


# Rhythmic modulation of visual discrimination is linked to individuals' spontaneous motor tempo

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## Abstract

The impact of external rhythmic structure on perception has been demonstrated across different modalities and experimental paradigms. However, recent findings emphasize substantial individual differences in rhythm-based perceptual modulation. Here, we examine the link between spontaneous rhythmic preferences, as measured through the motor system, and individual differences in rhythmic modulation of visual discrimination. As a first step, we measure individual rhythmic preferences using the spontaneous tapping task. Then we assess perceptual rhythmic modulation using a visual discrimination task in which targets can appear either in-phase or out-of-phase with a preceding rhythmic stream of visual stimuli. The tempo of the preceding stream was manipulated over different experimental blocks (0.77 Hz, 1.4 Hz, 2 Hz). We find that visual rhythmic stimulation modulates discrimination performance. The modulation is dependent on the tempo of stimulation, with maximal perceptual benefits for the slowest tempo of stimulation (0.77 Hz). Most importantly, the strength of modulation is also linked to individuals' spontaneous motor tempo. Individuals with slower spontaneous tempi show greater rhythmic modulation compared to individuals with faster spontaneous tempi. This finding suggests that different tempi affect the cognitive system with varying levels of efficiency and that self-generated rhythms impact our ability to utilize rhythmic structure in the environment for guiding perception and performance.

## KEYWORDS

active sensing, individual differences, rhythmic facilitation, tapping, visual discrimination

**Abbreviations:** ADHD, attention-deficit hyperactivity disorder; BIC, Bayesian information criteria; CV, coefficient of variation; ITI, inter-tap interval; OR, odds ratio.

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## 1 | INTRODUCTION

Rhythmic structure is present in everyday stimuli such as speech (Inbar et al., 2020; Poeppel & Assaneo, 2020), motion (Fraisse, 1982; Lakatos et al., 2019) and music (Jones, 2010). These external rhythms serve as natural

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cues for the guidance of behaviour (Haegens & Zion Golumbic, 2018; Jones, 2010; Large & Jones, 1999; Nobre & van Ede, 2017; Shalev et al., 2019). Numerous studies have demonstrated perceptual benefits for events that appear in synchrony with a preceding beat (Bauer et al., 2021; Cravo et al., 2013; Haegens & Zion Golumbic, 2018; Jones, 2010; Mathewson et al., 2010; Shalev & Nobre, 2022; Spaak et al., 2014). This phenomenon, termed 'rhythmic facilitation', has been documented in various modalities (Haegens & Zion Golumbic, 2018). However, recent findings emphasize substantial individual differences in rhythm-based perceptual modulation (Bauer, Jaeger, et al., 2015; Doelling & Poeppel, 2015; Lin et al., 2021; Saberi & Hickok, 2021; Sun et al., 2021). For example, in a study by Bauer, Jaeger, et al. (2015), only 40 out of 140 individuals showed classic rhythmic facilitation. Namely, they performed better for events appearing in-phase with a preceding auditory rhythmic stream, compared to events that appeared out-of-phase (both early and late targets). Similarly, Sun et al. (2021) showed rhythmic modulation of auditory detection in 36% of their experimental sample, with no rhythmic facilitation of performance at the group level. Here, we aim to test the hypothesis that these individual differences in rhythm-based perceptual modulation are linked to individual differences in spontaneous rhythmic preferences.

Rhythmic brain and behaviour patterns emerge even when there is no temporal structure in the environment. In the brain, spontaneous rhythmic fluctuations in neural excitability are demonstrated in different timescales from infra-slow to extremely fast (Buzsáki & Wang, 2012; Monto et al., 2008). In behaviour, spontaneous rhythmic structure is found in self-produced motion and speech (Fraisse, 1982; Poeppel & Assaneo, 2020), exploratory behaviours (Amit et al., 2017; Berg, 2002; Moore et al., 2014; Otero-Millan et al., 2008) and cognitive performance (Landau & Fries, 2012; Monto et al., 2008; VanRullen, 2016). Previous work has shown that individual differences in spontaneous rhythmic preferences account for variability in externally paced motor performance (McAuley et al., 2006; Zamm et al., 2015, 2016). For example, McAuley et al. (2006) showed that when individuals perform with external tempi that are close to their own spontaneous motor tempo they do better. Namely, they are more accurate and stable in tracking the external rhythmic stimulation. Similarly, in a series of studies, Zamm and colleagues showed that musicians perform optimally, both individually and in a dyad, at tempi that are close to their spontaneous rhythmic preferences (Zamm et al., 2015, 2016, 2018). Interestingly, activation of the motor system has been demonstrated during beat perception, even in the absence of motion (Bengtsson

et al., 2009; Cannon & Patel, 2021; Grahn & Brett, 2007). Therefore, individual differences in spontaneous motor tempi might impact not only motor performance but also modulation of perception within a rhythmic context.

To examine the hypothesis that individual differences in rhythmic facilitation are linked to individual differences in spontaneous motor tempi, we first assessed individuals' motor rhythmic preferences using the spontaneous tapping task (Fraisse, 1982; McAuley et al., 2006). Then, we characterized individual differences in rhythm-based perceptual modulation using different tempi of stimulation during a visual discrimination task. We designed a visual discrimination task in which targets could appear at different phases with respect to a rhythmic stream of stimuli (i.e. in-phase or out-of-phase). Then, for each individual, we assessed the impact of the external rhythm on performance and examined the relationship between their sensitivity to the external rhythm and their spontaneous tapping tempo.

## 2 | METHODS

### 2.1 | Participants

Fifty-six individuals (55% females, 86.6% right-handed, mean age = 25.26 [SD = 4.62]) participated in the study. We decided to exclude from the analysis participants who reported they are diagnosed with attention-deficit hyperactivity disorder (ADHD,  $n = 7$ ), based on previous studies that show reduced behavioural modulation in a rhythmic context in this population (Dankner et al., 2017; Shalev et al., 2022). No other neurological or psychiatric diseases were reported. In addition, participants reported normal or corrected-to-normal vision and normal hearing. We recruited participants using the university system for participant recruitment, as well as social media. We obtained written informed consent from all participants before the experimental session. Monetary compensation was provided for participation in the study. All experimental procedures were approved by the local Ethics Committee of the Hebrew University of Jerusalem.

