Neuroscience

A novel method for estimating properties of attentional oscillators reveals an age-related decline in flexibility

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Abstract

Auditory tasks such as understanding speech and listening to music rely on the ability to track sound sequences and adjust attention based on the temporal cues they contain. An entrainment approach proposes that internal oscillatory mechanisms underlie the ability to synchronize with rhythms in the external world. Here, we aimed to understand the factors that facilitate and impede rhythm processing by investigating the interplay between the properties of external and internal rhythms. We focused on two key properties of an oscillator: its preferred rate, the default rate at which it oscillates in the absence of input, and flexibility, its ability to adapt to changes in rhythmic context. We hypothesized that flexibility would be diminished with advancing age. Experiment 1 was a two-session duration discrimination paradigm where we developed methods to estimate preferred rate and flexibility and assessed their reliability. Experiment 2 involved a shorter version of this paradigm and a paced tapping task with matched stimulus conditions, in addition to a *spontaneous motor tempo* (SMT) and two *preferred perceptual tempo* (PPT) tasks that measured motor and perceptual rate preferences, respectively. Preferred rates, estimated as the stimulus rates with the best performance, showed a harmonic relationship across sessions (Experiment 1) and were correlated with SMT (Experiment 2). Interestingly, estimates from motor tasks were slower than those from the perceptual task, and the degree of slowing was consistent for each individual. To challenge an individual's oscillator flexibility, we maximized the differences in stimulus rates between consecutive trials in the duration discrimination and paced tapping tasks. As a result, performance in both tasks decreased, and performance on individual trials indicated a gravitation toward the stimulus rate presented in the preceding trial. Critically, flexibility, quantified as an individual's ability to adapt to faster-than-previous rates, decreased with age. Overall, these findings show domain-specific rate preferences for the assumed oscillatory system underlying rhythm perception and production, and that this system loses its ability to flexibly adapt to changes in the external rhythmic context during ageing.

eLife assessment

This **valuable** study has practical implications for understanding rhythm perception and production in human cognition. The evidence for individual frequency preferences and a deterioration in frequency adaptation with age is **solid**. These findings may inform existing models of rhythm perception and production, and the reported effects of age may have clinical implications.

Auditory tasks such as understanding speech and listening to music rely on our ability to allocate and adjust attention to rhythmic cues in complex auditory signals. However, listeners' tracking of and attention to rhythmic cues can fail when the signal is temporally disorganized[1], or with advancing age[2]. These failures of attention might result in reduced speech comprehension[2] as well as in diminished ability to solve the "cocktail party problem"[3]. However, speech perception[4] and production of musical sequences are improved when stimuli are presented at specific rates[5,6], indicating that these abilities might be "restored" in certain conditions. Here, we aimed to understand factors that facilitate and impede auditory rhythm processing from two different perspectives: those factors that arise from stimulus properties in the external world and those that stem from individual differences (the perceiver). Specifically, we tested how stimulus and the rhythmic context, in which a stimulus is presented, affects perception and production, and how temporal adaptation abilities change with advancing age. We found (1) a range of rates specific for each individual that yielded best performance, and (2) deteriorating performance when switching between stimulus rates that was further amplified by age.

Two main theoretical approaches explain how we perceive time and rhythm. A timekeeper account proposes that the duration between two events is represented by the count of accumulated pulses that are generated by an internal pacemaker[7]. An entrainment account, the Dynamic Attending Theory (DAT) proposes that biological systems consist of internal oscillations, i.e., rhythms, that adjust their phase and period to the temporal regularities of an external signal[8–10]. Synchronization between internal and external rhythms, termed *entrainment*, is the underlying mechanism for time and rhythm perception. Predictions of DAT have been confirmed in a number of studies that reported rhythmic facilitation effects, where a rhythmic cue improves perceptual timing of subsequent targets, with the highest accuracy for targets aligning with the entraining attentional oscillator's peaks[11–18].

The current study did not test whether timing abilities are governed by entrainment or timekeeper mechanisms. We rather adopt an entrainment approach as well as common assumptions of entrainment models[19] that derive from the general properties of limit-cycle oscillators:

Assumption 1: Oscillations are self-sustaining; they persist even when no stimulus is present. They induce series of periodic expectations at the peaks of this oscillation.

Assumption 2: Oscillators are adaptive; they respond to timing perturbations (e.g., changes in stimulus rate) by correcting their phase and period.

Assumption 3: Each oscillator has an intrinsic period[20] at which it oscillates in the absence of any input (see Assumption 1) and is most stable against perturbations.

Assumption 4: Oscillators can respond to stimulus rates with integer-ratio relationships (i.e., in nested hierarchies).

Two key properties of internal oscillators that were the focus of the current study, are their *preferred rate* and their *flexibility*. Preferred rate, also termed as natural frequency or *eigenfrequency* in different literatures, refers to the intrinsic period of the oscillator (Assumption 3), or group of nested oscillators[19], in the absence of any input (Assumption 1). Oscillators accomplish synchronization to periodicities in the external signal better when the signal's rate is similar to the oscillator's preferred rate (or harmonics of the preferred rate[14]) than when it is dissimilar[21]. The range of rates around the oscillator's preferred rate for synchronization is referred to as the *entrainment region*[22]. Theoretically, knowing the preferred rate of an individual's internal oscillator would allow predicting the rates at which they would most successfully interact in a real-world listening situation.

One common method to estimate the preferred rate is the spontaneous motor tapping task, where participants are asked to tap their finger[22–24] or a drumstick[20], on a desk or a sensor at a "comfortable rate". The preferred rate estimate, spontaneous motor tempo (SMT), measured as the mean or median of the intervals between the individual taps, tends to cluster around 500-600 ms in adults[22]. One potential short-coming of using SMT as a direct measure of an internal oscillator's preferred rate is that SMT reflects a "preference" for producing periodic movements in the absence of any interaction with the environment. Although this is indeed the definition of preferred rate, a stronger test of the degree to which SMT reflects the preferred rate of an internal oscillator would be to observe successful synchronization within – but not outside of – an entrainment region. SMT does predict timing preference and performance in other tasks: participants tend to prefer stimulus rates (i.e., preferred perceptual tempo, PPT[22]) closer to their SMT[22], drift back to their SMT during continuation tapping in synchronization-continuation paradigms[5], and over-and-underproduce stimuli that are faster and slower than their SMT, respectively[5,6]. However, in paradigms that involve comparison of individuals' rate preferences[22] and tapping performance[5,25] across stimulus rates, stimulus conditions are tailored to individuals' SMT and are low in number. This results in a resolution that is too poor to observe an entrainment region, and often confounds SMT with the global mean stimulus rate in an experiment[26]. We have previously proposed a synchronization-continuation paradigm where individuals' tapping behavior on a finely-sampled broad range of stimulus rates was assessed. We estimated the preferred rate as the stimulus rate with minimum tapping errors during continuation tapping[27]. However, estimating preferred rates based on a tapping paradigm cannot disentangle preferred rates of an auditory oscillator, a motor oscillator, or a coupled oscillatory system whose preferred rate would be influenced by the preferences and coupling strengths of its components[1]. Thus, here we applied the fine rate sampling to a perceptual paradigm (Experiment 1), estimated preferred rates in perceptual and motor versions of the paradigm with same stimulus rate conditions (Experiment 2), and compared the estimates to individuals' SMT and PPT (Experiment 2).

Based on Assumption 2, we defined flexibility as the internal oscillator's ability to adapt to rate changes in the external sound signal[27]. The logic is as follows: upon encountering a new rate, the oscillator gradually updates its phase and period to each upcoming interval. From a dynamical systems perspective, flexibility can be conceptualized as a complement to "stiffness", and might be quantified based on the presence of hysteresis, which refers to a system's tendency to stay in a previous state despite changes in stimulus parameters[28]. An inflexible oscillator would exhibit hysteresis and continue to respond in a way that reflects the properties of previously entrained stimuli. A fully flexible oscillator would not exhibit hysteresis as it would completely update its phase and period to the new stimulus, resulting in no discrepancy between the current stimulus and its internal representation. Thus, the extent to which timing performance would be affected by the stimulus history is inversely related to the underlying oscillator's flexibility.

Prior research reveals effects of preceding context (also referred to as serial dependence[29,30] and carryover effects[31]) on timing behavior in tasks with and without a motor synchronization component. Within individual trials of synchronized tapping paradigms, changes in stimulus rate (period perturbation), and stimulus onset times (phase perturbation) result in increased asynchronies between stimulus and tap onsets. This effect is more pronounced for phase than period perturbations[32,33], and for sequences that speed up than those that slow down[25,33]. Across trials, the tapping rate in each trial is biased toward the previous trial's stimulus rate[27,30]. Temporal judgments in the absence of motor synchronization are also affected by the stimulus properties presented in a preceding trial[31,34,35] and throughout the experiment[34,36], suggesting effects of local and global temporal contexts on duration perception. The majority of studies that revealed individual differences in proneness to history effects[29,37] have not aimed to explicitly estimate the extent and source of these individual differences, or have done so in shorter temporal contexts, using different operational definitions of flexibility than the one used here[6]. Finally, similar to methods proposed to estimate preferred rate[5,6,22,27,38], previous attempts to measure flexibility[6,25,27] involved only motor responses. Thus, we presented the same stimulus history to participants in two tasks, one with and one without the motor demands of synchronize-continue tapping. This design allowed assessing the effects of the same predictor (trial-to-trial rate change) on performance in different tasks, and thereby performing systematic comparisons of oscillator flexibility across perceptual and motor domains.

From the perceiver's side, we chose to focus on how properties of internal oscillators change with advancing age. Studies assessing age-related changes in timing abilities show that older, as compared to younger individuals, produce slower tapping rates when asked to tap at a comfortable rate[22,39] at the fastest rate[40] they can maintain; show worse performance in temporal-order judgments[41], gap detection[42], and discrimination and reproduction of time intervals[43]; and tend to prefer slower stimulus rates[22], which manifests in a breakdown in understanding fast speech. From an entrainment perspective, these results suggest that internal oscillators of older individuals have slower preferred rates, reduced flexibility, or both. While the current study did not incorporate neural measures, it is worth noting that literature on neural entrainment can offer insights into the dynamics of attention. This is particularly relevant as these physical measures often align with the predictions of the dynamic attending theory. (see Refs.[44,45] for reviews). Neural entrainment to external auditory signals is aberrant[46–48], and less responsive to top-down attention in older than younger adults[49]. Moreover, older adults exhibit reduced neural adaptation[50] and sensory gating[51], suggesting an age-related decline in neural inhibition[50] that leads to a reduced capacity of the auditory system to adapt based on context. Based on the behavioral findings converging on reduced temporal abilities and evidence for impaired neural entrainment in older individuals, we hypothesized that older adults would exhibit stronger hysteresis than younger adults, which should result in smaller estimates of oscillator flexibility.

The aim of the current study was to estimate individuals' preferred rate and flexibility in rhythmic tasks with and without a motor synchronization component, and in both preference and performance contexts: here, preference refers to SMT and PPT, whereas performance refers to tasks that require listeners to either synchronize with or make a perceptual judgment about rhythmic stimuli. Moreover, we aimed to assess how internal oscillator properties, specifically oscillator flexibility, change with advancing age.

We conducted two experiments. The main goal of Experiment 1 was to develop methods to estimate preferred rate and flexibility in a paradigm without a motor synchronization component, as a complement to our recent tapping study[27]. The task was a duration discrimination paradigm where participants compared the duration of a single comparison interval to the duration of intervals making up a standard stimulus. We assessed the effect of stimulus history on responses by comparing performance across two sessions with the same finely-sampled pool of stimulus rates, one where we maximized and the other where we minimized the amount of rate change across trials. Experiment 2 involved shorter versions of the duration discrimination

(Experiment 1) and paced tapping[27] tasks with matched stimulus rates and histories, unpaced tapping tasks including SMT, and two tasks where individuals' rate preferences (PPT) were measured.

In line with the *preferred period hypothesis*[22], if SMT captures the preferred rate of common mechanisms underlying rhythm perception and production, we should see better performance around an individual's SMT, as has previously been observed for motor tasks[5,6,22,52]. However, we did not necessarily expect a one-to-one correspondence between preferred rate estimates across tasks with and without a motor component, as individual differences in motor contributions to synchronization abilities are well documented[53].

We hypothesized that larger trial-to-trial changes in stimulus rate would lead to poorer performance due to hysteresis, in that both tapping and duration-discrimination responses should reflect the properties of the preceding stimuli. Thus, we expected that larger changes between consecutive trials' stimulus rates should decrease discrimination accuracy and increase tapping errors. We expected that the strength of these effects – the degree of inflexibility – should increase with age.

Experiment 1

Methods

Participants

Participants (N = 31) were recruited from the participant pool of Max Planck Institute for Empirical Aesthetics laboratories in Frankfurt, Germany. Written informed consent was obtained from all participants. The procedure was approved by the Ethics Council of the Max Planck Society and the Research Ethics Board at Toronto Metropolitan University in accordance with the Declaration of Helsinki. Out of 31 (age: M = 33, SD = 11) individuals who were recruited for the study, 27 participants (age: M = 33, SD = 12) completed both sessions. Upon completion of each session, participants received 7 euros for every 30 minutes of their participation (21 euros per session on average). Two participants volunteered to complete the study without compensation. Prior to the experimental sessions, participants completed an online survey. All participants self-reported normal hearing and proficiency in English.

Procedure

The study consisted of an online background survey that participants completed at home, and then two experimental sessions. During the in-lab experimental sessions, participants completed two types of tasks. A series of unpaced tapping tasks, consisting of SMT[54] and a 'forced' motor tempo (FMT) task, which was used to assess the range of free tapping rates within the participants' motor abilities. The main task was duration discrimination, where participants judged whether a comparison interval was 'shorter' or 'longer' than the intervals making up a standard sequence. Details of all tasks are provided below. Sessions were separated by 4-19 days. A single session started with the SMT and FMT tasks. Participants then set the sound volume to a level that they found comfortable for completing the task. Then, participants were presented with instructions on a computer screen that explained the main task with text and figures. A practice block, simulating the duration discrimination task, followed the instructions (details below). All instructions were in English. Once participants indicated that they understood the task, the main task blocks were initiated. Finally, unpaced tapping tasks were repeated in the same order. Participants were debriefed upon their request, only after the second session. An individual session lasted 90 minutes on average.

Duration discrimination task

The main task was a duration discrimination paradigm, where participants judged whether a comparison interval was longer or shorter than the intervals making up an isochronous standard sequence, by pressing either the L (longer) or S (shorter) key on a computer keyboard. The task procedure is illustrated in **Figure 1**. In each experimental session, 400 unique trials of this task were presented, each consisting of a combination of the three main independent variables: the inter-onset interval, IOI; amount of deviation of the comparison interval from the standard, DEV, and the amount of change in stimulus IOI between consecutive trials, ΔIOI. We explain each of these variables in detail in the next paragraphs.

Stimuli were made up of 50-ms woodblock sounds; first, an isochronous standard sequence and then a comparison interval, separated by a silent gap. The interval between the 5 woodblock sounds making up the 'standard' isochronous stimulus sequence is referred to as IOI. Each trial's IOI was drawn (without replacement) from a pool of all possible stimulus rates, linearly spaced between 200 to 998 ms in 2-ms steps. The silent interval between the last stimulus onset of the standard sequence and the first stimulus onset of the comparison pair was 6 times the standard IOI.

The comparison interval on each trial was longer or shorter than the standard IOI. DEV refers to the magnitude of the comparison interval's deviation from the standard IOI. DEV took on one of ten levels, which were proportional to IOI: ± 2%, 7%, 11%, 16%, 20%. Each DEV level was presented 40 times in each session. Since IOI was unique on each trial, IOI and DEV were not fully crossed factors. Instead, the IOI dimension was divided into 40 bins, each consisting of 10 consecutive IOIs. The 10 DEV levels were randomly assigned to the 10 IOI values in each bin. The correspondence between IOI and DEV pairs was unique for each participant.

While the mean (M = 599 ms), standard deviation (SD = 231 ms) and range (200, 998 ms) of the presented stimulus IOIs were identical between the sessions, the way IOI changed from trial to trial was different. Change in IOI between consecutive trials was referred to as ΔIOI. In one session, the 'linear-order' session, ΔIOI was always ±4 ms. In one half of the session, ΔIOI was fixed at +4 ms. That is, IOI was 200 ms in the first trial, 204 ms in the second, and so on. In the other half of the session, ΔIOI was fixed at –4 ms. On the first trial, IOI was 998 ms, 994 in the second, and so on. The starting point, either 200 ms or 998 ms (in fast-start and slow-start conditions, respectively), was counterbalanced across participants.

In the other session, the 'random-order' session, ΔIOI was maximized, and the direction of the change (i.e., whether a trial was faster or slower than the previous) alternated on every trial. That is, if the stimulus IOI on one trial was faster than the previous (-ΔIOI), it would be slower (+ΔIOI) in the following trial, and vice versa. Note that stimulus IOI was stable within the standard sequence, and only changed between trials. Session order, that is, whether a participant experienced the linear-order or random-order session first, was counterbalanced across participants. An example trajectory of stimulus IOI within linear-order and random-order sessions across trials is illustrated in **Figure 1**.

In each session, participants completed 407 trials, presented in 8 blocks with 50 trials in the first block, and 51 trials in the remaining 7 blocks. Except for the first block, the first trial of each block repeated the IOI that was presented as the last trial of the preceding block and was discarded from further analyses; this enabled preservation of the between-trial histories across blocks between which participants were allowed to take short breaks. Before the main task, participants were instructed about the task, and practiced the task for at least 6 trials. Instructions included two example trials with IOI of 500 ms, one with DEV of +.3 and another with DEV of -.3, illustrating 'comparison longer' and 'comparison shorter' conditions, respectively. DEV was fixed at -.2 in half of the practice trials, and at +.2 in the other half. Two practice trials each were presented at fast,

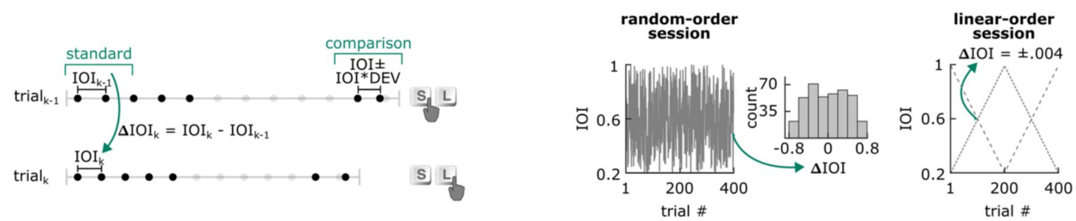


Figure 1

Design of the duration discrimination task in Experiment 1.

