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RESEARCH ARTICLE

Musical training enhances temporal adaptation of auditory-motor synchronization

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Abstract

To coordinate their actions successfully with auditory events, individuals must be able to adapt their behaviour flexibly to environmental changes. Previous work has shown that musical training enhances the flexibility to synchronize behaviour with a wide range of stimulus periods. The current experiment investigated whether musical training enhances temporal adaptation to period perturbations as listeners tapped with a metronome, and whether this enhancement is specific to individuals' Spontaneous Production Rates (SPRs; individuals' natural uncued rates). Both musicians and nonmusicians adapted more quickly to period perturbations that slowed down than to those that sped up. Importantly, musicians adapted more quickly to all period perturbations than nonmusicians. Fits of a damped harmonic oscillator model to the tapping measures confirmed musicians' faster adaptation and greater responsiveness to period perturbations. These results suggest that, even when the task is tailored to individual SPRs, musical training increases the flexibility with which individuals can adapt to changes in their environment during auditory-motor tasks.

Keywords Flexibility · Auditory-motor synchronization · Temporal adaptation · Musical training · Spontaneous production rates

Introduction

A key component of behavioural flexibility is the ability to adapt planned actions to achieve a specific goal (MacKay 1982). In conversational speech, rate adaptations help prevent interruptions. In joint music-making, rate adaptations help preserve synchronization. In each of these examples, individuals must quickly adapt the timing of their actions based on sensory feedback to achieve the desired outcome, a process called temporal adaptation. Music performance is a particularly good model of this process, as adaptation must occur at a very precise (millisecond-level) timescale (Large et al. 2002; Madison and Merker 2004; Palmer et al. 2014; Thaut et al. 1998). What mechanisms allow for this precise level of temporal adaptation?

Researchers often use perturbation tasks to investigate the mechanisms underlying temporal adaptation of auditory-motor synchronization (cf. Large et al. 2002; Palmer et al. 2014; Repp 2002; Thaut et al. 1998). In this paradigm, individuals synchronize their responses (e.g., finger taps) with an auditory stimulus that unexpectedly changes its period, phase, or both. Dynamical systems theory proposes that the mechanisms supporting temporal adaptation in these tasks are internal oscillations or rhythms that entrain or synchronize with stimulus rhythms by adjusting their period and phase to match stimulus changes (Large and Jones 1999; Strogatz and Stewart 1993). As predicted by these mathematical models, individuals adapt more quickly to phase than to period changes and to slowing than to speeding changes in an auditory stimulus (Large et al. 2002; Loehr et al. 2011; Palmer et al. 2014). Furthermore, comparison of nonlinear oscillator models with linear timekeeper models indicates that nonlinear oscillator models better explain adaptation to changing auditory stimuli than linear timekeeper models.

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Specifically, only nonlinear oscillator models correctly predict faster adaptation to slowing than to speeding period perturbations of the same magnitude (Loehr et al. 2011). This asymmetry arises because slowing perturbations are handled more efficiently by the sinusoidal period adaptation function in the nonlinear model.

A fundamental principle of dynamical systems theory states that these internal oscillations have a natural frequency at which movement is optimized and toward which individuals should be drawn (Hoyt and Taylor 1981). Natural frequencies have been measured by individuals' Spontaneous Production Rates (SPRs), or the rates at which performers produce regular rhythmic auditory sequences in the absence of external cues (cf. Palmer et al. 2019; Scheurich et al. 2018; Zamm et al. 2016, 2018). Individuals produce auditory sequences with least temporal variability at their SPRs compared with other rates and tend to drift back toward their SPRs when producing sequences at a different rate (Zamm et al. 2018). Individuals also synchronize more accurately with a partner whose SPR is similar to their own (Zamm et al. 2016). Furthermore, individuals tend to anticipate a metronome more when synchronizing with slower rates and lag more when synchronizing with faster rates relative to their SPRs (Scheurich et al. 2018). These findings suggest that natural frequencies measured as SPRs may represent an optimal coordination mode. Previous studies examining temporal adaptation of auditory-motor synchronization, however, have not accounted for individual differences in SPRs.