### 2.2 | Experimental tasks

#### 2.2.1 | Spontaneous tapping task

To assess participants' spontaneous rhythmic preferences, we used the spontaneous tapping task (Fraisse, 1982; McAuley et al., 2006). We asked participants to tap with the index finger of their dominant hand on a smartphone screen, at a comfortable and regular

tempo. We recorded tapping times using a touch-sensitive app developed in the lab. We placed the smartphone on a table in front of the participant, positioned at a comfortable distance. Before the recording, we asked the participants to do a short practice task to check that they understood the study task. The duration of the recording was 1 min.

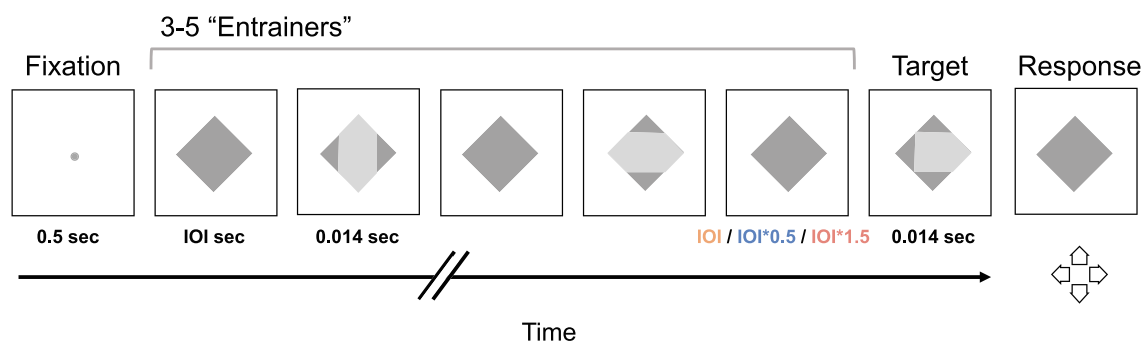
## 2.2.2 | Visual discrimination task

To assess the impact of rhythmic context on perception, we designed a visual discrimination task. On each trial, we presented a rhythmic, isochronous stream of visual stimuli. The last stimulus in each stream was the designated target—an arrow pointing to one of four possible directions (up, down, left or right). Each stream comprised three to five preceding events (i.e. ‘entrainers’) that set the rhythm of stimulation. We asked participants to report the direction of the target. We manipulated two aspects of temporal expectation. For the first, **context tempo**, we manipulated the tempo at which the entrainers were flashed on the screen. Overall, we used three tempi of stimulation, 0.77, 1.43 and 2 Hz, that were presented in three separate experimental blocks. Thus, the inter-onset intervals (IOIs) between subsequent stimuli in a trial were 1.3, 0.7 and 0.5 s for 0.77, 1.43 and 2 Hz, respectively. The order of experimental blocks was counterbalanced between participants. The tempi of stimulation were chosen to correspond with the rhythmic range of preferred tapping rhythms ( $\sim 0.7$ –5 Hz) as established on a separate sample. However, we had an upper limit on the stimulation tempo, as we found that stimulating at a tempo faster than 2.5 Hz resulted in chance performance in all presented conditions. Therefore, our final choice of stimulation tempi was impacted by both

the motor tempo range and task difficulty constraints. For the second, **target phase**, we manipulated the timing of the target with respect to the rhythmic context formed by the entrainers. The targets were distributed uniformly across three possible timings: A third of the targets appeared in-phase with the preceding stream (i.e. on beat), a third of the targets appeared half a cycle before the beat (early targets), and a third of the targets appeared half a cycle after the beat (late targets). The different target phases were presented in a random order within each block (i.e. within each context tempo).

## 2.3 | Stimuli and experimental protocol

Trial structure and stimulus are depicted in Figure 1. Each trial started with a 0.5 s fixation dot that was followed by the presentation of a dark-grey diamond (height: 5.5 cm, width: 5.5 cm). The rhythmic stream of stimuli consisted of light-grey double-sided arrows (length: 5.5 cm, width: 2.8 cm). The double-sided arrows flashed on top of the dark-grey diamond. The dark-grey diamond was present on the screen throughout the trial. The arrows were each presented for 0.014 s. The number of stimuli preceding the target stimulus was set to 3, 4 or 5 (10%, 80% and 10% of trials, respectively, within each block). We manipulated the number of events before the target to prevent formation of expectations based on the number of stimuli leading to the target. The last stimulus in each sequence was the designated target and was composed of a unidirectional arrow overlaid on the diamond. Participants were instructed to report the direction of the unidirectional arrow immediately after its appearance. When unable to perceive the direction of the arrow, participants were asked to guess. Overall, we presented participants with three experimental blocks, each containing a different



**FIGURE 1** Stimuli and trial structure: Each trial started with a fixation dot. The fixation dot was followed by a stream of visual stimuli. The first three to five stimuli consisted of arrows pointing in two directions (i.e. the entrainers). The last stimulus in each stream was the designated target and consisted of an arrow pointing in one direction only. Participants were asked to report the direction of the target immediately after its presentation. The inter-onset interval (IOI) between the entrainers set the tempo of stimulation and was manipulated across blocks ( $\text{IOI} = 0.5, 0.7$  or  $1.3$  s). The last IOI before the target was manipulated within each block and could be identical (blue), half a cycle shorter ( $\text{IOI} \times 0.5$ , orange) or half a cycle longer ( $\text{IOI} \times 1.5$ , pink), than the preceding IOIs in the trial. The entrainers and the target appeared on the screen for 0.014 s.

tempo of stimulation (i.e. context tempo). Each block consisted of 99 trials uniformly distributed across the three possible target times (in-phase, early and late targets). Therefore, each participant completed 297 trials. The order of trials within each block was randomized. Breaks were administered three times throughout the task.