Each trial consisted of an isochronous standard sequence of five sounds (four intervals), followed by silence and another pair of sounds. The comparison duration was either shorter or longer than the standard intervals and took on one of ten values (DEV) that were proportional to the inter-onset interval (IOI) between tones making up the standard sequence. The task was to press the S or L key to indicate whether the comparison interval was shorter or longer than the standard IOI. Over the course of 400 unique trials of a single session, IOI ranged from 200 to 998 ms. In random-order sessions, change in stimulus rate between a given trial n and immediately preceding trial n-1 (ΔIOI) was maximized, and the distribution of ΔIOI ranged from -778 ms to +770 ms. In linear-order sessions, IOI increased in each trial in the first 200 trials and decreased in the other half of the trials (or vice versa, counterbalanced across participants) in steps of 4 ms.

medium, and slow IOIs; randomly selected from ranges of [300 - 500 ms], [501 - 700 ms] and [701 - 900 ms], respectively. If participants failed on more than 3 of the first 6 practice trials, they completed another round of 6 practice trials. Both example and practice trials were randomly ordered within their respective blocks in each session.

The dependent variables were accuracy and bias. Accuracy coded whether a response on a trial was correct or not (1 = correct, 0 = incorrect). Bias, on the other hand, could take on one of three values per trial: if the response was correct, bias was 0. If the comparison interval in a trial was longer, and the participant's response was 'shorter', bias in that trial was -1. Similarly, if participant's response was 'longer' in a trial where comparison interval was shorter, bias was +1.

Unpaced tapping tasks

Unpaced tapping tasks consisted of a single SMT trial and two FMT trials, one each to estimate the 'slowest' and 'fastest' rates at which participants could maintain steady tapping. The unpaced tasks were repeated in the same order before and after completion of the duration discrimination task in both sessions. In the SMT task, participants were instructed to 'tap on the desk at a rate that is comfortable to maintain'. In the FMT tasks, the instruction was 'tap at the slowest rate that is comfortable to maintain' (FMT-slowest) and to 'tap at the fastest rate that is comfortable to maintain' (FMT-fastest). Participants tapped for 30 seconds in the SMT task and FMT-fastest task, and 45 seconds in the FMT-slowest task. For all unpaced tapping tasks, the dependent measures were tapping rate (median of the produced intervals) and coefficient of variation.

Apparatus

Stimuli were generated and presented on a Windows desktop computer, using the Psychophysics Toolbox extensions[55,56] for Matlab. Auditory stimuli were presented via Beyerdynamics 880 Pro headphones. The audio signal was presented and recorded by an RME Fireface UC soundcard. All instructions were presented on an ASUS VG24QE LCD screen. Keypress responses for the duration discrimination task were collected on a USB keyboard. Tapping responses for the unpaced tapping tasks were recorded via a Schaller Oyster S/P contact microphone at a sampling rate of 44100 Hz. The contact microphone was attached on the right half of the desk by default. Prior to the sessions, participants were asked to specify if they would like the microphone to be moved to the left half of the desk. None of the participants requested a relocation of the microphone.

Background survey

Prior to the first experimental session, participants completed an online survey. The survey consisted of two parts: the first part included questions about participants' demographics, language skills, hearing abilities, and psychological disorders. The second part was 'The Goldsmiths Musical Sophistication Index', 'Gold-MSI'[57]. The survey language was English by default, with an option to change the language to German. One question in the Gold-MSI was removed from the analyses due to contrasting Likert coding between the different languages in which the survey was completed.

Analysis

Data cleaning and exclusion criteria

The raw format of the tapping data was audio, since tapping responses were collected by a microphone. Individual taps were extracted from the audio files after visual inspection of the soundwave of each trial to set the noise floor for the recording on that trial. All peaks that exceeded the noise floor were retained. Inter-tap intervals (ITIs) were calculated as the difference between neighboring taps' timestamps. We developed an automated procedure that detects and removes single-trial ITI outliers while accounting for drift that may have occurred within tapping trials. The script first marked the ITIs whose deviation from the median ITI exceeded 3x the median absolute deviation (MAD) of all ITIs in the respective trial. Then, it fitted a linear regression to the unmarked ITIs as a function of tap count. Finally, it removed any ITI that was smaller than half or larger than 1.5 times the predicted ITI.

Exclusion criteria for the main task were (1) a decrease in accuracy with increasing absolute DEV, and (2) chance level performance for both deviation directions (trials where comparison interval was shorter, and those where it was longer). To assess the first criterion at the participant level, we fitted separate models to each individual's single-session data where accuracy was predicted by absolute deviation of the comparison interval for either shorter (|-DEV|) or longer (|+DEV|) comparison conditions. The models were fitted using Matlab's *fitglm* function, with the response variable distribution specified as 'binary', and link function specified as 'logit', since the response variable, accuracy, was binary. Next, we compared the slopes (β) obtained from the separate models where either or predicted accuracy against zero, using one-tailed one-sample t-tests. All participants had positive slopes for both directions in both session types, indicating that the probability of correct response increased with |DEV| in all conditions. To test for chance level performance, for each session type, we split all trials into negative and positive DEV conditions and compared each group of trials' accuracy against a mean of .5, using one-sample t-tests. Results showed that none of the participants had chance-level performance for both deviation directions. Finally, before applying group-level statistics such as t-tests and correlations, any datapoint that fell outside of the interquartile range was excluded from the respective distributions.

Preferred rate estimates

We conceptualized individuals' preferred rates as the stimulus rates where duration-discrimination accuracy was highest. To estimate preferred rate on an individual basis, we smoothed response accuracy across the stimulus-rate (IOI) dimension for each session type, using the *smoothdata* function in Matlab. Estimates of preferred rate were taken as the smoothed IOI that yielded maximum accuracy. Details of the smoothing procedure are provided in the Supplementary Information.

To compare the preferred rate estimates between session types, we first conducted a paired-samples t-test. Then, we assessed the correspondence between the estimates. However, conventional correlation methods are not able to capture possible harmonic relationships between variables. Thus, we used a permutation test[27] that accounted for the harmonic structure in data, in addition to the assessment of one-to-one correspondence between the datapoints. The test first calculates the perpendicular distance of the data points to the closest line among the y = x, y = 2*x and y = x/2 theoretical lines (referred to as residuals here, as in Ref.[27]) whose sum quantifies how much the datapoints deviate from a total harmonic correspondence. Then, the test shuffles the Y-axis values with respect to the X-axis values 1000 times and calculates summed residuals for each permutation. The p-value is the percentage of summed residuals smaller than the initial value computed from original data. To validate the results obtained from this test, we ran additional analyses using circular and modular approaches. Details of these analyses and their results are provided in the Supplementary Information.

In addition to estimating the preferred rate as stimulus rates with peak performance, we investigated whether accuracy increased as a function of detuning, namely, the difference between stimulus rate and preferred rate, as predicted by the entrainment models[8,58,59]. We tested this prediction by assessing the slopes of logistic regression models, fitted to conditions where stimulus rates, faster or slower than an individual's preferred rate estimate, predicted accuracy. The model was fitted to datasets from all participants and sessions, where IOIs that were faster and slower than the participant's preferred rate estimates were separately z-scored, and the direction (i.e., whether stimulus IOI was faster or slower than the preferred rate estimate) was coded as categorical. We expected a systematic increase in performance towards the preferred rate, which should result in an interaction between IOI and direction.

Flexibility estimates

We hypothesized that larger trial-to-trial changes in stimulus rate would reduce accuracy. To test this hypothesis, we first compared participants' average accuracy between session types, using a paired-sample t-test. Then, we assessed the effect of absolute rate change (|±ΔIOI|) on accuracy for each individual. To do so, we fitted generalized linear models to each participant's random-order session data and obtained slopes (β) that quantified the strength of the |±ΔIOI| effect for each participant. The models were fitted using Matlab's *fitglm* function, with the distribution of the response variable specified as 'binary', and link function specified as 'logit', since the response variable, accuracy was binary. We also fitted separate models for trials where the stimulus was faster or slower than the previous trial's stimulus, where the predictor was either |-ΔIOI| or |+ΔIOI|, respectively. The model formula was $P(Y=1|X) = e^{(\alpha+\beta x)} / e^{(\alpha+\beta x)}+1$, where Y is binary accuracy and X is the amount of rate change in trials that were faster than previous (|-ΔIOI|) or in trials that were slower (|+ΔIOI|). Next, using one-tailed one-sample t-tests, we tested whether models' β were smaller than zero, which would confirm a decrease in accuracy as a function of |-ΔIOI| or |+ΔIOI|. The β values, which quantified individuals' ability to adapt to changes in stimulus rate from one trial to the next, served as our single-individual estimate of oscillator flexibility. Finally, to investigate whether responses were affected by the previous trial's stimulus, we computed participants' average bias in trials where stimulus was faster than the previous one (|-ΔIOI|), and in trials where it was slower (|+ΔIOI|). We compared the distribution of average bias values against zero, using one-sample t-tests. Non-zero positive bias indicated that participants incorrectly responded as 'comparison interval was longer' in trials where comparison interval was in fact shorter than the standard interval; and non-zero negative bias indicated the opposite.

Results

We first assessed whether accuracy increased with increasing DEV. Comparison of the distribution of slopes (β) against zero showed that for both DEV directions, β were greater than zero. Descriptive and inferential statistics are shown in Table 1. Next, we compared participants' average accuracies from 'comparison shorter' (|-DEV|) and 'comparison longer' (|+DEV|) conditions. Although average accuracy from the latter conditions was higher in both sessions, these differences were nonsignificant for both sessions.

Preferred rate estimates

We expected that accuracy should depend on IOI differently for each participant, and estimated individuals' preferred rate as the IOI where smoothed accuracy was maximum. Between-session comparisons showed that estimates did not significantly differ between sessions ($p = .129$). When we directly compared preferred rate estimates from the two session types (**Fig. 2A**), we found that for most participants, the estimates were numerically close to each other. Interestingly, for some participants, estimates from one session were close to double or half of those from the other session, suggesting a harmonic relationship between the estimates. We applied a permutation test that accounted for the harmonic structure of the data and found a significant relationship between estimates from two session types ($p=.008$, **Fig. 2A**). Logistic models assessing a systematic increase in accuracy towards the preferred rate estimate revealed a significant main effect of IOI ($\beta= 0.195$, $p < .001$), and a significant interaction between IOI and direction ($\beta= -.378$, $p < .001$), indicating that accuracy increased in fast rates toward the preferred rate and decreased in slow rates. **Figure 2B** illustrates the preferred rate estimation method on an example participant's dataset, and shows the slices of regression surface, namely, predicted accuracy, given the model for each direction (i.e., with stimulus rates faster and slower than the preferred rate).

Session type	Predictor	Outcome	M	SD	T	df	p
Linear-order session	|-DEV|	accuracy	1.397	0.588	12.115	25	<.001
	|+DEV|	accuracy	1.118	0.430	13.253	25	<.001
Random-order session	|-DEV|	accuracy	0.672	0.315	11.083	26	<.001
	|+DEV|	accuracy	0.514	0.271	9.668	25	<.001
	|-**Δ**IOI|	accuracy	-0.165	0.138	-6.096	25	<.001
	|+**Δ**IOI|	accuracy	-0.138	0.126	-5.603	25	<.001

Table 1

Descriptive statistics and test results for comparison of Beta estimates against null distributions in Experiment 1 analyses.

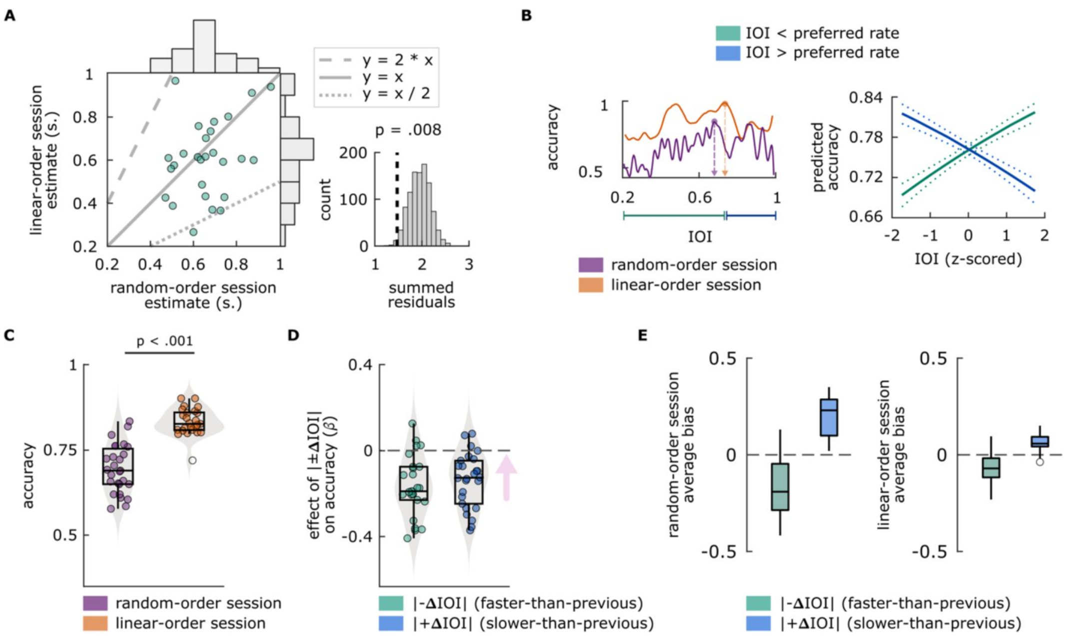


Figure 2

Main findings of Experiment 1.

A Left: Each circle represents a single participant's estimate from random-order session (x axis) and linear-order session (y axis). The histograms across the axes show the distributions of estimates for each session type. The dotted and dashed lines respectively represent 1:2 and 2:1 ratio between the axes, and the solid line represents one-to-one correspondence. Right: permutation test results. The distribution of summed residuals (distance of data points to the closest y=x, y=2*x and y=x/2 lines) of shuffled data over 1000 iterations, and the summed residual from original data (dashed line) which fell below .008 of the permutation distribution. **B** Left: Illustration of the preferred rate estimation method from one participant's random-order (purple) and linear-order (orange) session datasets. Estimates were obtained by the stimulus rates where smoothed accuracy (curved lines) was maximum (arrows). Green and blue lines respectively represent the stimulus rates that were faster and slower than the linear-order session estimate. Right: Slices of the regression surface, calculated from the model where accuracy was predicted by normalized IOIs that were faster than a participant's preferred rate estimate (green), and by those that were slower (blue). Solid lines show predicted accuracy given the model, and dotted lines represent 95% confidence intervals. **C** Average accuracy from random-order (left, purple) and linear-order (right, orange) sessions. Each circle represents a participant's average accuracy. **D** Flexibility estimates. Each circle represents an individuals' slope (β) obtained from logistic models, fitted separately to conditions where |-ΔIOI| (left, green) or |+ΔIOI| (right blue) predicted accuracy, with greater values (arrow's direction) indicating better oscillator flexibility. The distribution of β from both conditions were smaller than zero, indicating a negative effect of between-trial absolute rate change on accuracy. **E** Participants' average bias from |-ΔIOI| (left, green), and |+ΔIOI| (right, blue) conditions in both session types. Box plots in **C-E** show median (black vertical line), 25th and 75th percentiles (box edges) and extreme datapoints (whiskers). In **C** and **E**, empty circles show outlier values that remained after data cleaning procedures.

Flexibility estimates

Average accuracy (**Figure 2C**) was higher in linear-order (M = 0.834, SD = 0.039) sessions than in random-order (M = 0.695, SD = 0.072) sessions (t(24) = 12.5964, p < .001). β from models where |±ΔIOI| predicted accuracy was significantly smaller than zero for both |-ΔIOI| and |+ΔIOI| conditions and we found no significant differences between β from the former and latter conditions, showing that the probability of giving a correct response decreased with the amount of rate change across trials, regardless of whether a stimulus was faster or slower than the previous trial. Descriptive and inferential statistics are provided in **Table 1**. The distributions of β from individual fits are shown in **Figure 2D**. To investigate the source of the negative relationship between |±ΔIOI| and accuracy, we analyzed how rate change affected bias. In both session types, participants' average bias from faster-than-previous (|-ΔIOI|) conditions was significantly smaller than zero (random-order session: M = -0.179, SD = 0.144, t(26) = -6.4487, p < .001; linear-order session: M = -0.065, SD = 0.078, t(26) = -4.3159, p < .001); and average bias from slower-than-previous (|+ΔIOI|) conditions was significantly greater than zero (random-order session: M = 0.195, SD = 0.096, t(26) = 10.5406, p < .001; linear-order session: M = 0.063, SD = 0.046, t(23) = 6.6472, p < .001), as shown in **Figure 2E**. These results indicate that participants perceived longer comparison intervals as shorter on the trials where stimulus was faster than the previous trial; and vice versa on trials where stimulus was slower.

Unpaced tapping

Individuals completed a series of unpaced tapping tasks in the beginning and in the end of each session. Here, we focused on tapping rate from the spontaneous motor tempo (SMT) task. We first compared individuals' SMT before and after sessions. For both random- and linear-order sessions, SMT from before and after the session correlated and were not significantly different. Given the consistency of the measure, we averaged participants' SMT within sessions and compared the mean SMT across session types. We found a strong correlation between tapping rates from the random- and linear-order sessions. Test results of the unpaced tapping analyses are provided in **Table 2**.

Discussion

The results of **Experiment 1** showed that discrimination accuracy systematically increased with the difference between standard and comparison intervals (DEV) and decreased with the difference in stimulus rate between consecutive trials (|±ΔIOI|). Accuracy showed a nonlinear relationship with IOI: we observed improved accuracy at an individual-specific range of stimulus rates and in cases at their (sub)harmonics (IOI).

