly predictive of passage reading fluency (GORT) across all perturbation conditions. Nearly every perturbation condition contributed to this relationship; nearly all could independently predict passage reading fluency. However, stability of behavioral entrainment was predictive of word reading fluency only in the perturbation size = 8% condition. For native Mandarin speakers, entrainment stability predicted word reading fluency in the difficult conditions. Across all perturbation conditions, the relationship approached significance. Participants whose entrainment to an external rhythm is more stable are also better at coordinating the neural processes necessary to fluently generate speech from written text.

Although they manifest differently in each population, relationships between entrainment stability and reading fluency were observed in non-clinical adult populations of both English and Mandarin speakers. Differences were seen in word-level reading fluency between English and Mandarin speakers, however. One explanation for this apparent discrepancy is the different types of measures that were used to assess word reading fluency. Tests directly comparable to the Word-Letter ID and Word Attack tests are not available for Mandarin; thus, we used a test that is not standardized for this age group (Li et al. 2017; Song et al. 2015). Moreover, this test is timed, and the Word-Letter ID and Word Attack tests are not. Thus, the pressure of timing might contribute to the differences we see in the relationship between entrainment in these two language groups and word-level reading fluency.

Two previous studies with children and adolescents in non-clinical populations found relationships between behavioral entrainment and word reading fluency (David et al. 2007; Tierney and Kraus 2013b). For example, Tierney and Kraus (2013b) used an entrainment task and the same Word-Letter ID and Word Attack tasks to measure word reading fluency, reporting a strong relationship. However, these differences could be due to the different age ranges of the participants; the word reading fluency measures may not be as sensitive for adults as for adolescents. Also, different measures of entrainment stability were used in these studies. Wolff (2002)'s study is the only study that has used a perturbation task with children with dyslexia. The study showed that children with dyslexia had more taps after the perturbation point that were tracking

the stimuli instead of anticipating the stimuli, compared to the age-matched control group. The study did not correlate behavioral rhythmic entrainment to reading measurements.

Entrainment stability did not predict reading comprehension in either group. Using a similar comprehension assessment to ours, Goswami et al. (2013) found that the perception of beat structure in music predicted the development of reading comprehension in children with and without dyslexia. In their study, the rhythmic assessment was quite different, suggesting that rhythmic structure perception and entrainment stability may index different aspects of reading performance (Ding et al. 2016).

General discussion

What might the link be between overt behavioral entrainment to an auditory rhythm and reading fluency? One possibility is that the same neural systems that are entrained by external stimuli may also function to synchronize within large brain networks during other activities, for example during speaking or reading (Black et al. 2017). If this is the case, then the ability of a neural system to maintain an entrained or synchronized state may determine performance in any task in which it was involved.

Lack of stability due to weaker coupling may manifest in clinical populations as deficits in the ability to make fast and accurate changes in phase and period in response to external rhythms, or manifest as abnormal neuronal oscillations (e.g., Goswami 2019) due to reduced ability to synchronize with incoming signals from spatially distinct neuronal networks. Many studies have found that populations with dyslexia showed atypical neural entrainment to the rhythm of speech and music in the slow frequency range. For example, Molinaro et al. (2016) showed that, compared to a control group, children with developmental dyslexia demonstrated impaired neural entrainment (measured by the coherence between MEG signal and the envelope of the auditory sentence stimuli) to speech in the delta band. Power et al. (2016) found that children with developmental dyslexia showed poorer speech encoding (measured by correlation between reconstructed envelope from the EEG signal and the actual stimulus envelope) in the delta band, compared to the control group. These impairments in speech entrainment may limit the development of preliterate syllabic and phonological processing skills, ultimately leading to impaired reading ability (Di Liberto et al. 2018; Goswami 2011). On the other hand, the atypical entrainment to music rhythmic stimuli were also found in children with developmental dyslexia and adults with dyslexia (Colling et al. 2017; Hämäläinen et al. 2012; Soltész et al. 2013). This evidence of atypical neural entrainment to speech and music could be an outcome

of lack of stability of neural systems, while maintaining an entrained or synchronized state. Training stability, using an entrainment task, and specifically a perturbation methodology, may lead to rehabilitation of other abilities, including intrapersonal synchronization and reading fluency.

Another possibility that may contribute to the link between overt behavioral entrainment to an auditory rhythm and reading fluency is executive function and attentional resources, mainly given their importance in reading measurements (Cirino et al. 2019; Foy and Mann 2013; Krause 2015). Studies have also found a relationship between bilingualism, musical experience, and executive function (Moradzadeh et al. 2015). The link between executive function and overt behavioral entrainment is less clear depending on the type of stimuli. Repp and Keller (2004) suggested that, when encountering error correction in a metronome entrainment task, with stimuli IOI around 2 Hz, period correction (tempo perturbation condition in the current study) was strongly dependent on attentional resources and the awareness of tempo change (see also Pecenka et al. 2013). Phase correction (phase perturbation condition in the current study), on the other hand, was more automatic and less subject to cognitive control. Given that the tempo perturbation condition in general yielded stronger predictive power in reading measurements than the phase perturbation condition in the current study, and the fact that all the Mandarin speakers in this study were fluent in English to a certain extent, we cannot rule out the possibility that executive function and attentional resources may also contribute to the link we found between overt behavioral entrainment to an auditory rhythm and reading fluency.

Conclusions

We found a strong relationship between behavioral entrainment stability, tap to syllable task performance, and passage and word reading fluency for neurotypical native English and native Mandarin speakers, respectively. Entrainment stability significantly predicted tap to syllable task performance for all participants as well as passage reading fluency for English speakers, and word reading fluency for Mandarin speakers. Our perturbation paradigm tapped into individual differences in reading in the neurotypical population, which not only provides further evidence on the relationship between rhythmic skills and reading fluency, but also have theoretical and modeling significance. The strong relationship between entrainment and tap to syllable task performance explains the efficacy of rhythm-based speech and reading intervention. The

fact that increased musical experience is associated with temporal adaptability suggests that dynamical stability is trainable, specifically, training that involves responses to temporal perturbations may become a part of the intervention techniques in clinical settings.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00221-022-06369-9>.

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Declarations

Conflict of interest The questionnaire and methodology for this study was approved by the University of Connecticut Institutional Review Board (Protocol: H15-061). Informed consent was obtained from all individual participants included in the study. The datasets generated and/or analyzed for the current study are not publicly available due to possible compromise of individual privacy, but are available from the corresponding author on reasonable request.

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