## 2.4 | Procedure

Before arriving at the lab, participants signed a digital informed consent form. Upon arrival, they completed a personal information questionnaire. Participants were seated in a dimly lit room at ~47 cm from a 60" gamma calibrated monitor and completed the spontaneous tapping task. Then, they continued to the visual discrimination task. Stimulus presentation and response acquisition were controlled using Psychtoolbox (Version 3.20.20; Brainard, 1997; Kleiner et al., 2007) on MATLAB (Version 2018b, MathWorks, Natick, Massachusetts). Participants reported the direction of the target using keys that were located at the top of a Logitech joystick (model ATTACK3 simulator). The joystick was located near the participants' dominant hand, and they were instructed to use their thumb for responding. Before starting the task, participants performed a simplified version of the task in which the arrows forming the visual rhythmic stimulation were presented for longer durations (0.100 s instead of 0.014 s in the main experiment). This allowed participants to become familiarized with the task and response device. Then, participants continued to a second practice in which the timing parameters were identical to the actual experiment (each stimulus in the stream was presented for 0.014 s). The stimulation tempo in the practice was always set to the tempo with which the participants would start the actual experiment. Participants completed 10 practice trials before proceeding to the first experimental block.

## 2.5 | Data pre-processing

### 2.5.1 | Spontaneous tempo

We calculated the inter-tap intervals (ITIs) between the recorded taps and pre-processed the time course of performance using the following steps: (1) We removed ITIs that were longer than 3 s, as those were indicative of breaks in performance; and (2) we removed ITIs that were more than 1.5 interquartile ranges above the upper quartile or below the lower quartile. On average, these procedures resulted in the removal of 2.7% of taps ( $SD = 2.8\%$ ). Then, for each individual, we calculated two performance measures: (1) **mean tempo**, calculated based on the ITI

between the recorded taps; and (2) **variability**, calculated based on the coefficient of variation (CV). CV is a normalized measure that accounts for the produced mean tempo in the assessment of variability (the standard deviation of the ITI divided by the mean ITI). Two participants were excluded due to high variability in performance using the interquartile range method for outlier detection. Additionally, we removed two data sets due to a log failure. One of those data sets was replaced by a measurement of the same participant on a different day.

### 2.5.2 | Visual discrimination

We removed trials with extremely fast response times (<150 ms), as those were indicative of premature responses. We did not exclude trials based on other characteristics of response times, as participants were encouraged to take breaks when needed by withholding the response until they were ready to continue. Overall fast response times led to the removal of 2.9% of trials. Finally, we removed two participants who performed the task at chance level, as was determined using a binomial test. Altogether, the analysis was conducted on 44 participants. Analysis conducted on all trials, without excluding premature responses, led to the same results.

## 2.6 | Data analysis

To test the effect of target phase on visual discrimination as a function of context tempo and spontaneous tempo, we performed a mixed effect logistic regression (Jaeger, 2008). Our dependent measure was discrimination accuracy, with correct responses coded as 1 and incorrect responses as 0. Our independent measures included 'target phase', 'context tempo', 'spontaneous tempo' and all the interactions between them as fixed effects. It also included random intercepts for participants and random slopes for context tempo by participant. This random effect structure was the maximal structure to converge (Barr et al., 2013). The two categorical predictors, target phase (before, in-phase, after) and context tempo (0.77 Hz, 1.43 Hz, 2 Hz), were both 'treatment coded' (reference levels: 'in-phase' for target phase, '1.43 Hz' for context tempo). The numerical predictor 'spontaneous tempo' was centred.

To assess the contribution of each predictor to the model, we performed a likelihood ratio test between the maximal converged model and a nested model that excluded the specific predictor we were interested in. In what follows, we report for each predictor the Bayesian Information Criteria (BIC) difference, chi-square values and significance level (Meteyard & Davies, 2020).

In addition, to obtain comparisons of interest that were not covered by the contrast structure included in the model, we utilized the ‘emmeans’ package in R (Lenth, 2019). Specifically, we calculated the log odds difference between specific target phases (before, in-phase, after) for each tempo separately (0.77 Hz, 1.43 Hz, 2 Hz). Then we tested this difference for significance using the Wald Z-test and transformed the log odds difference into odds ratio. For each comparison, we report odds ratio (OR) with confidence intervals and adjusted significance levels using false discovery rate correction for multiple comparisons (Benjamini et al., 2001).

Finally, to assess the relationship between individual differences in rhythmic modulation by external rhythms and individuals’ spontaneous tempo, we used the Pearson correlation. Individual differences in rhythmic modulation were quantified based on the difference in performance between in-phase and out-of-phase targets (separately for early and late targets). This measure emphasizes the impact of rhythmic context by removing individual differences in baseline performance.

### 3 | RESULTS

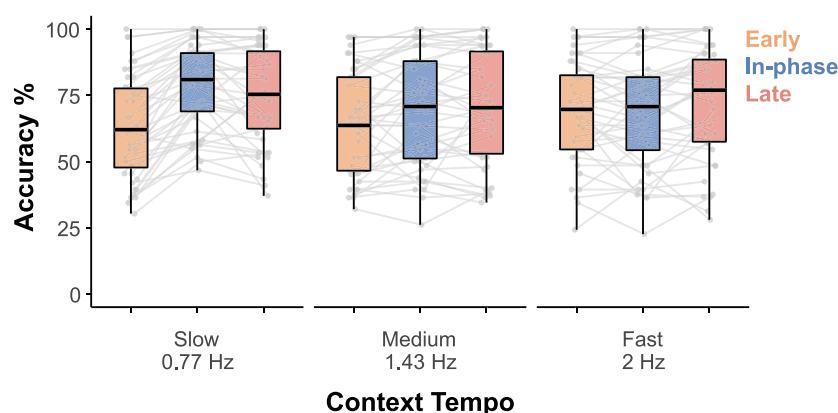
#### 3.1 | Rhythmic modulation of visual discrimination is dependent on context tempo

As can be seen in Figure 2, the impact of target phase on visual discrimination is highly dependent on the tempo of stimulation. To examine the relationship between context tempo and the rhythmic modulation of visual discrimination, we performed a model comparison between

the full converged model and a nested model excluding the interaction term between target phase and context tempo. We found that the interaction contributed significantly to the full model ( $\Delta\text{BIC} = 10$ ,  $\chi^2(8) = 64.87$ ,  $p < .001$ ). Therefore, context tempo impacts rhythmic modulation of visual discrimination.

To further characterize how performance changes by target phase (early, in-phase, late) for each tempo separately (0.77 Hz, 1.43 Hz, 2 Hz), we obtained log ratios between groups of interest. We found that the odds to discriminate targets that appear in-phase with the slow tempo (0.7 Hz) are **2.47** times higher than the odds to discriminate early targets ( $OR = 2.47$ , 95% CI: [2.06, 2.96],  $p < .001$ ) and **1.27** times higher than the odds to discriminate late targets ( $OR = 1.27$ , 95% CI: [1.05, 1.53],  $p = .02$ ). Therefore, individuals performed significantly better with targets that appeared in-phase with the slow tempo compared to targets that appeared out-of-phase.