For most participants, estimates from random-order sessions were close to double the estimates from the linear-order sessions (see **Figure 2A**). Correspondence between estimates from the two session types shows the reliability of the paradigm and robustness of the methods we developed for the preferred rate estimation, since we were able to obtain similar estimates in repeated measurements, and under conditions with major differences in stimulus history and task difficulty. The current findings support three key predictions of the entrainment account. First, similar estimates of preferred rate under different temporal contexts and repeated measurements as well as a systematic increase in accuracy towards the preferred rate suggest improved timing abilities in situations with smaller detuning between the oscillator's preferred rate and the stimulus rate[21]. Second, that the estimates from the more challenging random-order session were narrower while preserving the correspondence to those from other conditions indicates that the internal oscillators were able to adaptively[14,59] entrain to the range of rates around their preferred rate, i.e., their entrainment region[22]. Finally, the harmonic relationship between the

Experiment 1										
Session averages	Random-order		Linear-order		paired-samples t-test			Pearson correlation		
	M	SD	M	SD	T	df	p	r	df	p
SMT (s.)	0.555	0.189	0.189	0.194	-1.763	26	.090	.865	25	<.001
Measurement	1 (before)		2 (after)							
	M	SD	M	SD						
Random-order session										
SMT (s.)	0.534	0.199	0.563	0.214	-0.4174	25	.680	.549	24	.004
FMT ‘slowest’ (s.)	1.442	0.465	1.461	0.522	0.0202	24	.984	.493	23	.012
FMT ‘fastest’ (s.)	0.227	0.059	0.223	0.045	-0.0396	25	.969	.737	24	<.001
Linear-order session										
SMT (s.)	0.574	0.181	0.605	0.249	-0.8031	26	.429	.613	25	<.001
FMT ‘slowest’ (s.)	1.602	0.575	1.628	0.639	-0.5583	24	.582	.627	23	<.001
FMT ‘fastest’ (s.)	0.211	0.051	0.204	0.037	0.2351	23	.816	.611	22	.002
Experiment 2										
SMT (s.)	0.598	0.222	0.669	0.218	-2.6163	31	.014	.758	30	<.001
FMT ‘slowest’ (s.)	1.427	0.634	1.438	0.713	-0.1195	28	.906	.704	27	<.001
FMT ‘fastest’ (s.)	0.256	0.078	0.261	0.067	-0.5938	28	.557	.669	27	<.001

Table 2

Descriptive statistics of unpaced tapping measures in first and second experiments, and test results for pairwise comparisons.

estimates from the two session types suggest the oscillator's ability to respond to multiple nested rates, either due to the circular nature of oscillators[59] or by involvement of multiple nested oscillators in rhythmic entrainment[19].

Two sets of results confirmed the presence of history effects on timing performance. Accuracy was lower in random-order sessions where absolute rate change (|±ΔIOI|) was maximum, than in linear-order sessions where it was minimum. Moreover, accuracy in random-order sessions decreased as rate change increased. The difference in discrimination accuracy between sessions cannot be attributed merely to the effects of the global context, given that the global context was identical across session types. If the duration representations were drawn towards the mean of the rates presented in the session ('the central tendency effect[60]'), accuracy would be similar between the sessions with identical global means. Instead, we observed a drastic decrease in accuracy in the random-order session, which suggests a stronger influence of local than global context in the current paradigm. The analyses of bias confirmed this explanation by showing that internal duration representations on a given trial were biased towards the previous stimulus rate. Interestingly, rate change across trials affected bias even when it was small and fixed.

Experiment 2

Methods

Participants

32 participants were recruited from the participant pool of Max Planck Institute for Empirical Aesthetics laboratories. The procedure was approved by the Ethics Council of the Max Planck Society and the Research Ethics Board at Toronto Metropolitan University and was in accordance with the Declaration of Helsinki. Participants signed an informed consent prior to the session and received 21 euros on average as compensation after completing the session. Prior to the experimental sessions, they also completed an online survey. We targeted a uniform age distribution (M = 50, SD = 17): within the range of 20-80 years of age, we recruited 5 or 6 participants from each 10-year age bin.

Procedure

The study consisted of an online background survey; a series of unpaced tapping tasks including the SMT, two PPT tasks, a duration discrimination and a paced tapping task. Participants' hearing thresholds were measured using standard pure-tone audiometry. Participants were not excluded based on hearing threshold. The experiment procedure is illustrated in **Figure 3A**. Details of all tasks are provided below.

Participants completed an online survey prior to the session. The lab session started with the SMT and FMT tasks, respectively. Then, participants were asked to set the sound volume to be used in the auditory tasks throughout the experiment using a slider that they clicked with a mouse. The experiment proceeded with the slider PPT task, the keypress PPT task, then the duration discrimination and paced tapping tasks; and finally, with repetitions of the SMT, FMT and slider tasks. The order of the keypress, duration discrimination and paced tapping tasks was pseudo-randomized for each participant and all 6 order combinations were counterbalanced. Prior to each task, participants were presented with instructions on the screen. Short breaks were allowed between tasks. Upon completion of the experiment, participants were moved to another booth in the laboratory room to complete a pure-tone audiometry measurement. An individual session including audiometry lasted 90 minutes on average. Instructions (see **Appendix A**) were in German.

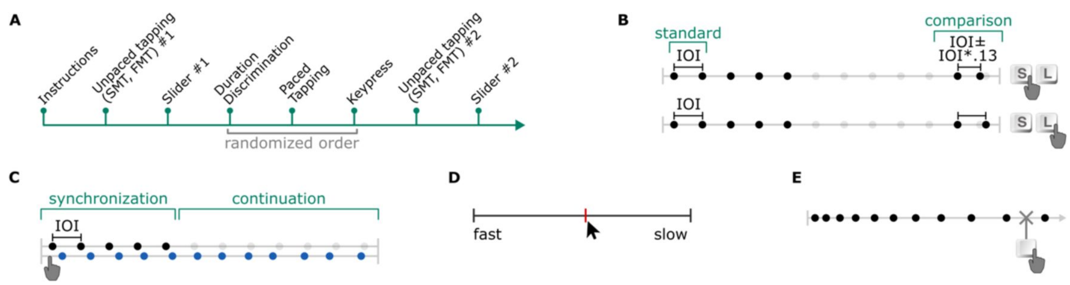


Figure 3

Experiment 2 (A) timeline, and illustrations of the (B) duration discrimination, (C) paced tapping, (D) slider and (E) keypress tasks.

Duration discrimination task

The stimuli for the duration discrimination task were the same as in **Experiment 1**. The conditions differed from **Experiment 1** random-order sessions in in three aspects: here, the pool of stimulus rates was linearly spaced between 200 to 1000 ms in 10-ms steps, comparison interval deviated from standard IOI at a fixed amount of DEV = ±13%, and there were two repetitions of each stimulus rate. For determining the spacing for IOI, we performed a bootstrapping analysis on data from our previous study, from which the current paced tapping paradigm was adapted[27]. The analysis revealed that 10 ms was the optimum step size that produced similar values to the original preferred rate estimates, while also preserving the between-session harmonic correlation. Details of the bootstrapping analysis are provided in Supplementary Information.

We selected the fixed deviation for comparison intervals as follows. First, we estimated thresholds for negative and positive deviations from Experiment 1. To do so, for each participant's (N=27) random-order session data, we averaged the accuracy at each deviation level, separately for negative and positive deviations. We fitted psychometric curves to the mean values and obtained the deviation amount that yielded 75% predicted accuracy from the fitted curve. From the resulting distributions of thresholds for negative and positive deviations, we removed outliers by excluding any value that exceeded 3x the median absolute deviation (MAD) of all threshold values in the respective distribution. Finally, we took the mean threshold value across participants and deviation directions. We then piloted the task on a small sample to confirm that the value of 13% was appropriate to be used in the duration discrimination task in Experiment 2 that would give an approximate accuracy of 75%.

The task (**Fig. 3B**) consisted of two blocks with complementary DEV conditions. Participants were presented with all 81 stimulus rates in the same order in each block. However, if the comparison interval for a given stimulus rate was longer in the first block, it was shorter in the second, and vice versa. As in **Experiment 1** random-order sessions, the change in IOI between consecutive trials (ΔIOI) was maximized, and the direction of the change alternated on every trial. For each participant, we generated a unique stimulus order which was constant across the blocks and was also used in the paced tapping task.

The instructions of the task included two example trials, and participants practiced the task for at least 6 trials. The properties and the procedure of the example and practice trials were identical to those in **Experiment 1**.

Paced tapping task

The task (**Fig. 3C**) was a shorter version of the synchronization-continuation paradigm we developed in a previous study[27]. On each trial, participants were presented with an isochronous stimulus sequence of 5 sounds, followed by silence. Sound stimuli were the woodblock samples used in Experiment 1. Participants were instructed to start tapping to the stimulus as soon as possible, and to continue tapping at the same rate once the sounds ceased, until the end of the trial, which was signaled by a change in the screen color. For each participant, the stimulus rates as well as their order were identical to those generated for the duration discrimination task. In these matched stimulus conditions, IOI ranged from 200 ms to 1000 ms in 10-ms steps. Allowed duration for continuation tapping was 6 times the stimulus IOI for fast (IOI < 300 ms) stimuli, and 7 times the IOI for slow (IOI > 300 ms) stimuli. Prior to the task, participants completed 6 practice trials, with specifications described in Ref.[27].

Unpaced tapping tasks

The procedure for the spontaneous motor tempo (SMT) task and ‘forced’ motor tempo (FMT) tasks were identical to those in Experiment 1.

Slider task

The slider task was a PPT task where participants dynamically adjusted the rate of stimulus sequences comprising the same woodblock samples used in Experiment 1. Each trial started with an isochronous stimulus sequence, and participants were presented with the instructions at the top of the screen. A horizontal slider (**Fig. 3D**) was displayed with labeled endpoints “schnell” (fast) and “langsam” (slow). Moving the mouse changed the indicator of the slider, marked in red; and each left-click produced an isochronous stimulus sequence with the selected rate. A right mouse click saved the final rate and terminated the trial. Participants completed two blocks of 8 trials of the task. In each block, the start-rate of the stimulus sequence was 200 ms in half of the trials and 1000 ms in the other half. The location of the labels also differed between trials, and the “fast” label was on the left end in half of the trials, and vice versa in the other half. Label locations and start-rates were counterbalanced within each block, and their combinations were ordered randomly.

Keypress task

The keypress task was also a PPT task where participants indicated their preferred rates by stopping stimulus sequences with dynamically changing rates. Stimulus samples making up the sequences were the woodblock samples used in **Experiment 1**. Each trial started with a stimulus sequence, and participants were presented with the instruction text on the top, and a dynamic figure on the middle of the screen that indicated the time left to respond. If no response was given during the stimulus, the trial was repeated. Stimuli started fast (IOI = 200) in half of the trials and slow (IOI = 1000) in the other half and increased or decreased by 10 ms in each interval, depending on the start-rate. That is, the stimulus got slower in each interval on fast-start trials, and vice versa on slow-start trials. Participants completed 6 trials of the keypress task. The order of the stimulus conditions was randomized. **Figure 3E** illustrates a fast-start condition of the keypress task.

Design

The stimulus IOIs presented in all tasks that involved an auditory stimulus ranged from 200 ms to 1000 ms. Thus, IOI was an independent variable, on which rate preferences and performances were assessed to be compared across tasks. The order of stimulus IOI, and thus ΔIOI, was matched between duration discrimination and paced tapping tasks, from which independent variables of +ΔIOI| and |-ΔIOI| were derived. Other independent variables were DEV direction (i.e., whether comparison interval was shorter or longer than the standard) in duration discrimination task, repetition for SMT, FMT and slider tasks; and start rate for slider and keypress tasks.

Dependent variables were the tapping rate in SMT and FMT, selected rate in slider and keypress, accuracy and bias in duration discrimination, and signed or absolute values of tempo-matching-errors, TME, in paced tapping tasks.

Apparatus

Apparatus for the presentation of sound stimuli, and collection of tapping and keyboard responses were identical to those of **Experiment 1**. Additionally, participants used a mouse for giving responses in the slider task, and for setting the desired sound volume. The background survey was a German translation of the survey used in **Experiment 1**. We conducted **Experiment 2** in German given that the participant sample consisted of older individuals who were less likely to fluently speak English than the mostly-student sample we recruited in **Experiment 1**.

Analysis

Data cleaning and exclusion criteria

As **Experiment 2** involved multiple tasks, participants were excluded from only the respective tasks where their performance met the exclusion criteria.

The duration discrimination task in **Experiment 2** had two exclusion criteria: (1) chance-level performance in both DEV directions, as in **Experiment 1** and (2) ceiling performance in overall response accuracy (average accuracy > .95). Two participants were excluded based on the first criterion; one participant was excluded based on the second.

On the trial-level, the paced tapping task had two exclusion criteria: first, any ITI that was smaller than half or bigger than 1.8 times the stimulus IOI was excluded. From the remaining ITIs, outliers were detected by the script described in *data cleaning and exclusion criteria* for unpaced tapping tasks under ***Experiment 1 Methods*** section. On the participant-level, criteria were incompatibility between stimulus rate and tapping rate, and low number of tapping intervals on average. To test the first criterion, we fitted models to overall task data where the tapping rate (i.e., the median of all intervals in each trial after trial-level data cleaning) was predicted by stimulus IOI and obtained slopes. 2 participants were excluded as they had slopes smaller than .5. One participant was excluded based on the second criterion, as the average number of intervals they produced across trials was smaller than 7.

The data cleaning procedure of unpaced tapping tasks was identical to that described for **Experiment 1**. In the slider task, we recorded whether participants listened to the different stimulus rates by clicking on the different locations on the slider. Exclusion criterion was not testing the stimulus rates on more than 75% of the trials by producing a minimum of one mouse click, which suggested that the participant did not engage with the task. One participant was excluded from the slider task based on this criterion. From the remaining participants' data, any trial without a mouse click was removed from further analyses. No exclusion criterion was defined for the keypress task.

Finally, before applying group-level statistics such as t-tests and correlations, any datapoint that fell outside of the interquartile range was excluded from the respective distributions.

Outcome measures

The outcome measures from the duration discrimination task were accuracy and bias. Response coding was same as in **Experiment 1**. Since the duration discrimination task in **Experiment 2** included two repetitions of each IOI (presented in different blocks with different DEV directions), accuracy and bias were averaged across IOI repetitions.

For each trial in the paced tapping task, we calculated the tempo-matching error, TME, following the analysis in our previous study[27]. TME was the difference between tapping rate (median inter-tap interval of all taps in a trial) and stimulus IOI, normalized by stimulus IOI, described by TME_k = ((median [ITI_1, ITI_1,..., ITI_n,])—IOI_k)/IOI_k where k is the trial index and n is the maximum number of intervals in a single trial. A positive TME indicated that the tapping rate was slower than stimulus rate, and a negative TME indicated that it was faster. For the unpaced tasks, the outcome measure from each trial was the tapping rate, calculated as the median ITI after trial-level data cleaning. From each trial of the SMT task, we also obtained the coefficient of variation

(CV), calculated as the standard deviation of all intervals divided by their mean. We further compared SMT across repetitions of the same task throughout the experiment using Pearson correlations and paired-samples t-tests.

The slider task had two start-rate conditions and two repetitions throughout the experiment (before and after main tasks). The dependent measure for each trial was the median of all final responses. We assessed the main effects and interactions of start-rate and repetition on slider responses across participants, using a repeated measures ANOVA. We calculated the rate preference on each trial of the keypress task as the presented stimulus' rate at the time of the keypress. The summary measure for each start-rate was the median of all rate preferences in trials with same start-rate.

Preferred rate estimates

Experiment 2 involved various tasks by which we aimed to estimate individuals' preferred rate. For the SMT task, we estimated preferred rate as median tapping rate; for the slider and keypress tasks (PPT), we averaged participants' indicated preference across conditions and repetitions. For both the duration discrimination and paced tapping tasks, we estimated preferred rate as the stimulus IOI yielding peak performance as follows.

Best-performance rates in the duration discrimination task were calculated by smoothing accuracy as a function of stimulus rate, as in Experiment 1. After excluding the study-specific outliers on the participant level, for each participant, we smoothed accuracy using 'gaussian' method in *smoothdata* function in Matlab. Following the optimization procedure used in Experiment 1, we assessed the window size that revealed a single-point maximum accuracy for each participant. The optimum window was 13 samples, which was used to smooth both the accuracy and IOI values in each participant's dataset.

The dependent measure in paced tapping task was TME, which was a signed, proportional error measure. Best-performance rates in this task were the conditions where participants tapped with the least errors, quantified by the absolute TME, |TME|. Since the paced tapping task shared the stimulus rate conditions with duration discrimination task, we used the optimum window size obtained for the duration-discrimination task for smoothing |TME| so that the estimates would be maximally comparable across tasks.

Flexibility estimates

Experiment 1 in the current study and the findings of our previous study[27] showed robust effects of stimulus history on rhythm perception and production. As in those analyses, flexibility in Experiment 2 was defined as the ability to adapt to changes in the rhythmic context.

In the duration discrimination task, we assessed flexibility by fitting logistic models to each participant's data where accuracy was predicted either by |-ΔIOI| or |+ΔIOI|, as in Experiment 1. A negative slope obtained from the models indicated that the probability of giving a correct response decreased as the |±ΔIOI| increased. Similarly, in the paced tapping task, we fitted linear models where |TME| was predicted either by |-ΔIOI| or |+ΔIOI|. A positive slope from the models indicated that the absolute tempo-matching error increased with |±ΔIOI|. However, as a final step, we inversed the slopes obtained from the paced tapping so that more negative beta estimates indicated less flexibility.

We tested the hypothesis of a decrease in oscillator flexibility with advancing age by correlating age and slopes from each |±ΔIOI| condition (flexibility estimates) in duration discrimination and paced tapping tasks (Pearson correlation, one-tailed). Since these analyses involved multiple comparisons, we controlled for the false discovery rate (FDR), using The Benjamini–Hochberg method[61,62]. To test whether overall performance decreased with age, we ran another series of correlations between age and average accuracy in duration discrimination task, and average |TME| in the paced tapping task, and FDR-corrected the p- values.