Because synchronization in music performance occurs at such a precise timescale, musical training may enhance temporal adaptation. Musicians synchronize more accurately with a regular auditory stimulus than nonmusicians (for reviews on sensorimotor synchronization and the role of musical training, see Aschersleben 2002; Palmer and Zamm 2017; Repp 2005; Repp and Su 2013). Only a few studies have addressed the impact of musical training on synchronization with a changing auditory stimulus. Madison and Merker (2004) compared musicians and nonmusicians synchronizing with a metronome containing both perceptible and imperceptible deviations in its beat period. Both groups performed similarly when deviations were imperceptible, but musicians adapted more than nonmusicians when deviations became perceptible. In that study, each deviation in the period of the metronome lasted at most two beats, allowing only for investigation of phase adjustment but not period adjustment. One study of temporal adaptation to longer period changes did not find differences between musicians and nonmusicians (Large et al. 2002). However, with a sample size of only three participants per group, it was not possible to draw conclusions about the influence of musical training. Repp's (2010) study showed that musicians adapted faster to period changes in an auditory stimulus than nonmusicians. Again, the sample size of musicians was small, and one-third of musicians were regular participants in similar studies. Furthermore, perturbations always occurred in the same sequence location, making them predictable to participants. Adaptation at individuals' SPRs was not considered in any of these studies.

Current research

The current study investigated effects of musical training on temporal adaptation to period perturbations while taking into account individuals' SPRs. We measured participants' SPRs with a previously validated musical tapping task developed for use with musicians and nonmusicians (Scheurich et al. 2018). Participants then synchronized their tapping with rates that were equal to, faster than, or slower than their SPRs, and continued synchronizing when the period unexpectedly changed. We focused only on period perturbations (not phase perturbations) to compare different predictions of nonlinear and linear models for slowing versus speeding perturbations (Loehr et al. 2011). Adaptation to period perturbations was measured by the phase of participants' taps relative to the metronome following period perturbations. Relative phase measures were then modeled with a damped harmonic oscillator model (Large et al. 2002; Palmer et al. 2014) and an exponential decay model (Pfordresher and Kulpa 2011) to test different mechanisms that may account for temporal adaptation.

Consistent with previous research, we predicted that (1) musicians would adapt more quickly to period perturbations than nonmusicians; (2) participants would lag the metronome more following speeding period perturbations and anticipate the metronome more following slowing period perturbations; (3) participants would adapt more quickly to slowing than to speeding period perturbations; and (4) participants would adapt more quickly to period perturbations that moved toward the SPR than away from the SPR. We also predicted that the damped harmonic oscillator model would better account for temporal adaptation to period perturbations than the exponential decay model because the exponential decay model does not contain a periodic component. Additionally, its parameters would indicate faster adaptation and closer return to baseline synchronization for musicians compared with nonmusicians following period perturbations.

Methods

Participants

Sixteen musicians (mean age = 22 years; SD = 2; 10 females) and 16 nonmusicians (mean age = 22 years; SD = 4; 11

females) participated in the study. Musicians with at least 6 years of private music instruction (mean years = 11; SD = 3) on an instrument were recruited. Percussionists were excluded because of their superior synchronization ability (Krause et al. 2010). Nonmusicians with no private music instruction in the past 6 years and less than 2 years of instruction overall (mean years = 0.21; SD = 0.44; one nonmusician who recalled having less than 2 years of training but not the exact amount was excluded from this calculation) were recruited. Participants had normal hearing sensitivity (< 30 dB HL threshold) within the frequency range of stimuli used in this study (125–750 Hz) as determined by an audiometry screening with a Maico MA-40 audiometer through headphones, normal pitch and meter perception as measured by the Montreal Battery of Evaluation of Amusia (MBEA; Peretz et al. 2003), and were familiar with the musical stimuli. The two groups did not differ significantly in age, $t(30) = 0.39$, $p = 0.54$, or in years of education, $t(30) < 0.01$, $p > 0.99$. An additional 4 musicians and 16 nonmusicians failed the screening criteria and were excluded.

Stimulus materials and equipment

The scale and meter tests of the MBEA were used to evaluate participants' pitch and meter perception. The test contained 31 "Scale" trials (one catch trial, 30 regular trials) and 30 "Meter" trials. Participants had to correctly answer the scale subtest catch trial, and achieve at least 73% and 67% accuracy on "Scale" and "Meter" tests, respectively (Peretz et al. 2003).

Musical stimuli included isochronous versions of "Mary Had a Little Lamb" (presented in F Major) and "Twinkle, Twinkle Little Star" (presented in G Major), which were chosen for their familiarity among participants. Each half note in "Mary Had a Little Lamb" (3 per repetition) and in "Twinkle, Twinkle Little Star" (6 per repetition) were replaced with two quarter-note beats, and each whole note in "Mary Had a Little Lamb" (1 per repetition) was replaced with four quarter-note beats, yielding a total of 32 beats ("Mary Had a Little Lamb") and 48 beats ("Twinkle, Twinkle Little Star") per repetition. "Mary Had a Little Lamb" was used as the practice melody to teach participants how to perform the tapping task and "Twinkle, Twinkle Little Star" was used as the melody for experimental trials.