Individuals also performed better with targets that appear in-phase with the medium tempo (1.43 Hz), compared to early targets ( $OR = 1.27$ , 95% CI: [1.07, 1.51],  $p = .01$ ). However, no difference in discrimination performance was found between targets that appeared in-phase with the rhythmic stream and targets that appeared late ( $OR = 0.93$ , 95% CI: [0.78, 1.12],  $p = .44$ ). Finally, for the fast tempo (2 Hz), we did not find evidence for rhythmic modulation of performance. Individuals discriminated similarly targets that appeared in-phase with a rhythmic stream and early targets ( $OR = .93$ , 95% CI: [0.78, 1.11],  $p = .44$ ). Furthermore, individuals discriminated targets that appeared in-phase worse than targets that appeared late ( $OR = .79$ , 95% CI: [0.67, 0.95],  $p = .02$ ).



**FIGURE 2** The impact of external rhythms on visual discrimination is dependent on the tempo of stimulation. Participants performed a visual discrimination task. For the slowest presented tempo (0.77 Hz), performance significantly increased for targets appearing ‘in-phase’ with the preceding stream (blue boxplot), compared to targets appearing half a cycle before (orange boxplot) or half a cycle after (pink boxplot). For the medium tempo (1.43 Hz), perceptual benefits were also found for targets appearing in-phase compared to early targets. No perceptual benefits were found for targets appearing in-phase with the fast tempo (2 Hz). Performance of individual participants is depicted by grey dots. Each grey line connects performance of an individual participant across different target phases within each context tempo.



In summary, the impact of rhythmic temporal expectation on visual discrimination is highly dependent on the tempo of stimulation. Maximal rhythmic modulation was found for the slowest tempo we presented with a **15.9%** benefit for in-phase targets compared to early targets and **3.6%** benefit compared to late targets. The medium tempo we presented elicited a **4.7%** benefit compared to early targets and no benefit compared to late targets. The fast tempo did not elicit a rhythmic modulation of performance. These results were replicated in another sample with a similar experimental design (Figure S1).

To further assess the impact of context tempo on rhythm-based expectation, we compared performance for targets that appeared in-phase with the three different context tempi. We found that the odds of correctly discriminating targets that appeared in-phase with the slow tempo were 1.69 times higher than the odds of correctly discriminating targets that appeared in-phase with the medium tempo ( $OR = 1.69$ , 95% CI: [1.35,2.12],  $p < .001$ ), and 1.8 times higher compared to the fast tempo ( $OR = 1.8$ , CI: [1.46,2.24],  $p < .001$ ). Therefore, the slowest tempo we used was the most effective tempo for forming a rhythm-based expectation for visual discrimination.

### 3.2 | Rhythmic modulation of visual discrimination is linked to individuals' spontaneous tempo

To assess the relationship between individuals' spontaneous tempo and rhythmic modulation of visual discrimination, we performed a model comparison between the full converged model and a nested model, excluding the interaction term between target phase and spontaneous tempo. We found that spontaneous tempo significantly affected the formation of rhythmic facilitation ( $\Delta BIC = 43$ ,  $\chi^2(6) = 13.01$ ,  $p = .04$ ). To further break down this significant interaction between spontaneous tempo and target phase, we calculated the Pearson correlation between individuals' spontaneous motor tempo and the strength of behavioural modulation by target phase. We calculated the strength of behavioural modulation by calculating for each individual the difference in accuracy between targets that appeared in-phase and targets that appeared out-of-phase, averaged across the three different context tempi. This measure emphasized the impact of rhythmic stimulation by removing individual differences in baseline performance. We found that the strength of behavioural modulation is linked to individuals' spontaneous tempo (Figure 3; *in-phase to early targets*:  $r(42) = .45$ ,  $p = .002$ , *in-phase to late targets*:  $r(42) = 0.43$ ,  $p = .004$ ). Specifically, individuals with slower spontaneous tempi exhibited greater differences between in-phase and out-of-phase targets, with reduced

performance for out-of-phase targets (difference between in-phase and out-of-phase performance greater than 0).

### 3.3 | The relationship between spontaneous tempo and rhythmic facilitation is independent of context tempo

We next assessed whether the relationship between spontaneous tempo and target phase is dependent on the tempo of external stimulation. To this end, we performed a model comparison between the full model and a nested model, excluding the three-way interaction term between target phase, spontaneous tempo and context tempo. This interaction did not contribute significantly to the model ( $\Delta BIC = 33$ ,  $\chi^2(4) = 3.88$ ,  $p = .42$ ). A closer inspection of the correlation between accuracy and spontaneous tempo for each target phase and context tempo separately indicated a similar relationship between spontaneous tempo and target phase across the different context tempi.

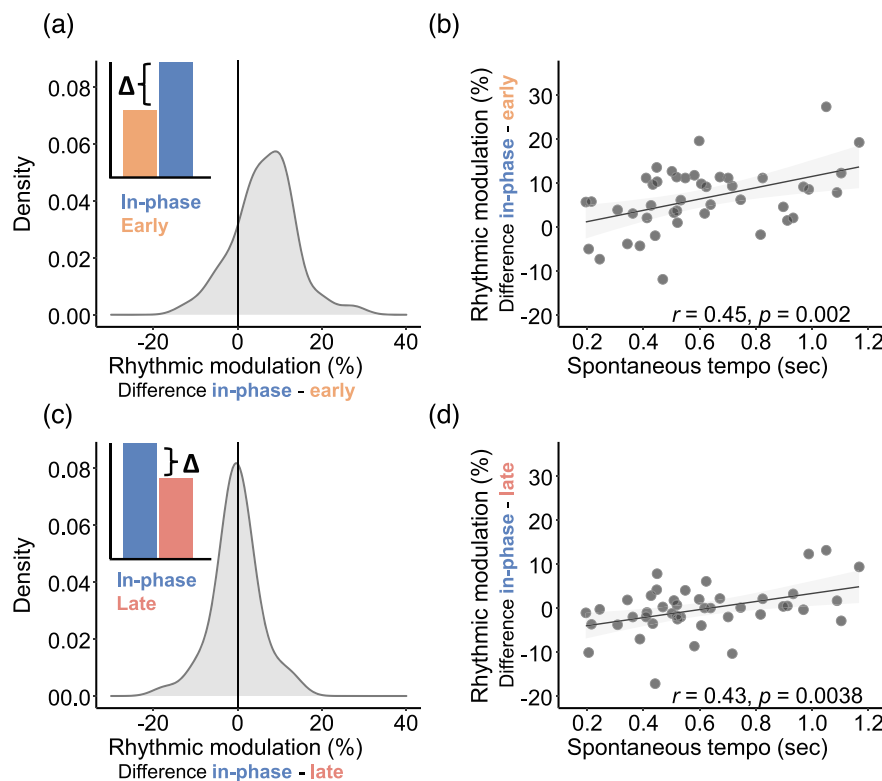
We also tested for the presence of a relationship between context tempo and spontaneous tempo independently of target phase. We compared the full model with a nested model, excluding the interaction between context tempo and spontaneous tempo. This interaction was not significant ( $\Delta BIC = 52$ ,  $\chi^2(6) = 4.64$ ,  $p = .59$ ). Therefore, individual differences in performance between the different context tempi are not accounted for by individual differences in spontaneous motor tempo.