Additionally, we explored the relationship between individuals' age and preferred rate estimates, by separate correlation analyses between age and preferred rate estimated from each condition and measurement of the slider and keypress (PPT) tasks, and preferred rate estimates from duration discrimination and paced tapping tasks. Since we defined no hypothesis for preferred rate and age relationships, we used two-tailed Pearson correlation and no correction.

Results

Unpaced tapping

Tapping rates from 'fastest' and 'slowest' FMT trials showed no difference between pre- and post-session measurements and were additionally correlated across repeated measurements. Given the consistency of the measures, rates from each FMT task from first and second measurements were averaged for further analyses. Tapping rates from SMT task were also correlated across measurements. However, rates from the second measurement were significantly slower than those from the first measurement. SMT CV did not correlate across measurements (p = .072), and CV from the second measurement (M = 0.070, SD = 0.033) was significantly higher (t(26) = -2.5116, p = 0.019 than CV from first measurement (M = 0.055, SD = 0.023). The results of the pairwise comparisons between tapping rates from all unpaced tapping tasks across measurements are provided in Table 2.

Preferred rate estimates

Individuals' PPT was measured by the slider and keypress tasks. In the slider task, rate preferences from the same start-rate conditions were significantly correlated and showed no systematic differences across repeated measurements. Within the first measurement block, rates from slow-start conditions (M = 0.732, SD = 0.165) were slower than those from fast-start conditions (M = 0.658, SD = 0.167) (t(25) = -2.109, p = 0.045), although they were significantly correlated (r(24) =0.691, p < .001). Rate preferences from the second measurement showed no difference between the start rate conditions (p=.709) and were significantly correlated (r(27) =0.521, p = 0.004). A repeated-measures ANOVA revealed no main effects of start-rate (p = 0.169) or repetition (p = 0.865), and no interaction (p = 0.067). In the keypress task, rate preferences from the fast-start condition (M = 0.467, SD = 0.092) were significantly faster than those from the slow-start condition (M = 0.840, SD = 0.111) (t(28) = -13.8046, p < 0.001), and we found no correlation between rate preferences across conditions (p = .803). The distributions of rate preferences from separate conditions of the slider and keypress tasks are shown in **Figure 4A**. Preferred rate estimates from both the duration discrimination and paced tapping tasks, measured by the stimulus rates with best performance, correlated significantly with SMT (**Fig. 4A**). Moreover, we found no significant differences between estimates from either task or SMT. However, estimates did not correlate between duration discrimination and paced tapping tasks, and were slower (t(26) = -2.7817, p = 0.099) in the latter (M = 0.641, SD = 0.173) than in the former task (M = 0.541, SD = 0.175). In **Figure 4B**, estimates from the two performance tasks and SMT (first measurement) are illustrated. In general, estimates from both the paced and unpaced tapping tasks were slower than those from the duration discrimination task. However, the nonparallel nature of the lines that connect single-participant preferred rates for each task (**Fig. 4B**, left) indicates that the amount of "slowing" in the tapping tasks relative to the discrimination task varied across individuals. We reasoned that if the degree of slowing for each individual arises from a common source for both tasks, which we will call 'the motor component', the differences between estimates for the discrimination versus both tapping tasks should be consistent. We quantified the contribution of the motor component to preferred rates each tapping task by subtracting the duration discrimination task estimates, which yielded two difference scores (paced tapping – duration discrimination and SMT – duration discrimination). These difference scores were significantly positively correlated, confirming that each individual had a consistent motor component contribution that slowed their preferred rate estimate in different tapping tasks in a similar manner.

Rate preferences in the slider task correlated with SMT only in fast-start conditions from the first measurement, and in slow-start conditions from the second measurement. Rate preferences from the keypress task only correlated with those from slider task conditions (i.e., within PPT tasks), but not with any SMT measurement or estimates from the performance tasks.

Flexibility estimates

We hypothesized negative effects of stimulus history on performance in both perceptual and motor tasks. We found similar effects of stimulus history in both tasks. β obtained from the separate models quantifying the effect of |-ΔIOI| and |+ΔIOI| on accuracy in the duration discrimination task were both significantly smaller than zero, indicating that accuracy decreased as |±ΔIOI| increased, both in trials where the stimulus was faster and slower than previous (**Fig. 5A**). In the paced tapping task, β from models where |TME| was predicted either by |+ΔIOI| or |-ΔIOI| were significantly greater than zero, indicating that tempo-matching errors increased as a function of |±ΔIOI| (**Fig. 5B**). Paired-samples t-tests revealed no significant differences between the strength of the effect of |-ΔIOI| vs |+ΔIOI| in either task. However, β from models where |+ΔIOI| predicted |TME| were numerically smaller, and significantly more variable than those models where |-ΔIOI| predicted |TME|; the difference in variability was assessed using a Brown-Forsythe test ($F(1,54) = 5.867$, $p = .019$). Descriptive statistics and test results for comparison of β estimates against zero are provided in **Table 3**.

To investigate the direction of history effects on performance, we compared perceptual and motor biases in trials with negative and positive rate change. In conditions where the stimulus on the current trial was faster than the previous one, average bias ($M = -0.166$, $SD = 0.094$) was significantly smaller than zero ($t(28) = -9.4985$, $p < .001$, **Fig. 5A**); and average TME ($M = 0.014$, $SD = 0.021$) was greater than zero ($t(27) = 10.587$, $p < .001$, **Fig. 5B**). The opposite was the case in conditions with slower-than-previous stimulus, as average bias ($M = 0.217$, $SD = 0.108$) was greater ($t(27) = 10.587$, $p < .001$, **Fig. 5A**) and average TME ($M = -0.013$, $SD = 0.018$) was smaller ($t(26) = -3.7556$, $p < .001$, **Fig 5B**) than zero.

In the duration discrimination task, we also assessed the differences in responses to shorter versus longer comparison intervals as an indicator of how individuals responded to phase perturbations, by comparing accuracy in trials with |-DEV| and |+DEV|. Participants' average accuracy from the latter conditions ($M = 0.746$, $SD = 0.070$) were higher ($t(25) = -2.5536$, $p = 0.017$) than those from the former conditions ($M = 0.694$, $SD = 0.116$).

Age-related changes in oscillator flexibility

One of the main goals of **Experiment 2** was to compare the estimates of preferred rate and flexibility across individuals to assess the age-related changes in oscillator properties. We recruited our participant sample to have a flat age distribution, with participants ranging in age from 20 to 76 years old.

The results revealed significant correlations (FDR-corrected for multiple comparisons) only between individuals' age and flexibility estimates from |-ΔIOI| conditions. β from logistic fits where |-ΔIOI| predicted accuracy in the duration discrimination task negatively correlated with age ($r(27) = -0.525$, $p = 0.002$, **Fig. 5C**). Similarly, we found a significant negative correlation

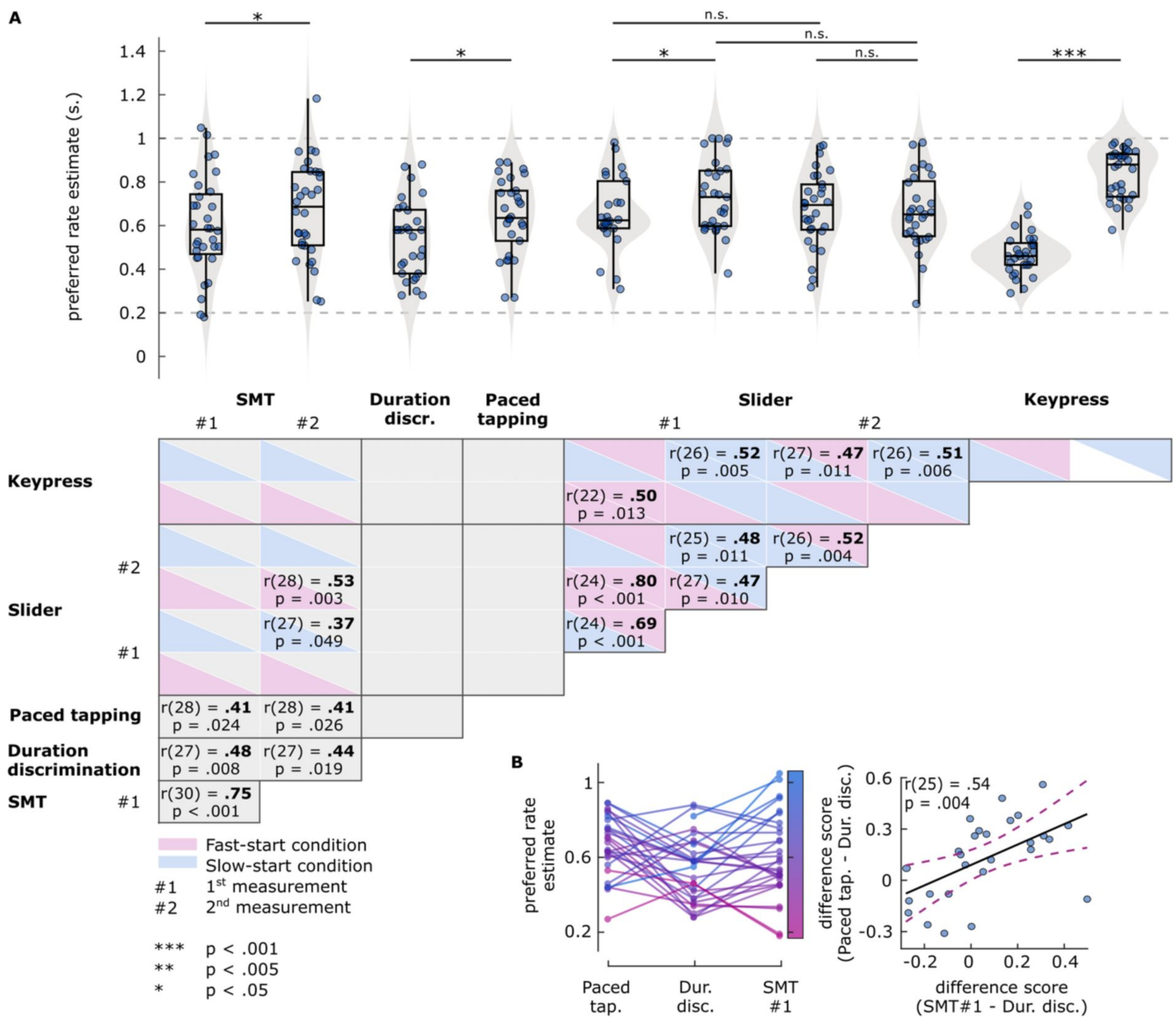


Figure 4

Results of Experiment 2 preferred rate analyses.

A Top: Estimates of preferred rate from each task condition. Box plots show median (black vertical line), 25th and 75th percentiles (box edges) and remaining data range (whiskers). Vertical lines above the box plots represent within-participants pairwise comparisons. The horizontal dashed lines represent the minimum and maximum stimulus rates presented in the experiment. Bottom: Pairwise correlations between preferred rates across tasks. For the slider and keypress tasks, boxes are colored to indicate fast-start (blue) and slow-start (pink) conditions. Correlations and p-values are reported for significant correlations only. **B** Relationship between the preferred rate estimates from the paced tapping, duration discrimination, and SMT (first measurement) tasks. Left: Participants' estimates from the three tasks. Each circle represents an individual's preferred rate estimate, connected by lines between the tasks. Both circles and lines are color-sorted by individuals' SMT, ranging from fast (pink) to slow (blue). Right: Correlation between the difference scores. Each circle represents a single participant's difference score, namely, how different the estimates from SMT (x axis) and paced tapping (y axis) tasks were than those from the duration discrimination task. Solid black line represents the regression line, dashed lines represent 95% confidence intervals.

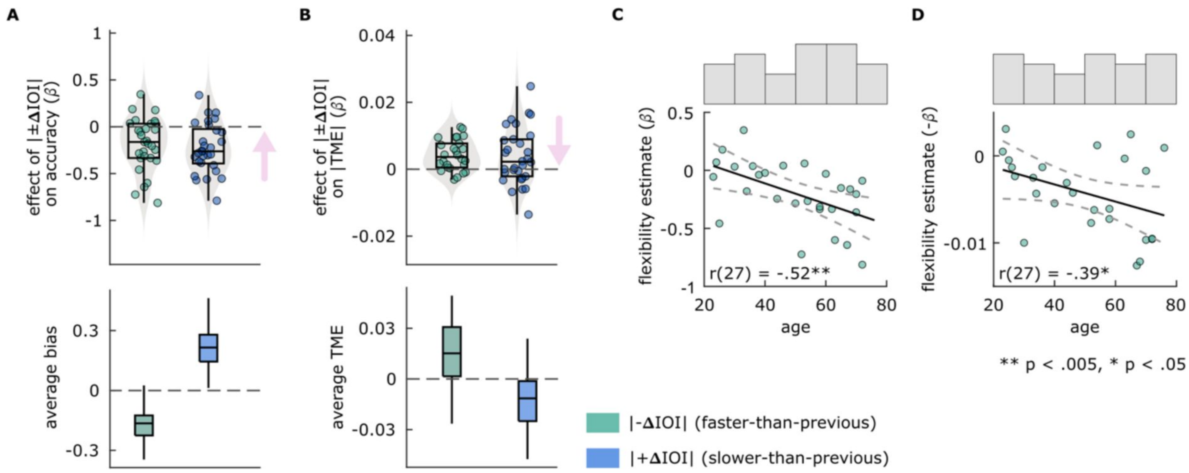


Figure 5

Results of Experiment 2 flexibility analyses.

A-B Effects of between-trial absolute rate-change (|±ΔIOI|) on performance in **Experiment 2** (**A**) duration discrimination and (**B**) paced tapping tasks. In the top panels, each circle represents an individuals' slope (β) obtained from models, fitted separately to conditions where |-ΔIOI| (left, green) or |+ΔIOI| (right, blue) predicted (**A**) accuracy in the duration discrimination or (**B**) |TME| in the paced tapping task. The arrow direction indicates better flexibility. In the bottom panels, box plots show (**A**) average bias in duration discrimination and (**B**) average TME in paced tapping tasks, from |-ΔIOI| (left, green) and |+ΔIOI| (right, blue) conditions. In all panels, box plots show the median (black vertical line), 25th and 75th percentiles (box edges) and extreme datapoints (whiskers). **C-D** Correlations between individuals' age and the flexibility estimates from (**C**) duration discrimination and (**D**) paced tapping tasks. Solid black lines represent the regression line, dashed lines represent 95% confidence intervals. Histograms above each plot show the distribution of participant ages after outlier corrections.

Task	Predictor	Outcome	M	SD	T	df	p
Duration discrimination	|-**Δ**IOI|	accuracy	-0.185	0.279	-3.5685	28	<.001
	|+**Δ**IOI|	accuracy	-0.230	0.261	-4.7417	28	<.001
Paced tapping	|-**Δ**IOI|	|TME|	0.004	0.005	4.7222	25	<.001
	|+**Δ**IOI|	|TME|	0.004	0.008	2.493	29	.009

Table 3

Descriptive statistics and test results for comparison of Beta estimates against null distributions in Experiment 2 analyses.

between the inversed β from models where |-ΔIOI| predicted |TME|, and age (r(24) =-0.389, p = 0.025, **Fig. 5D**). The findings indicate that the ability to adapt to faster-than-previous rates decreased with increasing age.

Discussion

The results of **Experiment 2** revealed correspondences between preferred rate measures from various tasks, and effects of stimulus history on performance that were stronger for older individuals. The findings on preferred rate are consistent with previous research assessing tapping behavior at stimulus rates near to or far from individuals' SMT. During synchronization to[6] or continuation of[5,22,52] a rhythmic stimulus, individuals overproduce stimulus rates that are faster, underproduce those that are slower than their SMT. During continuation tapping, produced intervals have also been also shown to drift back towards individuals' SMT[5,63]. However, these previous paradigms have generally used a rough sampling of stimulus rates (e.g. 3)[22,52,63], or those that predefine conditions around SMT[5,6]. Here, we used a wide and finely-sampled range of stimulus rates that were unrelated to individuals' SMT. Thus, that we found SMT to be the anchor rate with optimal rhythmic performance further supports the idea that perception and production of rhythms are governed by a common mechanism which responds similarly to a range of stimulus rates across various tasks. Most work comparing individuals' timing performance across stimulus rates with respect to their SMT has made use of paradigms that involve a rhythmic motor component. The current study is the first that compared individuals' duration discrimination abilities across intervals of a rhythmic stimulus with respect to their SMT.

Preferred rates from the preference tasks with and without a rhythmic motor component (SMT and PPT, respectively) were more similar than preferred rate estimates from performance tasks (duration discrimination and paced tapping) with and without rhythmic movement. Rate preferences from the same start-rate conditions of the slider task showed strong correspondence across repeated measurements. Interestingly, rates from the fast-start conditions showed the strongest correlation across measurements, and with SMT. We interpret this difference between the fast- and slow-start conditions as being in line with the scalar property of time perception[64], in that absolute timing accuracy is generally more accurate for faster rates and shorter intervals. Moreover, this finding is supported by similar findings of increased discrepancy between SMT and PPT at slow, as compared to fast stimulus rates[65]. Preferred rates from the keypress task showed large differences between start-rate conditions, although rates from slow-start trials were correlated with those from most slider task conditions. Given that the keypress task involved no dynamical adjustment of stimulus rate, preferences may have been constrained to a smaller range of stimulus rates around the start rate; nonetheless, individual differences were still observable, and preferred rates were still consistent with those measured in the other PPT (slider) task.

Analyses focused on flexibility revealed that both duration discrimination and paced tapping performance were worse when rate change from one trial to the next was large, regardless of the direction of the change (i.e., whether stimulus was faster or slower than the previous one). In cases where stimulus in each trial was faster than the previous, slower stimulus, participants tended to perceive longer comparison intervals as shorter and tap slower than the stimulus. In the opposite cases, they tended to perceive shorter comparison intervals as longer and tap faster than the stimulus. Thus, non-zero biases and signed tapping errors observed in response to rate changes suggest that internal representations and behavior in each trial reflected the properties of the preceding trial; we will return to this point in the General Discussion. These findings are mostly in line with findings of Experiment 1 (current study) and those from our previous tapping study[27], and further emphasize the presence of history effects on timing performance. The finding of signed tapping errors supports the idea that oscillators gradually adjust their phase and period to a newly encountered stimulus, resulting in discrepancy between the stimulus interval and oscillator period during synchronization to a rhythmic stimulus[14,33,59]. However, in our previous study[27], tapping performance was especially affected when stimulus rates were faster than the preceding trial. In that study, |TME| was calculated from only synchronization tapping for the flexibility analysis. Here, we calculated |TME| from all taps from both the synchronization and continuation segments of each trial due to the lower number of trials. That is, in our previous study, we focused only on the first produced intervals on each trial, whereas here we included intervals that were produced after participants had a longer period to adapt to the new stimulus rate.