Perturbation stimuli used in the synchronization-perturbation task, based on Large et al. (2002), were constructed to present period perturbations at unpredictable trial locations. Each trial began with eight clicks of the metronome presented at one of three fixed "Base rates" (SPR, 18% Faster than SPR, 18% Slower than SPR). After the first eight clicks, participants began tapping the melody with the metronome for 20–25 beats to establish the Base rate. Within each experimental trial, eight total period perturbations (where 1 perturbation equals an Away from plus Return to Base rate) occurred in the metronome with different Perturbation Types (8% Slower or Faster than Base rate). There were four period perturbations of each Perturbation Type (i.e., four 8% Slower and four 8% Faster). Within each Perturbation Type, half were of each Perturbation Direction. Period perturbations were defined as a single uniform change in the inter-onset interval (IOI) that lasted 13–22 beats. To make period perturbations within each trial as unpredictable as possible, the duration and order of period perturbations were quasi-randomized such that Perturbation Types never perfectly alternated throughout a trial and no more than two successive period perturbations lasted for the same duration. Additionally, half of all period perturbations were positioned to start on a weak metrical beat of the melody and the other half on a strong metrical beat. Each trial also contained one baseline section during which the Base rate continued without period perturbations for 13–20 beats. Nine unique experimental trials were constructed (three per Base rate), consisting of 285–315 metronome beats (See Fig. 1 for a sample experimental trial).

Six practice trials (two per Base rate) were also constructed. Three trials introduced each Base rate for two repetitions of the melody without period perturbations. Three additional practice trials introduced period perturbations. These trials were designed in the same way as experimental trials, except that each trial contained four rather than eight total period perturbations. Practice trials containing period perturbations consisted of 161–190 metronome beats.

Participants tapped melodies on a Force-Sensitive Resistor (FSR) of an Arduino connected via a MIDI cable to a Dell computer running FTAP (Finney 2001; see Online Resource for timing resolution). Auditory feedback associated with a metronome and participants' taps was delivered

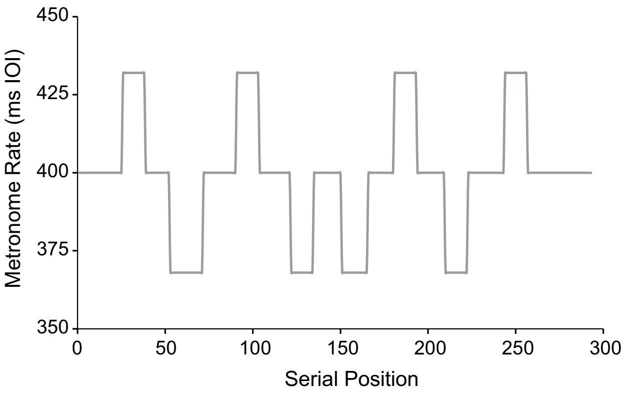

Fig. 1 Sample experimental trial from the synchronization-perturbation task at a 400 ms IOI Base rate. The solid line shows changes in the metronome rate from the Base rate. In this sample trial, the baseline section occurs after the final return to Base rate for an additional 21 beats until the end of the trial

in a woodblock timbre (timbre number 116) and piano timbre (timbre number 1), respectively, via an Edirol Studio-Canvas SD-80 tone generator at a comfortable listening level through AKG K271 Studio headphones.

Design

Participants completed three primary tasks: the spontaneous production rate task, the synchronization-perturbation task, and the maximal rate task, in this order. The between-subjects factor was Group (Musician and Nonmusician). The synchronization-perturbation task additionally contained four within-subjects factors: Base rate (SPR, 18% Slower than SPR, 18% Faster than SPR), Perturbation Direction (Away from and Return to Base rate), Perturbation Type (Slowing and Speeding), and Serial Position following each perturbation (1–12). The dependent variables were the SPRs (mean IOI) measured during the spontaneous production rate task and the relative phase between taps and metronome onsets following period perturbations in the synchronization-perturbation task. These variables were examined with parametric Analyses of Variance (ANOVAs). In addition, we examined parameter estimates from fits of the damped harmonic oscillator model to the relative phase data, and we compared fits of this model with the exponential decay model (see "Data analysis"). Model parameter estimates were examined with non-parametric Wilcoxon matched-pairs signed-ranks tests and Mann–Whitney tests. There were a total of 72 period perturbations across all experimental trials. Trials were blocked by Base rate. Half of each group's participants received Base rates ordered fastest to slowest, and the other half ordered slowest to fastest.