### 3.4 | Rhythmic modulation of visual discrimination is not related to the variability of spontaneous tapping

To examine whether the relationship between spontaneous tempo and rhythmic modulation of visual discrimination can be attributed to individual differences in the variability of spontaneous tapping, we calculated the correlation between the CV of spontaneous tapping and the rhythmic modulation indices. The CV was not related to the strength of rhythmic modulation (*in-phase to early targets*:  $r(42) = -.13$ ,  $p = .39$ , *in-phase to late targets*:  $r(42) = 0.25$ ,  $p = .1$ ). Individuals' CV was also independent of the mean tempo of spontaneous tapping ( $r(42) = -.015$ ,  $p = .33$ ).

## 4 | DISCUSSION

In this study, we examined whether individuals' ability to use external rhythmic structure for perception is dependent on context tempo and on individuals' spontaneous



**FIGURE 3** Behavioural modulation by external rhythms is linked to individuals' spontaneous tempo. (a) Density plot of the rhythmic modulation index, as calculated based on the difference in performance (accuracy scores) between in-phase and early targets, across all context tempi. (b) Individuals' rhythmic modulation index (difference in performance between in-phase and early targets, y-axis) is linked to individuals' spontaneous tempo (assessed through the spontaneous tapping task, x-axis). (c) Density plot of the rhythmic modulation index calculated based on the difference between in-phase and late targets. As can be seen, the group effect is centred at zero (no difference between in-phase and late targets). However, (d) the direction and magnitude of the rhythmic modulation is linked to individual's spontaneous tempo. Therefore, there are substantial individual differences in the impact of external tempo on visual discrimination. This variability can be captured through individual differences in spontaneous motor tempi (i.e. individuals' spontaneous tempo).

tempo. We found that visual rhythmic stimulation modulates discrimination performance. The modulation was dependent on the tempo of stimulation, with maximal perceptual benefits for the slowest tempo of stimulation (0.77 Hz). Most importantly, the strength of modulation was also affected by individuals' spontaneous tempo. Specifically, individuals with slower spontaneous tempi showed greater rhythmic modulation compared to individuals with faster spontaneous tempi. This relationship between spontaneous tempo and rhythmic modulation by external rhythms was not restricted or modulated by the specific tempo of stimulation and was best captured by the difference between 'in-phase' (i.e. on beat) and 'out-of-phase' performance across the different context tempi.

#### 4.1 | Tempo specificity in rhythm-based perceptual modulation

Although individuals can readily synchronize their motor performance with a wide range of tempi (Repp, 2009), we

find a clear advantage for slower tempi in guiding visual perception. Our results are consistent with a recent study by Zalta et al. (2020) that demonstrated optimal performance in an explicit timing task at a stimulation tempo of 0.7 Hz (i.e. beat-discrimination task). These results were interpreted as evidence in favour of the entrainment framework, which predicts optimal performance with external rhythms that are close to endogenous oscillatory activity (Farahbod et al., 2020; Haegens & Zion Golumbic, 2018; Large & Jones, 1999; McAuley et al., 2006; Tavano et al., 2021; Zalta et al., 2020). Such models posit a sampling frequency characteristic of a given system (motor or sensory) that constrains the rhythmic range for optimal perceptual benefits. Our findings are consistent with this conceptual framework and go beyond explicit timing judgements to perceptual discrimination within a rhythmic context.

Rhythmic facilitation in the visual modality has also been demonstrated with substantially faster frequencies (~10 Hz; De Graaf et al., 2013; Mathewson et al., 2010, 2012; Spaak et al., 2014). This putative discrepancy might

reflect two different sources for visual perceptual benefits. Given the short temporal scales, it is possible that entrainment by a 10-Hz stimulus generates local interactions within sensory cortices, while delta frequency stimulation results in the recruitment of top-down temporal anticipation (Fries & Bastos, 2021; Haegens & Zion Golumbic, 2018; Shalev et al., 2019). Future work could attempt to characterize rhythmic perceptual modulation at different temporal scales and address common principles and differences.

## 4.2 | Individual differences in rhythm-based perceptual modulation

Several recent studies that examined the role of external rhythmic structure in guiding perception show high variability across individuals (Bauer, Jaeger, et al., 2015; Lin et al., 2021; Saberi & Hickok, 2021). Different sources of variability were proposed, such as musical experience (Doelling & Poeppel, 2015) and the strength of neural coupling between frontal and auditory brain areas (Assaneo et al., 2019). Our findings indicate that an important source of variability lies in individuals' spontaneous motor preferences. This link between spontaneous rhythmic performance and perceptual modulation by external rhythms strengthens current models of beat perception. These models emphasize the role of the motor system and its spontaneous dynamics in the sensitivity of the perceptual system to external rhythmic structure (Bauer, Kreutz, & Herrmann, 2015; Cannon & Patel, 2021; Criscuolo et al., 2022; Grahn & Rowe, 2009; Morillon & Baillet, 2017; Patel & Iversen, 2014; Ross et al., 2016; Schwartz & Kotz, 2015).