A critical finding from the current study was that flexibility, estimated inversely from the strength of the effect of |-ΔIOI| on performance in both tasks with and without a motor component, decreased with age. Reduced performance in timing tasks for ageing individuals is a common finding across perceptual[41,43,49] and motor[40,66] tasks. However, overall timing performance measures, namely, task averages of duration discrimination accuracy and tapping errors showed no systematic relationships with individuals' age, suggesting that age-related changes in rhythm perception might be specific to adaptive mechanisms rather than general timing abilities.

In addition to focusing on deviations in stimulus rate between trials, we also assessed how participants responded to within-trial deviations, that is, how much comparison interval deviated from the stimulus IOI. As in Experiment 1, however, significantly here, accuracy was marginally higher in conditions with longer compared to shorter comparison intervals. That this difference reached significance only in the current study may be due to the age of the participant sample, given the finding that adapting to faster, but not slower stimulus was more challenging for older individuals.

Of note is that the paradigm in Experiment 2 was derived from two multi-session experiments through a series of reliability and bootstrapping analyses. The longer versions of the duration discrimination (Experiment 1, current study) and paced tapping (synchronization-continuation paradigm in Ref.[27]) involved around 400 trials in each of the two sessions, between which the estimates of preferred rate and flexibility were also consistent. Thus, the current paradigm can be used to assess internal oscillator properties in clinical settings or with participant samples where concerns for task difficulty or fatigue may arise.

General Discussion

The goal of the current set of studies was to highlight factors that impact auditory rhythm processing. To this end, we conducted two experiments, investigating the interplay between the properties of the external world (the stimulus) and the individual responding to the stimulus (the perceiver). Adopting an entrainment perspective that considers internal oscillators as the underlying mechanism for rhythm processing[11,67], we aimed to capture this interplay by characterizing the properties of internal oscillators, and to assess how they change with advancing age. Specifically, we estimated oscillators' preferred rates and flexibility for each individual in perceptual and motor tasks, assessed the relationship between rate preferences and optimal stimulus rates for timing performance, and tested the hypothesis that oscillator flexibility diminishes as we age.

Experiment 1 was a perceptual paradigm, where individuals' ability to discriminate between stimulus intervals over a wide range of finely-sampled stimulus rates was assessed in two temporal contexts: one that required rapid temporal adaptation, challenging oscillator flexibility, and one without such requirement. In Experiment 2, we combined shorter versions of the duration discrimination paradigm (Experiment 1) and a paced tapping paradigm (adapted from Ref.[27]), using matching stimulus conditions. Experiment 2 also involved a common measure of preferred rate, the 'spontaneous motor tempo' (SMT) task, and two 'preferred perceptual tempo' (PPT) tasks (slider, keypress) where individuals' rate preferences were assessed. From the performance paradigms, we estimated preferred rate as the stimulus rates with best performance, indexed by maximum accuracy in the duration discrimination tasks, and minimum tempo-matching errors in the paced tapping task. We defined flexibility as the ability to adapt to changes in stimulus rate, which was inversely related to how much single-trial performance was affected by trial-to-trial changes in stimulus rate.

Preferred rate estimates

In the rhythmic entrainment literature, preferred rate is typically estimated by SMT. However, two main aspects of the SMT task motivated us to question its explanatory power for predicting individuals' perceptual abilities in real-world listening situations. First, given that the task involves periodic motor actions, the relative contributions of an internal timekeeper versus constraints or resonances of an individual's motor system to the produced tapping rate cannot be separated. Second, SMT is a preference measure, since it measures the rate at which individuals prefer to tap at, without introducing any interaction with a stimulus. Although there is evidence for positive relationships between SMT and rates yielding best timing abilities in paced tapping tasks[5,6,63], rate preferences obtained from SMT task may not necessarily predict how individuals would perform at other auditory tasks, especially those that don't involve periodic motor actions. Here, we aimed to bridge this gap and understand the potential predictive power of SMT for perceptual performance situations with higher ecological validity, by directly comparing SMT to 'performance' measures of preferred rate both with and without motor component.

The results of Experiment 2 revealed that the stimulus rates for which individuals showed better timing performance were indeed correlated with SMT. However, we did not find one-to-one correspondences between SMT and preferred rate estimates from the performance tasks, and estimates were not correlated across the performance tasks. SMT was more variable across participants than preferred rates estimated from either of the performance tasks, and preferred rates estimated from tasks involving a motor component (SMT, paced tapping) tended to be slower than those estimated from the duration discrimination task. We discuss two possible primary dimensions along which these tasks differ and how these might preclude directly predicting performance on one task based on the rate preference for another: involvement of the motor system and indicating preference versus interacting with an environmental rhythm.

Both the unpaced (SMT) and paced tapping tasks required rhythmic motor responses, as compared to the duration discrimination task where perceptual judgments were assessed. We found that preferred rate estimates from both motor tasks were slower than for those obtained via duration discrimination. Interestingly, we found that the degree of 'slowing down' in the motor compared to the discrimination tasks was consistent within an individual: the degree of slowing from discrimination to SMT was correlated with the degree of slowing from discrimination to paced tapping. This suggests that the contribution of the 'motor component' to preferred rate is individually specific and quantifiable. This finding is in line with the proposal that perception and production of rhythms is governed by a system of multiple coupled oscillators[1,53], with the observed preferred rate in any task being jointly influenced by preferred rate of a perceptual (in this case, auditory) oscillator, preferred rate of a motor oscillator, and the coupling strength between these two nodes. Indeed, similar discrepancies between preferred rates of auditory and motor oscillators were observed in speech comprehension and were attributed to individual differences in auditory-motor coupling[68]. Under this assumption, we propose that the differences between preferred rate estimates from tasks with and without tapping (motor) responses, i.e., the degree of slowing when the motor component is added, will increase with the difference in eigenfrequencies of the perceptual and motor oscillators (their detuning), and decrease with increasing coupling strength.

The other difference between the tasks by which preferred rate was estimated was the requirement to interact with a stimulus rhythm in the performance tasks, whereas the SMT and PPT tasks only involved indicating a preference. Jones and McAuley argue that in the presence of a stimulus, the preferred rate can be 'pushed around' by the temporal context, given that the oscillators are adaptive and can perform within their entrainment regions[34]. Results of Experiment 1 confirmed this prediction by revealing an effect of temporal context on preferred rate: the distribution of estimates from the temporally-challenging condition was narrower than that from the condition that required minimal temporal adaptation. Thus, stimulus presentation in Experiment 2 duration discrimination and paced tapping tasks as opposed to SMT task may have contributed to the differences in preferred rate estimates. Additionally, in the paced tapping task, participants synchronized to the stimulus, which is shown to improve performance in tapping precision[69,70] and perceptual judgments[71,72], and thus may have contributed to the estimate differences.

Flexibility estimates

Another goal of the current study was to investigate the circumstances that negatively impact timing abilities. Specifically, we focused on trial-to-trial changes in stimulus rate, and to what extent individuals were able to adapt to such changes, which was our definition of oscillator flexibility. In line with previous literature which reveals effects of stimulus history on perceptual[31,34-36] and motor[25,27,30,32,33] responses, results of the current study showed that performance in duration discrimination and paced tapping tasks decreased as trial-to-trial changes in stimulus rate increased. Moreover, single-trial responses were biased such that they reflected the properties of the stimulus from the preceding trial. This set of findings is in line with predictions of oscillator models[59]. In a changing rhythmic context, the oscillator adapts to the newly encountered stimulus rate by gradually updating its phase and period[14]. The extent and time course of adaptation, however, will depend on the oscillator's flexibility, which might be modeled via error correction parameters in commonly used models of interval timing[14,59] or synchronized tapping[33]. An inflexible oscillator's period would adjust more slowly to a new rate, and so would continue to reflect the previously entrained rate, due to hysteresis. For the duration discrimination task, any comparison interval that is shorter than the oscillator's period would be classified as 'shorter', and vice versa, regardless of whether the interval was indeed shorter than the intervals making up the standard, isochronous rhythm. This means that when the previous trial was faster than the current one, the oscillator period would be relatively short, and participants would be biased to judge comparisons as "longer". Conversely, when the previous trial was slower than the current one, the oscillator period would be relatively long, and "shorter" responses would be more likely. The analysis of bias indicated that this was exactly the case for the current data. Similarly, tapping rates gradually updated from the preceding stimulus rate to a current one, resulting in tempomatching errors in the direction of the previous stimulus rate. That is, when the previous trial was faster than the current one, tapping rates would underestimate the stimulus rate, and when the previous trial was slower than the previous one, tapping rates would overestimate the stimulus rate. Again, the TME analysis confirmed this to be the case.

Age-related changes in oscillator flexibility

A critical finding of the current study was an age-related decline in a specific ability: temporal adaptation to faster-than-previous stimulus. In trials where the stimulus was faster than the previous one, accuracy in the duration discrimination task decreased, and tempo-matching errors in the paced tapping task increased as a function of the amount of rate difference between trials, more so for older individuals.

The timing literature reveals age-related changes in time perception, such as a decrease in the accuracy of temporal estimates[73], and slower tapping rates in spontaneous[22,39,74] or forced[40] unpaced tapping tasks. These changes are generally attributed to slowing of the internal timekeeper mechanisms[39,41] or a reduction of attentional resources[75]. Moreover, studies comparing older and younger individuals' preferences and performances in paced tapping paradigms reveal mixed results[66]. In the current study, we did not observe age-related changes in overall performance measures such as perceptual accuracy or tapping errors, and contrary to previous work we did not find a slowing of preferred rate no matter how it was estimated. Instead, these findings rather point to age-related changes in adaptive mechanisms underlying temporal processing. Studies assessing temporal adaptation abilities show that older individuals adapt their movements to temporal perturbations more slowly and less efficiently than younger individuals[76,77] and with less error correction[78]. We observed an age-related decline in temporal adaptation during both perception of and synchronization with auditory stimuli, suggesting a common source that affected the two means of responding.

Previous work has revealed age-related differences in neural entrainment to auditory rhythms. Most studies have focused on neural entrainment to amplitude modulated sounds, of which metronomic stimuli like those we used here are a special case and found that older adults entrain *more* strongly and in a more stereotyped (less flexible) way[46–48]. A similar pattern was observed for entrainment to the amplitude envelope of speech[79,80]. A mixed pattern of results has been reported for frequency modulated sounds; however, the existing data suggest that these differences might depend on parameters such as modulation rate and depth[49,81], which we will not further address here. Moreover, older adults show less neural adaptation than younger adults in temporal contexts where stimulus rate changes gradually and predictably[47]. Another functional difference between younger and older brains, potentially relevant here, are findings on “neural noise”. Variability in brain activity as measured in the BOLD signal using functional magnetic resonance imaging is higher in younger than older brains, again suggesting inflexible and stereotyped neural activity. Indeed, neural noise is associated with faster and more consistent performance across a variety of cognitive tasks[82,83]. Similarly, 1/f noise measured with EEG, associated with predictive processing in a lexical task, was lower for older than younger individuals[84]. Taken together, these results suggest that poorer performance in temporal tasks that involve prediction and adaptation might reflect less flexible, overly stereo-typed neural responses in older adults. This might indicate a loss of flexibility in the generating oscillator(s).

An interesting aspect of the current findings was that adaptation to faster, but not slower stimulus rates was more difficult for older individuals. Oscillator models predict this asymmetry, with increased tapping asynchronies to speeding up compared to slowing down stimuli due to the ‘period adaptation function’ of the oscillator[33]. This was the case for the paced tapping paradigm (current study), as the effect of rate change on tapping errors was smaller and significantly more variable when stimuli slowed down as opposed to sped up, paralleling previous findings[27]. In the duration discrimination tasks, although the magnitude of the effect of rate change was similar for both rate-change directions, only adaptation to faster stimuli worsened with age. Though evidence shows reduced adaptation to time-compressed[85] or artificially speeded[2] speech in older individuals, further research is needed to address the sources of adaptation to fast versus slow stimuli in ageing.

Individual differences in internal oscillator properties

One advantage of the current approach is its focus on individual variability. Previous work on rhythm perception and production, as well as aging, has largely used traditional statistical approaches involving group or condition comparisons of central tendency measures. In these cases, variability is attributed to measurement error or noise. In the current work, we opted to view variability as potentially attributable to individual differences in internal oscillator properties that may in future work be shown to have predictive power for successful outcomes in real-world listening situations. Taking this approach focused on individual differences revealed several novel findings that would have otherwise not been accessible. First, we found correspondence between the rates individuals prefer to tap their finger at, listen to, and perform perceptual and motor tasks most accurately, all pointing to preferred rates of potentially coupled, perceptual and motor internal oscillatory systems. Second, we observed harmonic relationships between the preferred rates estimated from the duration discrimination paradigm under two different temporal contexts (Experiment 1); this is in line with the assumption that oscillators are capable of entraining to multiple stimulus rates within a temporal hierarchy[59,86], and further strengthens our choice to adopt an entrainment approach here. Finally, we found that oscillator flexibility decreased with age; this finding is supported by evidence from neural entrainment research and adds to the narrative regarding the effects of ageing on the auditory system.

The pared-down versions of the duration discrimination and paced tapping paradigms described in Experiment 2 were carefully designed based on the analyses of their correspondence between Experiment 1 and our previous tapping study[27] in terms of their main results. That is, we designed the Experiment 2 tasks to be the streamlined versions that would yield the same main results as their longer counterparts. The reasons for minimizing the duration of the tasks were (1) it allowed us to test and compare perception and production in a within-participant manner in a single session, and (2) it improved suitability for testing older adults, who we did not want to subject to an overly long or multi-session experiment. That the results of Experiment 2 replicated those from Experiment 1 and Ref.[27] independently confirmed the robustness of the designs. Thus, we would propose that these minimized designs could be used in a more diagnostic capacity in future work to measure and test predictions about internal oscillator properties of older adults or a clinical population of interest.

Conclusion

To summarize, we adopted an entrainment approach to rhythm perception and production, which proposes that these abilities are governed by internal oscillatory mechanisms. We then developed a paradigm to estimate individuals' internal oscillator properties based on the common assumptions of the entrainment models. Performance in both duration discrimination and synchronized tapping tasks was best at a range of stimulus rates that was specific to each individual – their preferred rate – and was broadly consistent with preferred rates estimated from preference tasks (SMT). One important departure from this consistency was that involving a motor requirement slowed preferred rates, and we were able to quantify the contribution of this motor component, which was consistent within individuals across different tasks. Performance decreased as a function of change in stimulus rate between consecutive trials. The extent to which individuals were able to adapt to the changes – oscillator flexibility – decreased with age, in accordance with research on neural entrainment and neural noise.

Several aspects of the current findings speak against alternative explanations of timekeeper models. First, an increase in performance at certain stimulus rates that show consistency across multiple measurements (Experiment 1) and tasks with and without a motor component (Experiment 2) is predicted by entrainment models (Assumption 3), but not timekeeper theories as the latter models assume a flat performance profile across stimulus rates, following 'the Weber law'[7,87]. Second, best-performance rates (i.e., preferred rate estimates) showed harmonic relationships across multiple measurements, which is compatible with the properties of oscillator models (Assumption 4), and not predicted by timekeeper models. Finally, studies adopting a timekeeper approach suggest that timing responses should gravitate towards the mean of the presented stimulus rates in a given experimental session[60], which should have resulted in similar patterns of results in the two sessions of Experiment 1, where only the trial order differed. We found significant accuracy and bias differences between the sessions that cannot be solely attributed to the gravitation toward the mean as the temporal statistics for the stimuli were identical across sessions.

Overall, these findings support the general hypothesis of dynamic attending theory that an oscillatory system with a stable preferred rate underlies rhythm perception and production. We further show that this system loses its ability to flexibly adapt to changes in the external rhythmic context as we age.

Appendix A

Experiment 2 instructions

Welcome!	**Willkommen**
In this experiment, you will be asked to do several tasks:	In diesem Experiment werden Sie gebeten, mehrere Aufgaben zu erledigen:
• tapping your finger on the desk without hearing any sounds.	• tippen mit dem Finger auf den Tisch, ohne ein Geräusch zu hören.
• tapping your finger on the desk along with rhythms that you will listen to over headphones.	• tippen mit dem Finger auf den Tisch zu den Rhythmen, die Sie über die Kopfhörer hören.
• listening to rhythms and comparing time intervals.	• Rhythmen hören und Zeitabstände vergleichen Hören von Rhythmen und Vergleichen von Zeitabständen.
• adjusting the tempo of a rhythm.	• Anpassen des Tempos eines Rhythmus.
Press ENTER to proceed.	Drücken Sie die EINGABETASTE um fortzufahren.