Procedure

After giving informed consent, participants were seated next to the Arduino which was placed on a table where participants could rest their tapping arm. Participants were introduced to the tapping task and were given a chance to practice before completing the experimental tasks. They were instructed to tap each beat of the practice melody (rather than the melody rhythm) with the index finger of their dominant hand, and that each time they tapped they would hear the next melody tone. Participants were instructed to practice until they felt comfortable with the tapping task.

Participants then completed the spontaneous production rate task with the experimental melody. They were instructed to tap each beat of the melody at a comfortable and steady rate. Participants completed one practice trial in which they tapped the melody four times without stopping. Participants were offered more practice, after which they completed three experimental trials; in each experimental trial, they tapped the melody four times without stopping.

Participants then completed a musical background questionnaire that assessed their age, education, musical engagement (i.e., training, ensemble playing, and listening), musical ability (i.e., absolute pitch, and synchronization and singing abilities), and history of neurological or speech disorders. This took approximately 10–15 min to complete, during which the experimenter computed participants' SPRs (see "Data analysis") for use in the synchronization-perturbation task.

During the synchronization-perturbation task, participants were instructed to synchronize their tapping of the experimental melody with a steady (regular) metronome set at the first Base rate. Participants were told they would hear a metronome cue for eight beats, and that they should begin synchronizing with the metronome on the ninth beat, continuing until they no longer heard auditory feedback, signaling the end of the trial. After completing one practice trial, participants were given the option to do more practice trials with the steady metronome. Then participants completed a practice trial in which they were told that the metronome would sometimes speed up or slow down, and they should continue synchronizing when the rate changed. Participants finally completed three experimental trials with period perturbations. This procedure was repeated for each Base rate.

Participants then completed the maximal rate task. They were instructed to tap the same experimental melody as before, and that this time there would be no metronome and they should tap the melody as fast as possible. Participants completed one practice trial and one experimental trial in which they tapped the melody once through.

In the final part of the experiment, participants completed the scale and meter subtests of the MBEA. The entire experiment lasted approximately 1 h and 30 min and participants received compensation for their participation. All procedures were approved by the McGill University Research Ethics Board.

Data analysis

Participants' SPRs were calculated from the spontaneous production rate task as the mean IOI for the middle two repetitions of the melody in each experimental trial to capture participants' maximally stable behavior (Loehr and Palmer 2011; Scheurich et al. 2018; Zamm et al. 2015). Outlier IOI values that were more than three standard deviations from the mean were excluded from analysis (musicians = 0.52% of total IOIs; nonmusicians = 0.69% of total IOIs). Participants' maximal rates were calculated in the same way except that the analysis only included one repetition of the melody from the experimental trial.

Adaptation to period perturbations was assessed by examining relative phase between taps and metronome onsets following period perturbations. Taps in the synchronization-perturbation task were aligned with the metronome using a nearest neighbour approach (cf. Pecenka and Keller 2011; Scheurich et al. 2018). Relative phase was computed for the first twelve beats following each perturbation using Eq. 1 (Large et al. 2002; Palmer et al. 2014), where ϕ_n is the relative phase at tap n, T_n is the onset time of tap n, S_n is the stimulus (metronome) onset time closest to tap n, and S_{n+1} is the onset time of the next stimulus.

$$\phi_n = \frac{T_n - S_n}{S_{n+1} - S_n}. \tag{1}$$

As shown in Eq. 1, relative phase was computed as the tap onset T_n minus the stimulus onset S_n, leading to a signed asynchrony measure in the numerator where a negative value indicates that the tap preceded the stimulus; this signed asynchrony is represented as a proportion of the metronome IOI (the denominator). When there were one or more missed taps in the first 12 beats following a perturbation, the 12 serial positions were extended to include extra taps (as in Large et al. 2002 and Palmer et al. 2014). For cases in which those extra taps extended up to the final Serial Position of one stimulus period before the next stimulus period began, the calculation of the stimulus IOI was adjusted to reflect the period with which participants synchronized rather than the new stimulus period. For cases in which there were not enough extra taps to replace missing taps, any missing taps at the end of the perturbation were replaced with cell mean relative phase values for that serial position. Relative phase was then adjusted (ϕ_a in Eq. 2) by subtracting each participant's mean relative phase in the baseline sections that contained no perturbations (ϕ_b in Eq. 2) from the relative phase following each perturbation (ϕ_n in Eq. 2; similar to Large et al. 2002 and Palmer et al. 2014) to compare synchronization following perturbations with each participant's baseline synchronization performance.