Relatedly, according to the preferred period hypothesis (McAuley et al., 2006), when an individual is performing a rhythmic task close to their rhythmic motor preference, benefits on the rhythmic task should be maximal. Our results do not provide direct support for this hypothesis. They do, however, highlight that spontaneous tempo impacts cognition. We find that task tempo and spontaneous tempo impact performance orthogonally. Slower tempi generate larger performance benefits compared to faster tempi, and individuals with slower spontaneous tempi are more sensitive to rhythmic stimulation. In other words, our study demonstrates that motor rhythmic preferences can determine the impact of externally presented rhythms on sensory processing and thus affect cognition beyond the motor system.

Finally, our findings also extend current literature on the functional role of spontaneous rhythmic preferences. Previous work showed that spontaneous motor tempi can

affect externally paced motor performance in personal (Bardy et al., 2015; McAuley et al., 2006; Roman et al., 2021; Scheurich et al., 2018) and interpersonal settings (Alderisio et al., 2017; Roman et al., 2021; Zamm et al., 2015, 2016, 2018). In addition, previous work investigating the neural markers of rhythm perception found that neural markers modulated by the presence of a rhythm were also linked to individuals' spontaneous rhythmic preferences (Schwartz & Kotz, 2015). Here, for the first time to the best of our knowledge, we show that individuals' spontaneous motor tempi impact visual perception within a rhythmic context, even when overt-beat tracking (e.g. motor synchronization) is not necessary or beneficial for task performance. Therefore, individual differences in spontaneous motor rhythms might be linked to performance variability in a variety of scenarios such as lab-based experiments that include rhythmic temporal structure (e.g. statistical learning tasks; see Kirkham et al., 2002), computerized diagnostic tools (e.g. CPT; see Klee & Garfinkel, 1983) and everyday interpersonal interactions that require rhythmic perception and performance (e.g. communicating, moving and performing together; Keller et al., 2014).

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## CONFLICT OF INTEREST

The authors declare no competing interests.

## AUTHOR CONTRIBUTIONS

LS, SN and ANL conceived and designed the study. YK collected the data. LS analysed the data. LS and ANL wrote the manuscript.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ejn.15898>.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study and the code that was used to analyse them will be publicly available after publication on the OSF page at <https://osf.io/bqu6a/>.



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## REFERENCES

- Alderisio, F., Fiore, G., Salesse, R. N., Bardy, B. G., & Bernardo, M. D. (2017). Interaction patterns and individual dynamics shape the way we move in synchrony. *Scientific Reports*, 7(1), 1–10. <https://doi.org/10.1038/s41598-017-06559-4>
- Amit, R., Abeles, D., Bar-Gad, I., & Yuval-Greenberg, S. (2017). Temporal dynamics of saccades explained by a self-paced process. *Scientific Reports*, 7(1), 886. <https://doi.org/10.1038/s41598-017-00881-7>
- Assaneo, M. F., Ripollés, P., Orpella, J., Lin, W. M., de Diego-Balaguer, R., & Poeppel, D. (2019). Spontaneous synchronization to speech reveals neural mechanisms facilitating language learning. *Nature Neuroscience*, 22(4), 627–632. <https://doi.org/10.1038/s41593-019-0353-z>
- Bardy, G., Hoffmann, C. P., Moens, B., Leman, M., & Dalla, S. (2015). Sound-induced stabilization of breathing and moving. *Annals of the New York Academy of Sciences*, 1337(1), 94–100. <https://doi.org/10.1111/nyas.12650>
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. <https://doi.org/10.1016/J.JML.2012.11.001>
- Bauer, A. K. R., Jaeger, M., Thorne, J. D., Bendixen, A., & Debener, S. (2015). The auditory dynamic attending theory revisited: A closer look at the pitch comparison task. *Brain Research*, 1626, 198–210. <https://doi.org/10.1016/J.BRAINRES.2015.04.032>
- Bauer, A. K. R., Kreutz, G., & Herrmann, C. S. (2015). Individual musical tempo preference correlates with EEG beta rhythm. *Psychophysiology*, 52(4), 600–604. <https://doi.org/10.1111/PSYP.12375>
- Bauer, A. K. R., Van Ede, F., Quinn, A. J., & Nobre, A. C. (2021). Rhythmic modulation of visual perception by continuous rhythmic auditory stimulation. *Journal of Neuroscience*, 41(33), 7065–7075. <https://doi.org/10.1523/JNEUROSCI.2980-20.2021>
- Bengtsson, S. L., Ullén, F., Henrik Ehrsson, H., Hashimoto, T., Kito, T., Naito, E., Forssberg, H., & Sadato, N. (2009). Listening to rhythms activates motor and premotor cortices. *Cortex*, 45(1), 62–71. <https://doi.org/10.1016/J.CORTEX.2008.07.002>
- Benjamini, Y., Drai, D., Elmer, G., Kafkafi, N., & Golani, I. (2001). Controlling the false discovery rate in behavior genetics research. *Behavioural Brain Research*, 125(1–2), 279–284. [https://doi.org/10.1016/S0166-4328\(01\)00297-2](https://doi.org/10.1016/S0166-4328(01)00297-2)
- Berg, R. W. (2002). Rhythmic whisking by rat: Retraction as well as protraction of the vibrissae is under active muscular control. *Journal of Neurophysiology*, 89(1), 104–117. <https://doi.org/10.1152/jn.00600.2002>
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436. <https://doi.org/10.1163/156856897X00357>
- Buzsáki, G., & Wang, X. J. (2012). Mechanisms of gamma oscillations. *Annual Review of Neuroscience*, 35(1), 203–225. <https://doi.org/10.1146/annurev-neuro-062111-150444>
- Cannon, J. J., & Patel, A. D. (2021). How beat perception co-opts motor neurophysiology. *Trends in Cognitive Sciences*, 25(2), 137–150. <https://doi.org/10.1016/j.tics.2020.11.002>
- Cravo, A. M., Rohenkohl, G., Wyart, V., & Nobre, A. C. (2013). Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. *Journal of Neuroscience*, 33(9), 4002–4010. <https://doi.org/10.1523/JNEUROSCI.4675-12.2013>
- Criscuolo, A., Schwartze, M., & Kotz, S. A. (2022). Cognition through the lens of a body–brain dynamic system. *Trends in Neurosciences*, 45, 667–677. <https://doi.org/10.1016/J.TINS.2022.06.004>
- Dankner, Y., Shalev, L., Carrasco, M., & Yuval-Greenberg, S. (2017). Prestimulus inhibition of saccades in adults with and without attention-deficit/hyperactivity disorder as an index of temporal expectations. *Psychological Science*, 28(7), 835–850. <https://doi.org/10.1177/0956797617694863>
- De Graaf, T. A., Gross, J., Paterson, G., Rusch, T., Sack, A. T., & Thut, G. (2013). Alpha-band rhythms in visual task performance: Phase-locking by rhythmic sensory stimulation. *PLoS ONE*, 8(3), 29–32. <https://doi.org/10.1371/journal.pone.0060035>
- Doelling, K. B., & Poeppel, D. (2015). Cortical entrainment to music and its modulation by expertise. *Proceedings of the National Academy of Sciences of the United States of America*, 112(45), E6233–E6242. <https://doi.org/10.1073/pnas.1508431112>
- Farahbod, H., Saberi, K., & Hickok, G. (2020). The rhythm of attention: Perceptual modulation via rhythmic entrainment is low-pass and attention mediated. *Attention, Perception, & Psychophysics*, 82(7), 3558–3570. <https://doi.org/10.3758/s13414-020-02095-y>
- Fraisse, P. (1982). Rhythm and tempo. In D. Deutsch (Ed.), *The psychology of music* (pp. 149–180). Academic Press.
- Fries, P., & Bastos, A. M. (2021). Which rhythms reflect bottom-up and top-down processing? December. <https://doi.org/10.13140/RG.2.2.21306.52160>
- Grahn, J. A., & Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. *Journal of Cognitive Neuroscience*, 19(5), 893–906. <https://direct.mit.edu/jocn/article-abstract/19/5/893/4337>. <https://doi.org/10.1162/jocn.2007.19.5.893>
- Grahn, J. A., & Rowe, J. B. (2009). Feeling the beat: Premotor and striatal interactions in musicians and nonmusicians during beat perception. *Journal of Neuroscience*, 29(23), 7540–7548. <https://doi.org/10.1523/JNEUROSCI.2018-08.2009>
- Haegens, S., & Zion Golumbic, E. (2018). Rhythmic facilitation of sensory processing: A critical review. *Neuroscience and Biobehavioral Reviews*, 86, 150–165. <https://doi.org/10.1016/J.NEUBIOREV.2017.12.002>
- Inbar, M., Grossman, E., & Landau, A. N. (2020). Sequences of intonation units form a ~ 1 Hz rhythm. *Scientific Reports*, 10(1), 1–9. <https://doi.org/10.1038/s41598-020-72739-4>
- Jaeger, T. F. (2008). Memory and language categorical data analysis: Away from ANOVAs (transformation or not) and towards logit mixed models. *Journal of Memory and Language*, 59(4), 434–446. <https://doi.org/10.1016/j.jml.2007.11.007>
- Jones, M. R. (2010). Attending to sound patterns and the role of entrainment. In A. C. Nobre & J. T. Coull (Eds.), *Attention and time* (pp. 317–330). Oxford UP.
- Keller, P. E., Novembre, G., & Hove, M. J. (2014). Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal coordination. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 369(1658), 20130394. <https://doi.org/10.1098/rstb.2013.0394>