FREE TAPPING	TIPPEN OHNE GERÄUSCH
In this section, you will be asked to tap your finger on the desk without hearing any sounds.	In diesem Abschnitt werden Sie gebeten, mit dem Finger auf den Tisch zu tippen, ohne ein Geräusch zu hören.
First, you will tap at a comfortable rate, then at the slowest rate, finally at the fastest rate that is comfortable for you to maintain.	Tippen Sie zunächst mit einer angenehmen Geschwindigkeit, dann mit der langsamsten und anschließend mit der schnellsten Geschwindigkeit, die Sie bequem beibehalten können.
Please press the right arrow key to go to next page.	Bitte drücken Sie die rechte Pfeiltaste, um zur nächsten Seite zu gelangen.
The expected duration for TIPPEN OHNE GERÄUSCH task is ~3 minutes	Die voraussichtliche Dauer der Aufgabe TIPPEN OHNE GERÄUSCH beträgt ~3 Minuten
Throughout the section,	Im gesamten Abschnitt
• Please tap next to the microphone, within the area marked with tape.	• Bitte tippen Sie neben dem Mikrofon in dem mit Klebeband markierten Bereich.
• Please tap with only one finger. Choose the finger that is most comfortable for you to tap with.	• Bitte tippen Sie nur mit einem Finger. Wählen Sie den Finger, mit dem Sie am bequemsten tippen können.
• Please tap loud enough so that the microphone can pick up the taps.	• Bitte tippen Sie so laut, dass das Mikrofon das Tippen wahrnehmen kann.
• Please tap with equal strength.	• Bitte tippen Sie mit gleicher Stärke.
• Please make sure your clothes or accessories do not make sounds.	• Bitte achten Sie darauf, dass Ihre Kleidung oder Accessoires keine Geräusche verursachen.
• Please tap as evenly as possible.	• Bitte tippen Sie so gleichmäßig wie möglich.
If you have questions, please notify the experimenter.	Wenn Sie Fragen haben, wenden Sie sich bitte an den Versuchsleiter.
Otherwise, please press ENTER to proceed to the task.	Andernfalls drücken Sie bitte die EINGABETASTE, um mit der Aufgabe fortzufahren.
When you see the grey screen, please tap your finger on the desk at a rate that is comfortable for you to maintain.	Wenn Sie den grauen Bildschirm sehen, versuchen Sie bitte mit dem Finger auf den Tisch zu tippen mit einer Geschwindigkeit die für Sie angenehm ist.
You can stop tapping when the screen changes color.	Sie können mit dem Tippen aufhören, wenn sich die Farbe des Bildschirms ändert.
Press ENTER when you are ready.	Drücken Sie die EINGABETASTE wenn sie bereit sind.
When you see the grey screen, please tap your finger at the slowest rate that is comfortable for you.	Wenn Sie den grauen Bildschirm sehen, tippen Sie bitte mit der LANGSAMSTEN Geschwindigkeit, die für Sie am angenehmsten ist.
When you see the grey screen, please tap your finger at the fastest rate that is comfortable for you.	Wenn Sie den grauen Bildschirm sehen, tippen Sie bitte mit der SCHNELLSTEN Geschwindigkeit, die für Sie am angenehmsten ist.

SOUND VOLUME	EINSTELLUNG DER LAUTSTÄRKE
Now, please wear the headphones and adjust them for your comfort.	Setzen Sie bitte jetzt die Kopfhörer auf und stellen Sie diese auf Ihren Komfort ein.
In this section, you will adjust the sound volume. Note that this level can not be changed later.	In diesem Abschnitt stellen Sie die Lautstärke des Tons ein. Beachten Sie, dass dieser Wert später nicht mehr geändert werden kann.
Click on different locations on the slider to change the sound volume. You will hear a sound every time you change the volume.	Klicken Sie auf verschiedene Stellen des Schiebereglers, um die Lautstärke zu ändern. Sie hören jedes Mal einen Ton, wenn Sie die Lautstärke ändern.
Please press ENTER to start adjusting the volume.	Bitte drücken Sie die EINGABETASTE, um mit der Einstellung der Lautstärke zu beginnen.
Click on the left button to CHANGE the sound volume	Klicken Sie auf die linke Taste um die Lautstärke zu VERÄNDERN
Click on the right button to SET the sound volume	Klicken Sie auf die rechte Taste um die Lautstärke EINZUSTELLEN
Please DO NOT click and drag the mouse at the same time. Move the mouse and then click on different locations on the slider.	Bitte klicken und ziehen Sie die Maus NICHT gleichzeitig. Bewegen Sie die Maus und klicken Sie dann auf verschiedene Stellen des Schiebereglers.

TAPPING TO RHYTHM	TIPPEN ZUM RHYTHMUS
In the current section, you will be instructed about the task. Please read the instructions carefully.	Im aktuellen Abschnitt werden Sie in die Aufgabe eingewiesen. Bitte lesen Sie die Anweisungen sorgfältig durch.
You can travel between pages with the arrow keys freely until the practice section.	Bis zum Übungsteil können Sie mit den Pfeiltasten frei zwischen den Seiten wechseln.
The expected duration for TAPPING TO RHYTHM task is ~ 15 minutes (7,5 minutes x 2 blocks with a break in between)	Die voraussichtliche Dauer für die Aufgabe TIPPEN ZUM RHYTHMUS beträgt ~ 15 Minuten (7,5 Minuten x 2 Blöcke mit einer Pause dazwischen)
On each trial, you will hear a sequence of five sounds.	Bei jedem Durchgang hören Sie eine Folge von fünf Töne.
Your task is to start tapping along with the sounds, and then keep going at the same rate once the sounds stop.	Ihre Aufgabe ist es, mit den Tönen zu tippen und dann mit der gleichen Geschwindigkeit weiterzumachen, sobald die Töne aufhören.
You should keep tapping as evenly as possible until the screen changes color.	Sie sollten so gleichmäßig wie möglich tippen, bis der Bildschirm seine Farbe ändert.
Here is a graphical representation of the task. Remember, you should start tapping your finger soon as you can and tap along with the sounds. Keep tapping after the sounds stop.	Hier sehen Sie eine graphische Darstellung der Aufgabe. Denken Sie daran, dass Sie so schnell wie möglich anfangen mit dem Finger zu tippen, sobald Sie mit den Tönen mittippen können.
	Tippen Sie weiter, nachdem die Töne aufgehört haben.
You have completed the instructions. If you have understood the task, please press ENTER to proceed to the practice section.	Sie haben die Anweisungen abgeschlossen. Wenn Sie die Aufgabe verstanden haben, drücken Sie bitte EINGABETASTE, um mit dem Übungsteil fortzufahren.
PRACTICE	ÜBUNG
In this section, you will practice the task for at least 6 trials. After each trial, you will be given feedback regarding your performance.	In diesem Abschnitt üben Sie die Aufgabe für mindestens 6 Durchgänge. Nach jedem Versuch erhalten Sie eine Rückmeldung zu Ihrer Leistung.
Press ENTER to start the practice trials.	Drücken Sie die EINGABETASTE, um die Übungsversuche zu starten.
FEEDBACK	RÜCKMELDUNG
Something went wrong. Please notify the experimenter!	Etwas ist schief gelaufen. Bitte benachrichtigen Sie die Versuchsleiterin!
You did not start tapping before the sounds ended. Please try to start tapping as soon as you hear the sounds.	Sie schienen nicht zu tippen, bevor der Ton aufgehört hat. Bitte versuchen Sie zu tippen, sobald Sie den Ton hören.
Press ENTER to proceed.	Drücken Sie die EINGABETASTE um fortzufahren.
Not enough taps were recorded. Please do not stop tapping until the screen changes color.	Es wurden nicht genügend Tippgeräusche aufgezeichnet. Bitte hören Sie nicht auf zu tippen bis der Bildschirm seine Farbe ändert.
You were too fast!	Sie waren zu schnell!
You were too slow!	Sie waren zu langsam!
Let's try another.	Versuchen wir es mit einem anderen.
Good job!	Gut gemacht!
You have completed the practice section. If you have questions, please notify the experimenter.	Sie haben den Übungsteil abgeschlossen. Wenn Sie noch Fragen haben, informieren Sie bitte die Versuchsleiterin.
Otherwise, please press ENTER to proceed to the main task.	Andernfalls drücken Sie bitte die EINGABETASTE, um mit der Hauptaufgabe fortzufahren.
Note that no feedback will be given throughout this section.	Beachten Sie, dass es keine Rückmeldung während des Experiments geben wird.
You have successfully completed the TAPPING TO RHYTHM section.	Sie haben erfolgreich den Abschnitt tippen ZUM RHYTHMUS abgeschlossen.
You can take a short break before the next section.	Vor dem nächsten Abschnitt können Sie eine kurze Pause einlegen.
Press ENTER to end the break and proceed to the next section.	Drücken Sie die EINGABETASTE um die Pause zu beenden und fahren Sie mit dem nächsten Abschnitt fort.

DURATION DISCRIMINATION	DAUERDISKRIMINIERUNG
In the current section, you will be instructed about the task. Then, you will hear some examples. Finally, before the main task, you will practice the task. Please read the instructions carefully.	Im aktuellen Abschnitt werden Sie in die Aufgabe eingewiesen. Dann werden Sie einige Beispiele hören. Anschließend werden Sie vor der Hauptaufgabe die Aufgabe üben. Bitte lesen Sie die Anweisungen sorgfältig durch.
The expected duration for DAUERDISKRIMINIERUNG task is ~ 30 minutes (7,5 minutes x 4 blocks with breaks in between)	Die voraussichtliche Dauer für die Aufgabe DAUERDISKRIMINIERUNG beträgt ~ 30 Minuten (7,5 Minuten x 4 Blöcke mit Pausen dazwischen)
You can travel between pages with the arrow keys freely until you learn the task.	Sie können mit den Pfeiltasten frei zwischen den Seiten wechseln, bis Sie die Aufgabe gelernt haben.
In each trial, you will first hear a rhythm consisting of 5 drum sounds, followed by a short pause. Then, you will hear another interval with 2 drum sounds. Your task is to decide whether this final interval is longer or shorter than the intervals making up the rhythm. If the final interval is LONGER, press L key. If it is SHORTER, press S key.	Bei jedem Versuch hören Sie zunächst einen Rhythmus, der aus 5 Trommelklängen besteht, gefolgt von einer kurzen Pause. Dann hören Sie ein weiteres Intervall mit 2 Trommelklängen. Ihre Aufgabe ist es, zu entscheiden, ob dieses letzte Intervall länger oder kürzer ist als die Intervalle, aus denen der Rhythmus besteht. Wenn das letzte Intervall LÄNGER ist, drücken Sie die Taste L. Wenn es KÜRZER ist, drücken Sie die Taste S.
next page / previous page	nächste Seite / vorherige Seite
Here is a graphical representation of one trial: You will first hear the drum sounds, then respond on the keyboard. The end of the trial will be signaled by a screen color change.	Hier sehen Sie eine grafische Darstellung eines Versuchs: Zuerst hören Sie die Trommelklänge, dann antworten Sie mit der Tastatur. Das Ende des Versuchs wird durch einen Farbwechsel des Bildschirms signalisiert.
Please do not count, and do not get help from any movement in your body while doing this task.	Zählen Sie bitte nicht und lassen Sie sich bei dieser Aufgabe nicht von einer Bewegung Ihres Körpers helfen.
If you understood the task, please press ENTER to listen to the examples.	Wenn Sie die Aufgabe verstanden haben, drücken Sie bitte die EINGABETASTE, um sich die Beispiele anzuhören.
You can not go back to the current section once you proceed.	Sie können nicht zum aktuellen Abschnitt zurückkehren, wenn Sie fortfahren.
Press S key when the interval between the final pair of sounds is SHORTER than the ones making up the rhythm.	Drücken Sie die Taste S, wenn das Intervall zwischen dem letzten Tonpaar KÜRZER ist als das Intervall zwischen den Tönen, die den Rhythmus bilden.
Press L key when the interval between the final pair of sounds is LONGER than the ones making up the rhythm.	Drücken Sie die Taste L, wenn das Intervall zwischen dem letzten Tonpaar LÄNGER ist als das Intervall zwischen den Tönen, die den Rhythmus bilden.
You have completed the instructions. In the following section, you will practice the task for at least 6 trials. At the end of each trial, you will be given feedback regarding your responses.	Sie haben die Anweisungen abgeschlossen. Im folgenden Abschnitt werden Sie die Aufgabe für mindestens 6 Versuche üben. Am Ende eines jeden Versuchs erhalten Sie eine Rückmeldung zu Ihren Antworten.
When you are ready, please press ENTER to proceed	Wenn Sie bereit sind, drücken Sie bitte die EINGABETASTE, um fortzufahren.
Your response was correct.	Ihre Antwort war richtig.
The final interval was shorter than the previous intervals. Your response was incorrect.	Das letzte Intervall war kürzer als die vorherigen Intervalle. Ihre Antwort war falsch.
The final interval was longer than the previous intervals. Your response was incorrect.	Das letzte Intervall war länger als die vorherigen Intervalle. Ihre Antwort war falsch.
You were too late to respond. Please try to respond fast and accurately.	Sie haben zu spät geantwortet. Bitte versuchen Sie, schnell und genau zu antworten.
You have completed the practice section. If you have questions, please notify the experimenter.	Sie haben den Übungsteil abgeschlossen. Wenn Sie Fragen haben, informieren Sie bitte den Versuchsleiter.
Otherwise, please press ENTER to proceed to the main task	Andernfalls drücken Sie bitte die EINGABETASTE, um mit der Hauptaufgabe fortzufahren.
Note that no feedback will be given throughout this section	Beachten Sie, dass während dieses Abschnitts kein Feedback gegeben werden kann.
You have successfully completed the DURATION DISCRIMINATION section.	Sie haben den Abschnitt DURATION DISCRIMINATION erfolgreich abgeschlossen.
You can take a short break before the next section.	Sie können vor dem nächsten Abschnitt eine kurze Pause einlegen.
Press ENTER to end the break and proceed to the next section.	Drücken Sie die EINGABETASTE um die Pause zu beenden und fahren Sie mit dem nächsten Abschnitt fort.
BREAK.	PAUSIEREN. >> PAUSE
Now, you will repeat the task you completed at the beginning of the experiment, where you tapped without listening to any sound.	Jetzt wiederholen Sie die Aufgabe, die Sie zu Beginn des Experiments durchgeführt haben, bei dem Sie getippt haben ohne einen Gerausch zu hören.
PREFERRED TEMPO	BEVORZUGTES TEMPO

SLIDER	SCHIEBEREGLER
In the following trials, you will hear a continuous rhythm that will start with either fast or slow tempo.	Bei den folgenden Versuchen; hören Sie einen fortlaufenden Rhythmus, der entweder mit schnellem oder langsamem Tempo beginnt.
Your task is to click on different locations on the slider to change the tempo, and finally, to indicate the tempo that you prefer the most (you are most comfortable with).	Ihre Aufgabe ist es, auf verschiedene Stellen des Schiebereglers zu klicken, um das Tempo zu ändern, und schließlich das Tempo anzugeben, das Ihnen am besten gefällt (mit dem Sie sich am wohlsten fühlen).
Press ENTER to proceed to the task.	Drücken Sie ENTER, um mit der Aufgabe fortzufahren.
Click on the left button to CHANGE the tempo	Klicken Sie auf die linke Taste, zum Ändern des Tempos
Click on the left button to SET the tempo to a comfortable rate	Klicken Sie auf die linke Taste um das Tempo auf eine angenehme Geschwindigkeit einzustellen

KEYPRESS	TASTENDRUCK
In the following trials, you will hear a continuous rhythm that will start with either fast or slow tempo and change its tempo gradually.	In den folgenden Versuchen hören Sie einen fortlaufenden Rhythmus, der entweder mit einem schnellen oder einem langsamen Tempo beginnt und sein Tempo schrittweise ändert.
Your task is to press ENTER when the tempo is not too fast or too slow, but is at a comfortable rate that feels 'just right'.	Ihre Aufgabe ist es, die EINGABETASTE zu drücken, wenn das Tempo nicht zu schnell oder zu langsam ist, sondern eine angenehme Geschwindigkeit hat, die sich "genau richtig" anfühlt.
A circle will show how much time is left to give a response. Please specify your preferred tempo before the circle disappears.	Ein Kreis zeigt an, wie viel Zeit noch für eine Antwort bleibt. Bitte geben Sie Ihr bevorzugtes Tempo an, bevor der Kreis verschwindet.
The next trial will play automatically once you press enter. Please get ready and press ENTER to continue.	Der nächste Versuch wird automatisch abgespielt, sobald Sie die Eingabetaste drücken. Bitte machen Sie sich bereit und drücken Sie ENTER, um fortzufahren.
Press ENTER when the tempo is not too fast or too slow, but is at a comfortable rate that feels 'just right'.	Drücken Sie die EINGABETASTE, wenn das Tempo nicht zu schnell oder zu langsam ist, sondern ein angenehmes Tempo hat, das sich "genau richtig" anfühlt.
There was no response. Press ENTER to try again.	Es gab keine Antwort. Drücken Sie ENTER, um es erneut zu versuchen.
The next trial will play automatically once you press enter. Please get ready and press ENTER to continue.	Der nächste Versuch wird automatisch abgespielt, sobald Sie die Eingabetaste drücken.
You have completed the experiment. Thank you for your participation.	Sie haben das Experiment abgeschlossen. Vielen Dank für Ihre Teilnahme.
Press ENTER to exit.	Drücken Sie die EINGABETASTE zum Beenden.

Supplementary Information

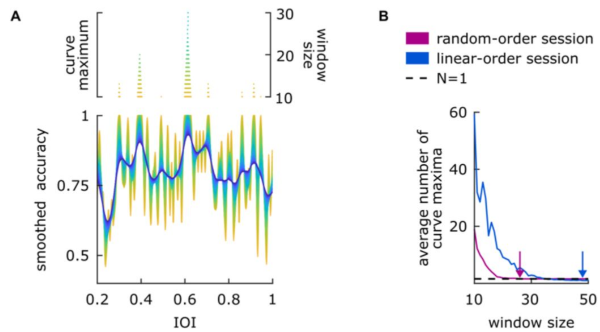
Smoothing procedure to obtain preferred rate estimates from Experiment 1 datasets

By default, the *smoothdata* function in Matlab outputs the moving average of the neighboring data points within a specified window size. Here, we used 'gaussian' as the method for smoothing that calculates the Gaussian-weighted moving average over each window. Both moving average and gaussian smoothing are forms of convolution, where each data point in a given window (number of elements) is multiplied by the specified array of numbers, namely, the 'mask' (Smith, 1997). In moving average method, the mask is flat, giving the weight of 1 to each element. Gaussian-weighted moving average gives higher values into the midpoint of the window, which enhances the fluctuations in the data that are the focus of the current analysis.

As we were interested in a single-point maximum accuracy for each individual and session, we optimized the window size for each session type such that the smoothed data revealed a single global maximum. Starting from a window size of 10 samples for each window size, we recorded the IOIs with the maximum accuracy value in each dataset. An illustration of the optimization for an example participant's dataset is shown in **Supplementary Figure S1A**. For small windows, smoothed data included IOI multiple values where accuracy was 1, especially in the linear-order sessions. The optimization procedure revealed that, to obtain a single global maximum for each individual's dataset, accuracy should be smoothed by windows of 26 samples in the random-order sessions and 48 samples in linear-order sessions, as shown in **Supplementary Figure S1B**. To equalize the smoothing across the variables of accuracy and IOI, we also smoothed IOI with the same window size. Estimates of preferred rate were taken as the smoothed IOI that yielded maximum accuracy.