$$\phi_a = \phi_n - \phi_b. \tag{2}$$

A damped harmonic oscillator model was fitted to the adjusted relative phase time series in a similar way to previous studies (Large et al. 2002; Palmer et al. 2014). Equation 3 shows the model, where n is the serial position following a perturbation and $\phi_a(n)$ is the adjusted relative phase at serial position n. The model contains five free parameters: A, oscillator amplitude; b, damping coefficient (inversely related to adaptation time); f, oscillation frequency; θ, phase; and c, intercept (related to relative phase after adaptation).

$$\phi_a(n) = Ae^{-bn}\cos(2\pi fn + \theta) + c. \tag{3}$$

The model was fitted to the adjusted relative phase time series using the Levenberg–Marquardt nonlinear least squares algorithm in R (R Core Team 2012) using the package minpack.lm (Elzhov et al. 2016), weighting the first four taps following each perturbation more heavily than the remaining eight taps and setting initial parameter values of $A = 0.08$ (matching the stimulus perturbation magnitude), $b = 1$, $f = 0.15$, and $\theta = 0$. Initial values of c were systematically varied between − 0.1 and 0.1 to account for individual differences observed across Musicians and Nonmusicians in return to baseline synchronization following perturbations. Finally, b was constrained to be greater than 0, and f to be between 0 and 0.5.

The primary parameters of interest were the damping coefficient (b parameter), final adaptation achieved following perturbations (c parameter), and oscillation frequency (f parameter). Outlier parameter values for b, c, and f were defined as values more than four standard deviations from the mean parameter estimate and the model's goodness of fit was evaluated using Variance Accounted For (VAF). Only model fits for which the model converged, VAF values reached significance, and there were no outlier parameter values for the parameters of interest were included in analyses of parameter values (Musicians = 90.63% of fits; Nonmusicians = 69.27% of fits).

Fits of the damped harmonic oscillator model were compared with fits of an exponential decay model shown in Eq. 4, originally formulated to model temporal adaptation following removal of delayed auditory feedback, which reflects similar dampening but contains no periodic component (Pfordresher and Kulpa 2011).

$$\phi_a(n) = (\phi_{\text{initial}} - \alpha) \times 2\left[1 - \frac{1}{1 + \exp(-\beta n)}\right] + \alpha. \tag{4}$$

In Eq. 4, n is the serial position following a perturbation and $\phi_a(n)$ is the adjusted relative phase at serial position n. The model contains two free parameters: α, asymptote (related to relative phase after adaptation, comparable to c in the damped harmonic oscillator model); and β, slope (related to adaptation time, comparable to b in the damped harmonic oscillator model). The model also contains one fixed variable, ϕ_{initial}, which is the initial relative phase value following a perturbation (comparable to A in the damped harmonic oscillator model). Fits of this model were carried out as for the damped harmonic oscillator model. Initial values of α, like c of the damped harmonic oscillator model, were systematically varied between − 0.1 and 0.1 to account for individual differences observed across Musicians and Nonmusicians in return to baseline synchronization following perturbations. The initial value of β was set equal to 1. The parameter α was unconstrained, and the parameter β was constrained to be greater than 0.

The damped harmonic oscillator and exponential decay models were compared using the Akaike Information Criterion (AIC; Akaike 1973) to account for the difference in number of free parameters between models. Smaller values of AIC are considered better fits. VAF was used for across-group comparison of the damped harmonic oscillator model. Only model fits for which models converged and there were no outlier parameter values for parameters of interest (*b*, *c*, and *f* parameters for the damped harmonic oscillator model; α and β parameters for the exponential decay model) were included in model comparisons and across-group comparisons within model (damped harmonic oscillator model: Musicians = 92.71% of fits and Nonmusicians = 80.21% of fits; exponential decay model: Musicians = 99.48% of fits and Nonmusicians = 98.96% of fits). If the damped harmonic oscillator model performs better than the exponential decay model, this would suggest that the periodic component of the model, which is not present in the exponential decay model, may be needed to describe participants' adaptation to period perturbations.

Results

Spontaneous production rates

We first investigated the stability of SPRs within and across individuals with different musical backgrounds by comparing SPRs across Trials and Groups. Figure 2 shows the distribution of SPRs across all participants. There were large individual differences in SPRs, which ranged from 254 to 616 ms across participants. A mixed ANOVA on mean IOIs by Trial (1, 2, and 3) and Group (Musician and Nonmusician) showed a significant main effect of Trial, $F(2, 60) = 14.40$, $p < 0.001$. Post hoc comparisons revealed that participants' SPRs became slightly faster from Trial 1 (mean = 432 ms) to Trials 2 (mean = 418 ms) and 3 (mean = 405 ms; Holm-adjusted *p*'s < 0.001; Holm 1979), and from Trial 2 to Trial 3 (Holm-adjusted $p < 0.05$). The main effect of Group was non-significant, $p = 0.27$, as was the interaction between Group and Trial, $p = 0.68$.