- Kirkham, N. Z., Slemmer, J. A., & Johnson, S. P. (2002). Visual statistical learning in infancy: Evidence for a domain general learning mechanism. *Cognition*, 83(2), B35–B42. [https://doi.org/10.1016/S0010-0277\(02\)00004-5](https://doi.org/10.1016/S0010-0277(02)00004-5)
- Klee, S. H., & Garfinkel, B. D. (1983). The computerized continuous performance task: A new measure of inattention. *Journal of Abnormal Child Psychology*, 11(4), 487–495. <https://doi.org/10.1007/BF00917077>
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., Broussard, C., & Cornelissen, F. (2007). What's new in Psychtoolbox-3? *Perception*, 36(14), 1–16. [https://pure.mpg.de/rest/items/item\\_1790332/component/file\\_3136265/content](https://pure.mpg.de/rest/items/item_1790332/component/file_3136265/content)
- Lakatos, P., Gross, J., & Thut, G. (2019). A new unifying account of the roles of neuronal entrainment. *Current Biology*, 29(18), R890–R905. <https://doi.org/10.1016/j.cub.2019.07.075>
- Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology*, 22(11), 1000–1004. <https://doi.org/10.1016/j.cub.2012.03.054>
- Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track time-varying events. *Psychological Review*, 106(1), 119–159. <https://doi.org/10.1037/0033-295X.106.1.119>
- Lenth, R. (2019). Emmeans: Estimated marginal means. In *R package version 1.4.2* (p. <https://cran.r-project.org/package=emmeans>). <https://github.com/rvleenth/emmeans%0Ahttps://cran.r-project.org/package=emmeans>
- Lin, W. M., Oettringer, D. A., Bakker-Marshall, I., Emmerzaal, J., Wilsch, A., Elshafei, H. A., Rassi, E., & Haegens, S. (2021). No behavioural evidence for rhythmic facilitation of perceptual discrimination. *European Journal of Neuroscience*, 55(11–12), 3352–3364. <https://doi.org/10.1111/EJN.15208>
- Mathewson, K. E., Fabiani, M., Gratton, G., Beck, D. M., & Lleras, A. (2010). Rescuing stimuli from invisibility: Inducing a momentary release from visual masking with pre-target entrainment. *Cognition*, 115(1), 186–191. <https://doi.org/10.1016/j.cognition.2009.11.010>
- Mathewson, K. E., Prudhomme, C., Fabiani, M., Beck, D. M., Lleras, A., & Gratton, G. (2012). Making waves in the stream of consciousness: Entraining oscillations in EEG alpha and fluctuations in visual awareness with rhythmic visual stimulation. *Journal of Cognitive Neuroscience*, 24(12), 2321–2333. [https://doi.org/10.1162/jocn\\_a\\_00288](https://doi.org/10.1162/jocn_a_00288)
- McAuley, J. D., Jones, M. R., Holub, S., Johnston, H. M., & Miller, N. S. (2006). The time of our lives: Life span development of timing and event tracking. *Journal of Experimental Psychology: General*, 135(3), 348–367. <https://doi.org/10.1037/0096-3445.135.3.348>
- Meteyard, L., & Davies, R. A. I. (2020). Best practice guidance for linear mixed-effects models in psychological science. *Journal of Memory and Language*, 112, 104092. <https://doi.org/10.1016/j.jml.2020.104092>
- Monto, S., Palva, S., Voipio, J., & Palva, J. M. (2008). Very slow EEG fluctuations predict the dynamics of stimulus detection and oscillation amplitudes in humans. *Journal of Neuroscience*, 28(33), 8268–8272. <https://doi.org/10.1523/JNEUROSCI.1910-08.2008>
- Moore, J. D., Kleinfeld, D., & Wang, F. (2014). How the brainstem controls orofacial behaviors comprised of rhythmic actions. *Trends in Neurosciences*, 37(7), 370–380. <https://doi.org/10.1016/J.TINS.2014.05.001>
- Morillon, B., & Baillet, S. (2017). Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences of the United States of America*, 114(42), E8913–E8921. <https://doi.org/10.1073/pnas.1705373114>
- Nobre, A. C., & van Ede, F. (2017). Anticipated moments: Temporal structure in attention. *Nature Reviews Neuroscience*, 19(1), 34–48. <https://doi.org/10.1038/nrn.2017.141>
- Otero-Millan, J., Troncoso, X. G., Macknik, S. L., Serrano-Pedraza, I., & Martinez-Conde, S. (2008). Saccades and microsaccades during visual fixation, exploration, and search: Foundations for a common saccadic generator. *Journal of Vision*, 8(14), 21. <https://doi.org/10.1167/8.14.21>
- Patel, A. D., & Iversen, J. R. (2014). The evolutionary neuroscience of musical beat perception: The action simulation for auditory prediction (ASAP) hypothesis. *Frontiers in Systems Neuroscience*, 8, 57. <https://doi.org/10.3389/fnsys.2014.00057>
- Poeppel, D., & Assaneo, M. F. (2020). Speech rhythms and their neural foundations. *Nature Reviews Neuroscience*, 21(6), 322–334. <https://doi.org/10.1038/s41583-020-0304-4>
- Repp, B. H. (2009). Rate limits of sensorimotor synchronization. *Advances in Cognitive Psychology*, 2(2), 163–181. <https://doi.org/10.2478/v10053-008-0053-9>
- Roman, I. R., Roman, A. S., & Large, E. W. (2021). Hebbian learning with elasticity explains how the spontaneous motor tempo affects music performance synchronization. *BioRxiv* [Preprint]. <https://doi.org/10.1101/2020.10.15.341610>
- Ross, J. M., Iversen, J. R., & Balasubramaniam, R. (2016). Motor simulation theories of musical beat perception. *Neurocase*, 22(6), 558–565. <https://doi.org/10.1080/13554794.2016.1242756>
- Saberi, K., & Hickok, G. (2021). Forward entrainment: Evidence, controversies, constraints, and mechanisms. *BioRxiv*, 2021.07.06.451373. <https://doi.org/10.1101/2021.07.06.451373>
- Scheurich, R., Zamm, A., & Palmer, C. (2018). Tapping into rate flexibility: Musical training facilitates synchronization around spontaneous production rates. *Frontiers in Psychology*, 9, 1–13. <https://doi.org/10.3389/fpsyg.2018.00458>
- Schwartz, M., & Kotz, S. A. (2015). The timing of regular sequences: Production, perception, and covariation. *Journal of Cognitive Neuroscience*, 27(9), 1697–1707. [https://doi.org/10.1162/JOCN\\_A\\_00805](https://doi.org/10.1162/JOCN_A_00805)
- Shalev, N., Bauer, A. K. R., & Nobre, A. C. (2019). The tempos of performance. *Current Opinion in Psychology*, 29, 254–260. <https://doi.org/10.1016/J.COPSYC.2019.06.003>
- Shalev, N., Boettcher, S., Wilkinson, H., Scerif, G., & Nobre, A. C. (2022). Be there on time: Spatial-temporal regularities guide young children's attention in dynamic environments. *Child Development*, 93(5), 1414–1426. <https://doi.org/10.1111/cdev.13770>
- Shalev, N., & Nobre, A. C. (2022). Eyes wide open: Regulation of arousal by temporal expectations. *Cognition*, 224, 105062. <https://doi.org/10.1016/J.COgnITION.2022.105062>
- Spaak, E., de Lange, F. P., & Jensen, O. (2014). Local entrainment of alpha oscillations by visual stimuli causes cyclic modulation of perception. *Journal of Neuroscience*, 34(10), 3536–3544. <https://doi.org/10.1523/JNEUROSCI.4385-13.2014>
- Sun, Y., Michalareas, G., & Poeppel, D. (2021). The impact of phase entrainment on auditory detection is highly variable: Revisiting a key finding. *European Journal of Neuroscience*, 55(11–12), 3373–3390. <https://doi.org/10.1111/EJN.15367>