Additional analyses for assessment of harmonic relationships between the preferred rate estimates obtained from two sessions of Experiment 1

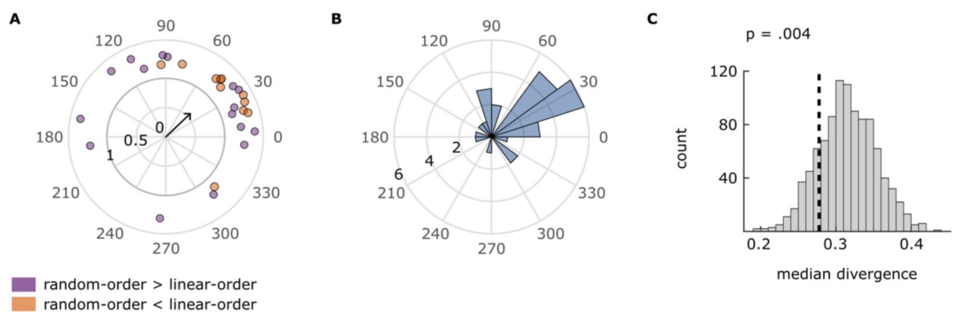
The harmonic correspondence between the preferred rate estimates obtained from random- and linear-order sessions of **Experiment 1** was analyzed by a permutation test, which tested whether the observed pattern where estimates from one session was duplicate (Y = 2*X) or half (Y = X/2) of the one from the other session, was due to chance. We ran additional analyses to validate this method. The first analysis involved a circular approach. We first normalized each participant's estimates by rescaling the slower estimate with respect to the faster one and converting the values to radians, using max(X)_radian = 2*pi*max(X)/min(X) where X represents a vector with a single participant's estimates from both sessions. **Supplementary Figure S2A** shows the normalized estimates. We reasoned that values with integer-ratio relationships should correspond to the same phase on a unit circle. Then, we assessed whether the resulting distribution of normalized values, shown in **Supplementary Figure S2B**, differed from a uniform distribution, using Rayleigh's test. Test statistic (p = .004) was significant, indicating that the distribution (**Supplementary Fig. S2B**) was not uniform. The circular mean of the distribution was 43.77 (SD = 53.42) degrees (M = 0.764, SD = 0.932 radians), indicating that the slower estimates were slightly slower than the fast estimate or its duplicates. This was an expected outcome since the normalization procedure that involved rescaling the maximum to minimum was biased towards a positive value, which rendered tests to compare the resulting distribution against zero inapplicable. Thus, we ran a second test, which was a modular approach, to assess integer-ratio relationships between the preferred rate estimates. We first calculated how much the slower estimate diverts, proportionally from the faster estimate or its multiples (i.e., subharmonics) by normalizing the estimates from both sessions by the faster estimate. The outcome measure was the modulus of the slower, with respect to the faster estimate, divided by the faster estimate, described as mod(max(X)/min(X))/min(X) where X represents each participant's estimates from the two sessions. Since the resulting distribution was non-normal, we used 'median' as the statistic summarizing the central tendency for percentage diversion of slow from fast preferred rate estimates. Then, we ran a permutation test where linear-order session estimates were shuffled over 1000 iterations, and median percentage diversion values for each iteration (**Supplementary Fig. S2C**) was retrieved. Test statistic was significant (p = .004), indicating that the harmonic relationships we observed in the estimates were not due to chance or dependent on the assessment method.



Supplementary Figure S1

Illustration of the optimization procedure and parameter choices for smoothing accuracy in Experiment 1.

A Bottom: An example participant's linear-order session dataset. Each color represents an output of the smoothing function that uses a window size, ranging from 10 (yellow) to 50 (dark blue). Top: The number of maximum values on the smoothed accuracy for each window size. **B** Participants' average number of curve maxima for random-order (pink) and linear-order (blue) sessions. Arrows show the optimized window sizes for the session types, where each individual's dataset had only one curve maximum (dashed line).



Supplementary Figure S2

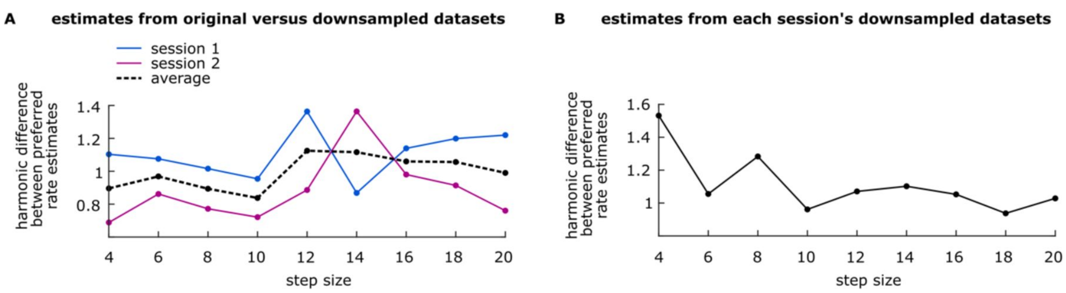
Result of the analyses of harmonic relationships in Experiment 1 preferred rate estimates.

A In circular analyses, each participant's slower estimates, regardless of whether they were obtained from either random-order (purple) or linear-order (orange) sessions, were normalized by the faster estimate. Mean vector angle (arrow) was 43 degrees. **B** Resulting distribution of normalized estimates from the circular analyses. **C** Permutation test results from the modular approach. The histogram shows the distribution of median percentage divergence, obtained from 1000 iterations, and the dashed line represents the median percentage divergence from original data.

Details of the bootstrapping analyses for Experiment 2 paradigm

The experiment in Kaya & Henry (2022) was a longer version of the paced tapping paradigm from **Experiment 2** (current study). The IOI of the isochronous stimulus sequences were sampled from a range of 200 ms to 1000 ms with a step size of 2 and varied in each trial. We estimated up to 3 preferred rates for each individual by fitting curves to continuation tapping tempo-matching errors ($|TME_{continuation}|$) and obtaining the IOIs at the curves' local minima. Estimates from two identical sessions that each participant completed showed strong correspondence and harmonic relationships, as measured by the permutation test described in **Experiment 1 methods** section.

For the bootstrapping analysis, we first downsampled each participant's single-session data, with each even step size between 4 and 20 ms. That is, for the respective step size, we filtered data where IOI corresponded to the spacing value added to the smallest (200 ms) to the largest (1000 ms) IOI. (e.g., trials with IOI = 200, 204, 208 ms and so on, for step size of 4 ms). We performed the preferred rate estimation procedure for each downsampled dataset, used in the experiment analyses. To assess the optimum step size that would represent the experiment's findings, we assessed the correspondences between (1) preferred rate estimates from the original and downsampled datasets for each session and (2) estimates from downsampled datasets between sessions. In both steps, the correspondence between estimates was quantified by their harmonic difference (i.e., the sum of the datapoints Euclidian distances to the closest line among y=x, y=2x and y=x/2 lines). A smaller difference value indicated that the estimates subject to comparison were similar, or close to doubles or halves of each other. Harmonic differences obtained from the first and seconds steps of the bootstrapping analysis are shown in **Supplementary Figure S3a** and **S3b**, respectively. Together, the bootstrapping analyses showed that the average harmonic difference between estimates from original versus downsampled datasets was smallest at the step size of 10, where harmonic difference between downsampled sessions' estimates was also small.



Supplementary Figure S3

Results of the bootstrapping analysis.

In **A**, each circle shows harmonic difference between preferred rate estimates from the original and downsampled datasets for session 1 (blue) and session 2 (pink) and their average (dotted black line) at the respective step size. In **B**, each circle shows harmonic difference between preferred rate estimates from the downsampled session 1 and session 2 datasets at the respective step size.

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Reviewer #1 (Public Review):

Summary:

This study assumes but also demonstrates that auditory rhythm processing is produced by internal oscillating systems and evaluates the properties of internal oscillators across individuals. The authors designed an experiment and performed analyses that address individuals' preferred rate and flexibility, with a special focus on how much past rhythms influence subsequent trials. They find evidence for such historical dependence and show that we adapt less well to new rhythms as we age. While I have some doubts about the entrainment-based interpretation of the results, this work offers a useful contribution to our understanding of individual differences in rhythm processing regardless.

Strengths:

The inclusion of two tasks -- a tapping and a listening task -- complement each other methodologically. By analysing both the production and tracking of rhythms, the authors emphasize the importance of the characteristics of the receiver, the external world, and their interplay. The relationship between the two tasks and components within tasks are explored using a range of analyses. The visual presentation of the results is very clear. The age-related changes in flexibility are useful and compelling.

The paper includes a discussion of the study assumptions, and it contextualizes itself more explicitly as taking entrainment frameworks as a starting point. As such, even if the entrainment of oscillators cannot be decisively shown, it is now clear that this is nevertheless adopted as a useful theoretical lens.

Weaknesses:

The newly included analyses that justify an entrainment or oscillator-based interpretation of the result could be presented in a clearer manner so that readers can parse their validity better. For example, in line with an entrainment interpretation, the regression lines in Figure 2B show accuracy increases as the IOI moves towards the preferred rate -- but then beyond the preferred rate, accuracy appears to increase further still. Furthermore, the additional analyses on harmonic relationships could be enriched with justification and explanation of each of its steps.

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Reviewer #2 (Public Review):

Summary:

The current work describes a set of behavioral tasks to explore individual differences in the preferred perceptual and motor rhythms. Results show a consistent individual preference for a given perceptual and motor frequency across tasks and, while these were correlated, the latter is slower than the former one. Additionally, the adaptation accuracy to rate changes is proportional to the amount of rate variation and, crucially, the amount of adaptation decreases with age.

Strengths:

Experiments are carefully designed to measure individual preferred motor and perceptual tempo. Furthermore, the experimental design is validated by testing the consistency across tasks and test-retest, what makes the introduced paradigm a useful tool for future research. The obtained data is rigorously analyzed using a diverse set of tools, each adapted to the specificities across the different research questions and tasks.
This study identifies several relevant behavioral features: (i) each individual shows a preferred and reliable motor and perceptual tempo and, while both are related, the motor is consistently slower than the pure perceptual one; (ii) the presence of hysteresis in the adaptation to rate variations; and (iii) the decrement of this adaptation with age. All these observations are valuable for the auditory-motor integration field of research, and they could potentially inform existing biophysical models to increase their descriptive power.

Weaknesses:

To get a better understanding of the mechanisms underlying the behavioral observations, it would have been useful to compare the observed pattern of results with simulations done with existing biophysical models. However, this point is addressed if the current study is read along with this other publication of the same research group: Kaya, E., & Henry, M. J. (2024, February 5). Modeling rhythm perception and temporal adaptation: top-down influences on a gradually decaying oscillator. https://doi.org/10.31234/osf.io/q9uvr

https://doi.org/10.7554/eLife.90735.2.sa0

Author Response

The following is the authors' response to the original reviews.

General response:

We thank the reviewers for their thorough evaluation of our manuscript. Working on the raised concerns has improved the manuscript greatly. Specifically, the recommendations to clarify the adopted assumptions in the study strengthened the motivation for the study; further, following up some of the reviewers' concerns with additional analyses validated our chosen measures and strengthened the compatibility of the findings with the predictions of the dynamic attending framework. Below, you will find our detailed point-by-point responses, along with information on specific revisions.

The reviewers pointed out that study assumptions were unclear, some of the measures we chose were not well motivated, and the findings were not well enough explained considering possible alternatives. As suggested, we reformulated the introduction, explained the common assumptions of entrainment models that we adopted in the study, and further clarified how our chosen measures for the properties of the internal oscillators relate to these assumptions.

We realized that the initial emphasis on the compatibility of the current findings with predictions of entrainment models might have led to the wrong impression that the current study aimed to test whether auditory rhythmic processing is governed by timekeeper or oscillatory mechanisms. However, testing these theoretical models to explain human behavior necessitates specific paradigms designed to compare the contrasting predictions of the models. A number of studies do so by manipulating regularity in a stimulus sequence or expectancy of stimulus onsets, or assessing the perceived timing of targets that follow a stimulus rhythm. Such paradigms allow testing the prediction that an oscillator, underlying perceptual timing, would entrain to a regular but not an irregular sequence. This would further lead to stronger expectancies at the peak of the oscillation, where 'attentional energy' is the highest. These studies report 'rhythmic facilitation', where targets that align with the peaks of the oscillation are better detected than those that do not (see Henry and Herrmann (2014) and Haegens and Zion Golumbic (2018) for reviews). Additionally, unexpected endings of standard intervals, preceded by a regular entraining sequence, lead to a biased estimation of subsequent comparison intervals, due to the contrast between the attentional oscillator's phase and a deviating stimulus onset (Barnes & Jones, 2000; Large & Jones, 1999; McAuley & Jones, 2003). Even a sequence rate that is the multiple of the to-be-judged standard and comparison intervals give rise to rhythmic facilitation (McAuley & Jones, 2003), and the expectancy of a stimulus onset modulates duration judgments. These findings are not compatible with predictions of timekeeper models as time intervals in these models are represented arbitrarily and are not affected by expectancy violations.

In the current study, we adopted an entrainment approach to timing, rather than testing predictions of competing models. This choice was motivated by several aspects of entrainment models that align better with the aims of the current study. First, our focus was on understanding perception and production of rhythms, for which perception is better explained by entrainment models than by timekeeper models, which excel at explaining perception of isolated time intervals (McAuley, 2010). Moreover, we wanted to leverage the fact that entrainment models elegantly include parameters that can explain different aspects of timing abilities, and these parameters can be estimated in an individualized manner. For instance, the flexibility property of oscillators can be linked to the ability to adapt to changes in external context, while timekeeper or Bayesian timing approaches lack a specific mechanism to quantify temporal adaptation across perceptual and motor domains. Finally, that entrainment is observed across theoretical, behavioral, and neural levels renders entrainment models useful in explaining and generalizing behavior across different domains. Nevertheless, some results showed partial compatibility with predictions of the timekeeper models, such as the modulation of 'bestperformance rates' by the temporal context, observed in Experiment 1’ random-order sessions, where stimulus rates maximally differed across consecutive trials. However, given that the mean, standard deviation, and range of stimulus rates were identical across sessions, and timekeeper models assume no temporal adaptation in duration perception, we should have observed similar results across these sessions. Conversely, we found significant accuracy differences, biased duration judgments, and harmonic relationships between the best-performance rates. We elaborate more on these results with respect to their compatibility with the contrasting models of human temporal perception in the revised discussion.

> ***Responses to specific comments:***
>
> *(1.1) At times, I found it challenging to evaluate the scientific merit of this study from what was provided in the introduction and methods. It is not clear what the experiment assumes, what it evaluates, and which competing accounts or predictions are at play. While some of these questions are answered, clear ordering and argumentative flow is lacking. With that said, I found the Abstract and General Discussion much clearer, and I would recommend reformulating the early part of the manuscript based on the structure of those segments.*
>
> *Second, in my reading, it is not clear to what extent the study assumes versus demonstrates the entrainment of internal oscillators. I find the writing somewhat ambiguous on this count: on the one hand, an entrainment approach is assumed a priori to design the experiment ("an entrainment approach is adopted") yet a primary result of the study is that entrainment is how we perceive and produce rhythms ("Overall, the findings support the hypothesis that an oscillatory system with a stable preferred rate underlies perception and production of rhythm..."). While one could design an experiment assuming X and find evidence for X, this requires testing competing accounts with competing hypotheses -- and this was not done.*

We appreciate the reviewer’s concerns and suggestion to clarify the assumptions of the study and how the current findings relate to the predictions of competing accounts. To address these concerns:

• We added the assumptions of the entrainment models that we adopted in the Introduction section and reformulated the motivation to choose them accordingly.

• We clarified in the Introduction that the study’s aim was not to test the entrainment models against alternative theories of rhythm perception.

• We added a paragraph in the General Discussion to further distinguish predictions from the competing accounts. Here we discussed the compatibility of the findings with predictions of both entrainment and timekeeper models.

• We rephrased reasoning in the Abstract, Introduction, and General Discussion to further clarify the aims of the study, and how the findings support the hypotheses of the current study versus those of the dynamic attending theory.

> *(1.2) In my view, more evidence is required to bolster the findings as entrainment-based regardless of whether that is an assumption or a result. Indeed, while the effect of previous trials into the behaviour of the current trial is compatible with entrainment hypotheses, it may well be compatible with competing accounts as well. And that would call into question the interpretation of results as uncovering the properties of oscillating systems and age-related differences in such systems. Thus, I believe more evidence is needed to bolster the entrainment hypothesis.*
>
> *For example, a key prediction of the entrainment model -- which assumes internal oscillators as the mechanism of action -- is that behaviour in the SMT and PTT tasks follows the principles of Arnold's Tongue. Specifically, tapping and listening performance should worsen systematically as a function of the distance between the presented and preferred rate. On a participant-by-participant, does performance scale monotonically with the distance between the presented and preferred rate? Some of the analyses hint at this question, such as the effect of ΔIOI on accuracy, but a recontextualization, further analyses, or additional visualizations would be helpful to demonstrate evidence of a tongue-like pattern in the behavioural data. Presumably, non-oscillating models do not follow a tongue-like pattern, but again, it would be very instructive to explicitly discuss that.*

We thank the reviewer for the excellent suggestion of assessing 'Arnold's tongue' principles in timing performance. We agree that testing whether timing performance forms a pattern compatible with an Arnold tongue would further support our assumption that the findings related to preferred rate stem from an entrainment-based mechanism. We rather refer to the 'entrainment region', (McAuley et al., 2006) that corresponds to a slice in the Arnold tongue at a fixed stimulus intensity that entrains the internal oscillator. In both representations of oscillator behavior across a range of stimulus rates, performance should systematically increase as the difference between the stimulus rate and the oscillator's preferred rate, namely, 'detuning' decreases. In response to the reviewer's comment, we ran further analyses to test this key prediction of entrainment models. We assessed performance at stimulus rates that were faster and slower than an individual's preferred rate estimates from in Experiment 1. To do so, we ran logistic regression models on aggregated datasets from all participants and sessions, where normalized IOI, in trials where the stimulus rate was faster than the preferred rate estimate, and in those where it was slower, predicted accuracy. Stimulus IOIs were normalized within each direction (faster- versus slower-than-preferred rate) using z-score transformation, and the direction was coded as categorical in the model. We reasoned that a positive slope for conditions with stimulus rates faster than IOI, and a negative slope from conditions with slower rates, should indicate a systematic accuracy increase toward the preferred rate estimate. This is exactly what we found. These results revealed significant main effect for the IOI and a significant interaction between IOI and direction, indicating that accuracy increased towards the preferred rate at fast rates and decreased as the stimulus rate diverged from the preferred rate at slow rates. We added these results to the respective subsections of Experiment 1 Methods and Results, added a plot showing the slices of the regression surfaces to Figure 2B and elaborated on the results in Experiment 1 Discussion. As the number of trials in Experiment 2 was much lower (N = 81), we only ran these additional analyses in Experiment 1.