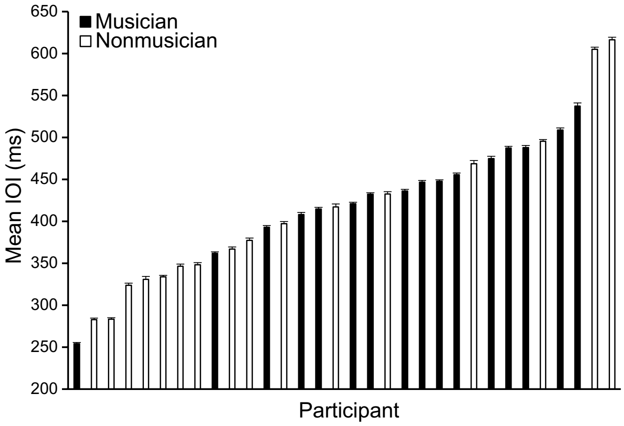

Fig. 2 Distribution of mean IOIs from the Spontaneous Production Rate task across participants, ordered from fastest to slowest. Each bar represents a single participant; black bars represent Musicians and white bars represent Nonmusicians. Error bars represent standard error

Synchronization-perturbation performance

Baseline synchronization accuracy

We next investigated whether baseline synchronization accuracy, measured during the stable (no perturbation) portion of each trial, differed across Groups and Base rates by examining the last 12 taps in the baseline section of each trial. A mixed ANOVA on mean unadjusted relative phase values by Group and Base rate (SPR, 18% Slower, and 18% Faster) showed a significant main effect of Group, $F(1, 30) = 48.20$, $p < 0.001$. Nonmusicians anticipated the metronome more (mean = − 0.12 or 12% early) than Musicians (mean = − 0.04 or 4% early) in the absence of perturbations. The main effect of Base rate was non-significant, $p = 0.74$, as was the interaction between Group and Base rate, $p = 0.85$.

Adaptation to rate perturbations

We next investigated adaptation to period perturbations. A mixed ANOVA on mean adjusted relative phase values by Group, Base rate, Perturbation Direction (Away from and Return to Base rate), Perturbation Type (Slowing and Speeding), and Serial Position (1–12) indicated multiple significant main effects and interactions. We focus on the main effects and interactions relevant to the primary questions of Group and Base rate effects on temporal adaptation; all significant main effects and interactions can be found in Table 1. A significant main effect of Group, $F(1, 30) = 8.81$, $p < 0.01$ showed closer return to baseline synchronization for Musicians (mean = − 0.0006 or less than 1% early) than Nonmusicians (mean = 0.0371 or more than 3% late). Results also showed a significant main effect of Base rate, $F(2, 60) = 3.96$, $p < 0.05$, with closer return to baseline synchronization for the 18% Slower Base rate (mean = 0.008 or less than 1% late) than the SPR (mean = 0.019 or less than 2% late) and 18% Faster Base rates (mean = 0.028 or more than 2% late), and closer return to baseline synchronization for the SPR Base rate than the 18% Faster Base rate (Holm-adjusted *p*'s < 0.001).

The significant interaction among Base rate, Perturbation Type, and Serial Position, $F(22, 660) = 2.25$, $p < 0.01$, is shown in Fig. 3. Adaptation tended to take longer and participants tended to lag the metronome cue more at faster than at slower Base rates. In addition, Fig. 3 shows that taps following a Speeding period perturbation tended to initially lag the cue more, and taps following a Slowing period perturbation tended to initially lead the cue more. There was

Table 1 Summary of significant main effects and interactions in the synchronization-perturbation task

Main effect or interaction	F value	p value
Group	8.81	0.006
Base rate	3.96	0.024
Perturbation Type	45.79	< 0.001
Serial Position	3.95	< 0.001
Group × Serial Position	2.06	0.023
Base rate × Serial Position	1.97	0.005
Perturbation Type × Serial Position	81.27	< 0.001
Group × Perturbation Type × Serial Position	7.32	< 0.001
Base rate × Perturbation Type × Serial Position	2.25	0.001
Perturbation Direction × Perturbation Type × Serial Position	2.69	0.003
Group × Perturbation Direction × Perturbation Type × Serial Position	2.53	0.004

also a significant interaction among Group, Perturbation Type, and Serial Position, $F(11, 330) = 7.32$, $p < 0.001$, and among Group, Perturbation Direction, Perturbation Type, and Serial Position, $F\ (11, 330) = 2.53$, $p < 0.01$.