- Tavano, A., Maess, B., Poeppel, D., & Schröger, E. (2021). Neural entrainment via perceptual inferences. *European Journal of Neuroscience*, 2022, 3277–3287. <https://doi.org/10.1111/ejn.15630>
- VanRullen, R. (2016). Perceptual cycles. *Trends in Cognitive Sciences*, 20(10), 723–735. <https://doi.org/10.1016/j.tics.2016.07.006>
- Zalta, A., Petkoski, S., & Morillon, B. (2020). Natural rhythms of periodic temporal attention. *Nature Communications*, 11(1), 1051. <https://doi.org/10.1038/s41467-020-14888-8>
- Zamm, A., Pfordresher, P. Q., & Palmer, C. (2015). Temporal coordination in joint music performance: Effects of endogenous rhythms and auditory feedback. *Experimental Brain Research*, 233(2), 607–615. <https://doi.org/10.1007/s00221-014-4140-5>
- Zamm, A., Wang, Y., & Palmer, C. (2018). Musicians' natural frequencies of performance display optimal temporal stability. *Journal of Biological Rhythms*, 33(4), 432–440. <https://doi.org/10.1177/0748730418783651>
- Zamm, A., Wellman, C., & Palmer, C. (2016). Endogenous rhythms influence interpersonal synchrony. *Journal of Experimental*

*Psychology: Human Perception and Performance*, 42(5), 611–616. <https://doi.org/10.1037/xhp0000201>

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