> *(1.3) Fourth, harmonic structure in behaviour across tasks is a creative and useful metric for bolstering the entrainment hypothesis specifically because internal oscillators should display a preference across their own harmonics. However, I have some doubts that the*

> *analyses as currently implemented indicate such a relationship. Specifically, the main analysis to this end involves summing the residuals of the data closest to y=x, y=2*x and y=x/2 lines and evaluating whether this sum is significantly lower than for shuffled data. Out of these three dimensions, y=x does not comprise a harmonic, and this is an issue because it could by itself drive the difference of summed residuals with the shuffled data. I am uncertain whether rerunning the same analysis with the x=y dimension excluded constitutes a simple resolution because presumably there are baseline differences in the empirical and shuffled data that do not have to do with harmonics that would leak into the analysis. To address this, a simulation with ground truths could be helpful to justify analyses, or a different analysis that evaluates harmonic structure could be thought of.*

We thank the reviewer for pointing out the weakness of the permutation test we developed to assess the harmonic relationship between Experiment 1's preferred rate estimates. Datapoints that fall on the y=x line indeed do not represent harmonic relationships. They rather indicate one-to-one correspondence between the axes, which is a stronger indicator of compatibility between the estimates. Maybe speaking to the reviewer's point, standard correlation analyses were not significant, which would have been expected if the permutation results were being driven by the y=x relationship. This was the reason we developed the permutation test to include integer-ratio datapoints could also contribute.

Based on reviewer's comment, we ran additional analyses to assess the harmonic relationships between the estimates. The first analysis involved a circular approach. We first normalized each participant's estimates by rescaling the slower estimate with respect to the faster one by division; and converted the values to radians, since a pair of values with an integer-ratio relationship should correspond to the same phase on a unit circle. Then, we assessed whether the resulting distribution of normalized values differed from a uniform distribution, using Rayleigh's test, which was significant ($p = .004$). The circular mean of the distribution was 44 (SD = 53) degrees (M = 0.764, SD = 0.932 radians), indicating that the slower estimates were slightly slower than the fast estimate or its duplicates. As this distribution was skewed toward positive values due to the normalization procedure, we did not compare it against zero angle. Instead, we ran a second test, which was a modular approach. We first calculated how much the slower estimate deviated proportionally from the faster estimate or its multiples (i.e., subharmonics) by normalizing the estimates from both sessions by the faster estimate. The outcome measure was the modulus of the slower, relative to the faster estimate, divided by the faster estimate. Then, we ran a permutation test, shuffling the linear-order session estimates over 1000 iterations and taking the median percent deviation values for each iteration. The test statistic was significant ($p = .004$), indicating that the harmonic relationships we observed in the estimates were not due to chance or dependent on the assessment method. We added these details of additional analyses to assess harmonic relationships between the Experiment 1 preferred rate estimates in the Supplementary Information.

> *(2.1) The current study is presented in the framework of the ongoing debate of oscillator vs. timekeeper mechanisms underlying perceptual and motor timing, and authors claim that the observed results support the former mechanism. In this line, every obtained result is related by the authors to a specific ambiguous (i.e., not clearly related to a biophysical parameter) feature of an internal oscillator. As pointed out by an essay on the topic (Doelling & Assaneo, 2021), claiming that a pattern of results is compatible with an "oscillator" could be misleading, since some features typically used to validate or refute such mechanisms are not well grounded on real biophysical models. Relatedly, a recent study (Doelling et al., 2022) shows that two quantitatively different computational algorithms (i.e., absolute vs relative timing) can be explained by the same biophysical model. This demonstrates that what could be interpreted as a timekeeper, or an oscillator can represent the same biophysical model working under different conditions.*

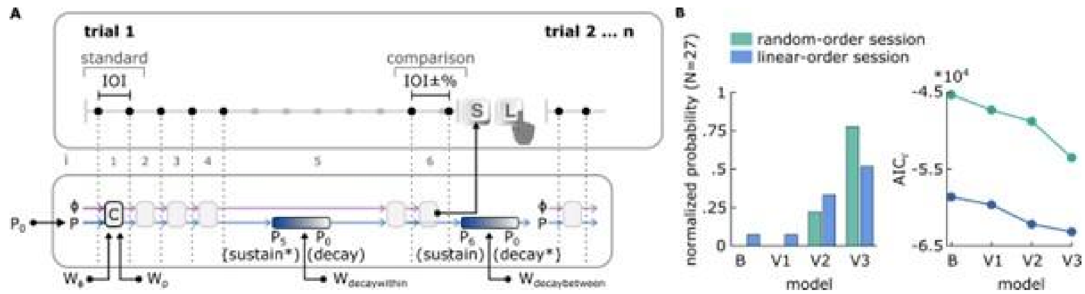
> *For this reason, if authors would like to argue for a given mechanism underlying their observations, they should include a specific biophysical model, and test its predictions against the observed behavior. For example, it's not clear why authors interpret the observation of the trial's response being modulated by the rate of the previous one, as an oscillator-like mechanism underlying behavior. As shown in (Doelling & Assaneo, 2021) a simple oscillator returns to its natural frequency as soon as the stimulus disappears, which will not predict the long-lasting effect of the previous trial. Furthermore, a timekeeper-like mechanism with a long enough integration window is compatible with this observation.*
>
> *Still, authors can choose to disregard this suggestion, and not testing a specific model, but if so, they should restrict this paper to a descriptive study of the timing phenomena.*

We thank the reviewer for their valuable suggestion of to include a biophysical model to further demonstrate the compatibility of the current findings with certain predictions of the model. While we acknowledge the potential benefits of implementing a biophysical model to understand the relationships between model parameters and observed behavior, this goes beyond the scope of the current study.

We note that we have employed a modeling approach in a subsequent study to further explore how the properties and the resulting behavior of an oscillator map onto the patterns of human behavior we observed in the current study (Kaya & Henry, 2024, February 5). In that study, we fitted a canonical oscillator model, and several variants thereof, separately to datasets obtained from random-order and linear-order sessions of Experiment 1 of the current submission. The base model, adapted from McAuley and Jones (2003), assumed sustained oscillations within the trials of the experiment, and complete decay towards the preferred rate between the trials. We introduced a gradual decay parameter (Author response image 1A) that weighted between the oscillator's concurrent period value at the time of decay and its initial period (i.e., preferred rate). This parameter was implemented only within trials, between the standard stimulus sequence and comparison interval in Variant 1, between consecutive trials in Variant 2, and at both temporal locations in Variant 3. Model comparisons (Author response image 1B) showed that Variant 3 was the best-fitting model for both random- and linear-order datasets. Crucially, estimates for within- and between-trial decay parameters, obtained from Variant 3, were positively correlated, suggesting that oscillators gradually decayed towards their preferred rate at similar timescales after cessation of a stimulus.

Author response image 1.

(A) Illustration of the model fitted to Experiment 1 datasets and (B) model comparison results. In each trial, the model is initialized with a phase (ϕ) and period (P) value. A At the offset of each stimulus interval i, the model updates its phase (pink arrows) and period (blue arrows) depending on the temporal contrast (C) between the model state and stimulus onset and phase and period correction weights, Wϕ and Wp. Wdecaywithin updates the model period as a weighted average between the period calculated for the 5th interval, P5, and model's preferred rate, P0. C, calculated at the offset of the comparison interval. Wdecaybetween parameter initializes the model period at the beginning of a new trial as a weighted average between the last period from the previous trial and P0. The base model's assumptions are marked by asterisks, namely sustained oscillation during the silence (i=5), and complete decay between trials. B Left: The normalized probability of each model having the minimum BIC value across all models and across participants. Right: AICc, calculated from each model's fit to participants' single-session datasets. In both panels, random-order and linear-order sessions were marked in green and blue, respectively. B denotes the base model, and V1, V2 and V3 denote variants 1, 2 and 3, respectively.



Although our behavioral results and modeling thereof must necessarily be interpreted as reflecting the mechanics of an attentional, but not a neural oscillator, these findings might shed light on the controversy in neuroscience research regarding the timeline of entrainment decay. While multiple studies show that neural oscillations can continue at the entrained rate for a number of cycles following entrainment (Bouwer et al., 2023; Helfrich et al., 2017; Lakatos et al., 2013; van Bree et al., 2021), different modeling approaches reveal mixed results on this phenomenon. Whereas Doelling and Assaneo (2021) show that a Stuart-Landau oscillator returns immediately back to its preferred rate after synchronizing to an external stimulus, simulations of other oscillator types suggest gradual decay toward the preferred rate (Large, 1994; McAuley, 1995; Obleser et al., 2017) or self-sustained oscillation at the external stimulus rate (Nachstedt et al., 2017).

While the Doelling & Assaneo study (2021) provides insights on entrainment and behavior of the Stuart-Landau oscillator under certain conditions, the internal oscillators hypothesized by the dynamic attending theory might have different forms, therefore may not adhere to the behavior of a specific implementation of an oscillator model. Moreover, that a phase-coupled oscillator does not show gradual decay does not preclude that models with period tracking behave similarly. Adaptive frequency oscillators, for instance, are able to sustain the oscillation after the stimulus ceases (Nachstedt et al., 2017). Alongside with models that use Hebbian learning (Roman et al., 2023), the main implementations of the dynamic attending theory have parameters for period tracking and decay towards the preferred rate (Large, 1994; McAuley, 1995). In fact, the u-shaped pattern of duration discrimination sensitivity across a range of stimulus rates (Drake & Botte, 1993) is better explained by a decaying than a non-decaying oscillator (McAuley, 1995). To conclude, the literature suggests that the emergence of decay versus sustain behavior of the oscillators and the timeline of decay depend on the particular model used as well as its parameters and does therefore not offer a one-for-all solution.

> ***Reviewer #2 (Recommendations For The Authors):***
>
> - *Are the range, SD and mean of the random-order and linear-order sessions different? If so, why?*

Information regarding the SD and mean of the random-order and linear-order sessions was added to Experiment 1 Methods section.

"While the mean (M = 599 ms), standard deviation (SD = 231 ms) and range (200, 998 ms) of the presented stimulus IOIs were identical between the sessions, the way IOI changed from trial to trial was different." (p. 5)

> - *Perhaps the title could mention the age-related flexibility effect you demonstrate, which is an important contribution that without inclusion in the title could be missed in literature searches.*

We have changed the title to include age-related changes in oscillator flexibility. Thanks for the great suggestion.

> - *Is the statistical analysis in Figure 4A between subjects? Shouldn't the analyses be within subjects?*

We have now better specified that the statistical analyses of Experiment 2's preferred rate estimates were across the tasks, in Figure 4 caption.

"Vertical lines above the box plots represent within-participants pairwise comparisons." (p. 17)

> - *It says participants' hearing thresholds were measured using standard puretone audiometry. What threshold warranted participant exclusion and how many participants were excluded on the basis of hearing skills?*

We have now clarified that hearing threshold was not an exclusion criterion.

"Participants were not excluded based on hearing threshold." (p. 11)

> - *"Tapping rates from 'fastest' and 'slowest' FMT trials showed no difference between pre- and postsession measurements, and were additionally correlated across repeated measurements" - could you point to the statistics for this comparison?*

Table 2 includes the results from both experiments' analyses on unpaced tapping. (p. 10)

"The results of the pairwise comparisons between tapping rates from all unpaced tapping tasks across measurements are provided in Table 2." (p. 15)

> - *How was the loudness (dB) of the woodblock stimuli determined on a participant-by-participant basis? Please ignore if I missed this.*

Participants were allowed to set the volume to a comfortable level.

"Participants then set the sound volume to a level that they found comfortable for completing the task." (p. 4)

> - *Please spell out IOI, DEV, and other terms in full the first time they are mentioned in the manuscript.*

We added the descriptions of abbreviations before their initial mention.

"In each experimental session, 400 unique trials of this task were presented, each consisting of a combination of the three main independent variables: the inter-onset interval, IOI; amount of deviation of the comparison interval from the standard, DEV, and the amount of change in stimulus IOI between consecutive trials, ΔIOI. We explain each of these variables in detail in the next paragraphs." (p. 4)

> - *Small point: In Fig 1 sub-text, random order and linear order are explained in reverse order from how they are presented in the figure.*

We fixed the incompatibility between of Figure 1 content and caption.

> - *Small point: I found the elaborate technical explanation of windowing methods, including alternatives that were not used, unnecessary.*

We moved the details of the smoothing analysis to the Supplementary Information.

> - *With regard to the smoothing explanation, what is an "element"? Is this a sample? If so, what was the sampling rate?*

We reworded ‘element’ as ‘sample’. In the smoothing analyses, the sampling rate was the size of the convolution window, which was set to 26 for random-order, 48 for linear-order sessions.

> - *Spelling/language error: "The pared-down", "close each other", "always small (+4 ms), than".*

We fixed the spelling errors.

> ***Reviewer #3 (Recommendations For The Authors):***
>
> - *My main concern is the one detailed as a weakness in the public review. In that direction, if authors decide to keep the mechanistic interpretation of the outcomes (which I believe is a valuable one) here I suggest a couple of models that they can try to adapt to explain the pattern of results:*
>
> *a. Roman, Iran R., et al. "Hebbian learning with elasticity explains how the spontaneous motor tempo affects music performance synchronization." PLOS Computational Biology 19.6 (2023): e1011154.*
>
> *b. Bose, Amitabha, Áine Byrne, and John Rinzel. "A neuromechanistic model for rhythmic beat generation." PLoS Computational Biology 15.5 (2019): e1006450.*
>
> *c. Egger, Seth W., Nhat M. Le, and Mehrdad Jazayeri. "A neural circuit model for human sensorimotor timing." Nature Communications 11.1 (2020): 3933.*
>
> *d. Doelling, K. B., Arnal, L. H., & Assaneo, M. F. (2022). Adaptive oscillators provide a hard-coded Bayesian mechanism for rhythmic inference. bioRxiv, 2022-06*

Thanks for the suggestion! Please refer to our response (2.1.) above. To summarize, although we considered a full, well-fleshed-out modeling approach to be beyond the scope of the current work, we are excited about and actively working on exactly this. Our modeling take is available as a preprint (Kaya & Henry, 2024, February 5).

> - *Since the authors were concerned with the preferred rate they circumscribed the analysis to extract the IOI with better performance. Would it be plausible to explore how is the functional form between accuracy and IOI? This could shed some light on the underlying mechanism.*

Unfortunately, we were unsure about what the reviewer meant by the functional form between accuracy and IOI. We interpret it to mean a function that takes IOI as input and outputs an accuracy value. In that case, while we agree that estimating this function might indeed shed light on the underlying mechanisms, this type of analysis is beyond the scope of the current study. Instead, we refer the reviewer and reader to our modeling study (please see our response (2.1.) above) that includes a model which takes the stimulus conditions, including IOI, and model parameters for preferred rate, phase and period correction and within- and between-trial decay and outputs predicted accuracy for each trial. We believe that such modeling approach, as compared to a simple function, gives more insights regarding the relationship between oscillator properties and duration perception.

> - *Is the effect caused by the dIOI modulated by the distance to the preferred frequency?*

We thank the reviewer for the recommendation. We measured flexibility by the oscillator's ability to adapt to on-line changes in the temporal context (i.e., effect of **Δ**IOI on accuracy), rather than by quantifying the range of rates with improved accuracy. Nevertheless, we acknowledge that distance to the preferred rate should decrease accuracy, as this is a key prediction of entrainment models. In fact, testing this prediction was recommended also by the other reviewer, in response to which we ran additional analyses. These analyses involved assessment of the relationship between accuracy and detuning. Specifically, we assessed accuracy at stimulus rates that were faster and slower than an individual's preferred rate estimates from in Experiment 1. We ran logistic regression models on aggregated datasets from all participants and sessions, where accuracy was predicted by z-scored IOI, from trials where the stimulus rate was faster than the preferred rate estimate, and in those where it was slower. The model had a significant main effect of IOI and an interaction between IOI and direction (i.e., whether stimulus rate was faster or slower than the preferred rate estimate), indicating that accuracy increased towards the preferred rate at fast rates and decreased as the stimulus rate diverged from the preferred rate at slow rates. We added information regarding this analysis to the respective subsections of Experiment 1 Methods and Results, added a plot showing the slices of the regression surfaces to Figure 2B and elaborated on the results in Experiment 1 Discussion. As the number of trials in Experiment 2 was insufficient, we only ran these additional analyses in Experiment 1. We agree that a range-based measure of oscillator flexibility would also index the oscillators' adaptive abilities. However, the current paradigms were designed for assessment of temporal adaptation. Thus, comparison of the two approaches to measuring oscillator flexibility, which can be addressed in future studies, is beyond the scope of the current study.

> - *Did the authors explore if the "motor component" (the difference between the motor and perceptual rates) is modulated by the participants age?*

In response to the reviewer's comment, we correlated the difference between the motor and perceptual rates with age, which was nonsignificant.

> - *Please describe better the slider and the keypress tasks. For example, what are the instructions given to the participant on each task, and how they differ from each other?*

We added the Experiment 2 instructions in Appendix A.

> - *Typos: The caption in figure one reads 2 ms, while I believe it should say 200. Page 4 mentions that there are 400 trials and page 5 says 407.*

We fixed the typos.

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