Figure 4 shows the interaction among Group, Perturbation Direction, Perturbation Type, and Serial Position. Four additional repeated measures ANOVAs were conducted that separated the data by Group and Perturbation Type to focus on effects of Perturbation Direction and Serial Position on temporal adaptation. As shown in Fig. 4, both Musicians and Nonmusicians tended to lag the cue more initially following Speeding perturbations and lead the cue more initially following Slowing perturbations. Musicians showed a significant interaction between Perturbation Direction and Serial Position for Speeding, $F(11, 165) = 5.39$, Bonferroni-adjusted $p < 0.001$, and Slowing period perturbations, $F(11, 165) = 7.41$, Bonferroni-adjusted $p < 0.001$. Musicians tended to adapt faster to period perturbations when they returned to the Base rate. For Nonmusicians, the interactions between Perturbation Direction and Serial Position for Speeding, Bonferroni-adjusted $p = 0.29$, and Slowing period perturbations, Bonferroni-adjusted $p > 0.99$, were non-significant. There was no advantage of returning to the Base rate for Nonmusicians.

Model Comparisons

We compared fits of the simpler exponential decay model (Pfordresher and Kulpa 2011) with fits of the damped harmonic oscillator model (Large et al. 2002; Palmer et al. 2014). A Wilcoxon matched-pairs signed-ranks test showed that the damped harmonic oscillator model provided a better fit to the data (median AIC = − 80.74) than the exponential decay model (median AIC = − 63.84; $Z = 4.93$, $p < 0.001$, one-tailed); all 32 participants demonstrated smaller AIC values for the damped harmonic oscillator model than for the exponential decay model.

Damped harmonic oscillator model fits

Next, we addressed the modulating influences of musical training on temporal adaptation, reflected in the complex interactions, with the damped harmonic oscillator model fits. First, we examined the overall fits of the damped harmonic oscillator model to adjusted relative phase values following period perturbations across groups (Large et al. 2002; Palmer et al. 2014). A Mann–Whitney test on mean VAF values showed that the damped harmonic oscillator model provided a better fit to Musician data (median VAF = 0.83) than to Nonmusician data (median VAF = 0.75; Mann–Whitney $U = 186$, $p < 0.05$, one-tailed).

Next, we examined parameter values resulting from fitting the damped harmonic oscillator model to each experimental condition per participant. Example b parameter estimates are shown for one condition in Fig. 5 for a Musician (top) and Nonmusician (bottom). Musicians had significantly larger b parameter estimates (median = 0.54) than Nonmusicians (median = 0.32), indicating faster adaptation to period perturbations (Mann–Whitney $U = 207$, $p < 0.01$, one-tailed). Example c parameter estimates are shown for one condition in Fig. 6 for a Musician (top) and Nonmusician (bottom). Musicians had significantly smaller c parameter estimates (median = 0.00) than Nonmusicians (median = 0.02), indicating closer return to baseline synchronization following period perturbations (Mann–Whitney $U = 186$, $p < 0.05$, one-tailed). Finally, example f parameter estimates are shown for one condition in Fig. 7 for a Musician (top) and Nonmusician (bottom). Musicians had significantly larger f parameter estimates (median = 0.13) than Nonmusicians (median = 0.10), perhaps indicating greater responsiveness to period perturbations (Mann–Whitney $U = 182$, $p < 0.05$, one-tailed). To confirm that results were not driven by larger removal of non-significant model fits for Nonmusicians than Musicians, we ran the same analyses including both significant and non-significant fits. Results were similar for b and c parameters; the f parameter was no longer significantly

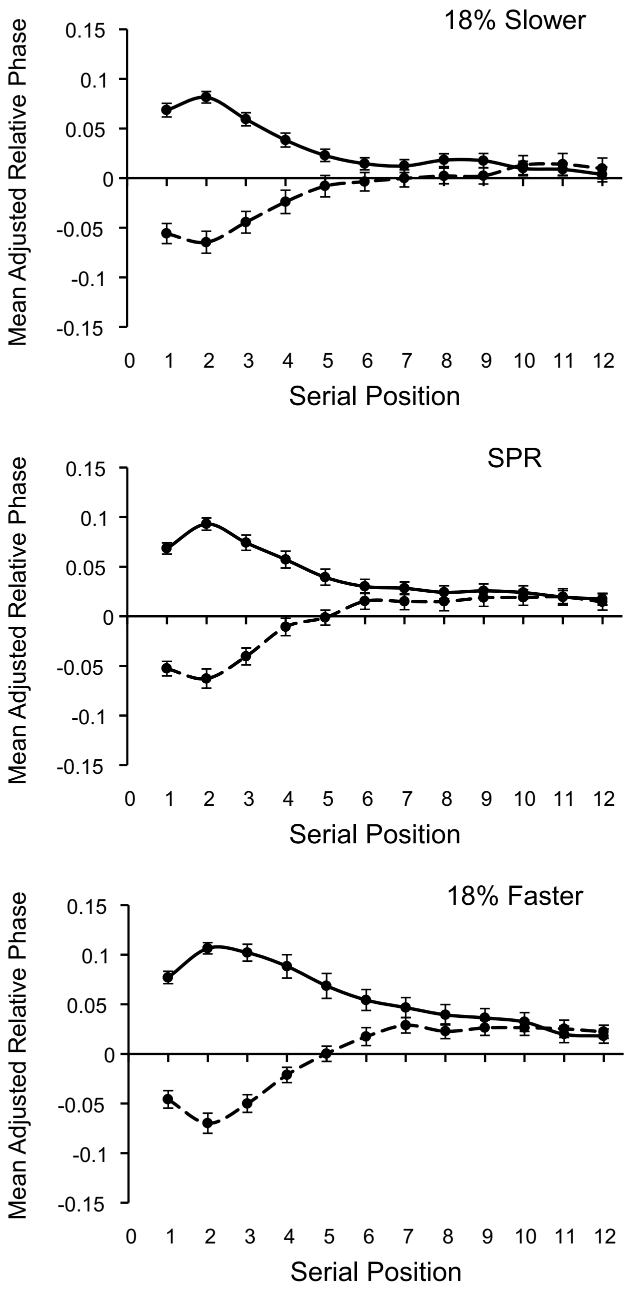

Fig. 3 Mean relative phase by Base rate, Perturbation Type, and Serial Position following perturbations. Solid lines show responses to Speeding perturbations, and dashed lines show responses to Slowing perturbations. Error bars represent standard error

different across groups (median for both groups = 0.13, $p = 0.43$, one-tailed).

Finally, we tested whether *b*, *c*, and *f* parameter estimates were correlated. None of the correlations between mean values of *b*, *c*, and *f* reached significance between or within groups (range of *p* values = 0.19–0.61). Thus, these parameters appear to account for different aspects of individual variability.

Additional correlations were run between *b*, *c*, and *f* parameter estimates and individual difference variables for the musician group to further examine the relationship between temporal adaptation and musical experience. These variables included: years of private music instruction, number of hours per week spent training on the primary instrument, number of ensembles currently involved with, and the frequency of ensemble performance. Frequency of ensemble performance was coded on a scale from 0 to 5 (0 = never; 1 = less than once a month; 2 = once a month; 3 = once a week; 4 = twice a week; and 5 = more than twice a week). One participant was excluded from correlations with frequency of ensemble performance as they did not specify an answer. Only the correlation of musicians' *c* parameter estimates with the number of ensembles they were currently involved with approached significance ($r = -\ 0.48$, uncorrected $p = 0.06$) prior to correction for number of tests (see Supplementary Table 1 for a summary of these results).

Maximal rates

To confirm that effects did not reflect participants' biomechanical limits reached during the synchronization-perturbation task, we compared participants' maximal rates with their prescribed (metronome) synchronization rate in the fastest condition (8% Faster than 18% Faster Base rate). Thirty-one of 32 participants showed faster maximal rates than the fastest prescribed synchronization rate. For the one exception (Nonmusician), we compared this participant's maximal rate with their mean tapping rate across the final 6 serial positions following all 8% Faster than 18% Faster Base rate perturbations (i.e., the fastest observed synchronization rate after adaptation). This participant's fastest observed synchronization rate was faster than their maximal rate (fastest observed synchronization rate = 233 ms; maximal rate = 242 ms), confirming that the participant could indeed tap faster than their measured maximal rate.

Discussion

The current study investigated influences of musical training on temporal adaptation of auditory-motor synchronization, implementing a perturbation paradigm. In contrast to previous studies (for reviews see Repp 2005; Repp and Su 2013), individual differences were taken into account by measuring participants' Spontaneous Production Rates and by subsequently tailoring the rates in the perturbation task to each individual's SPR. We examined musicians' and nonmusicians' temporal adaptation following unexpected period changes in the metronome. Findings indicated more rapid and accurate temporal adaptation for musicians than nonmusicians. Musicians also showed greater sensitivity

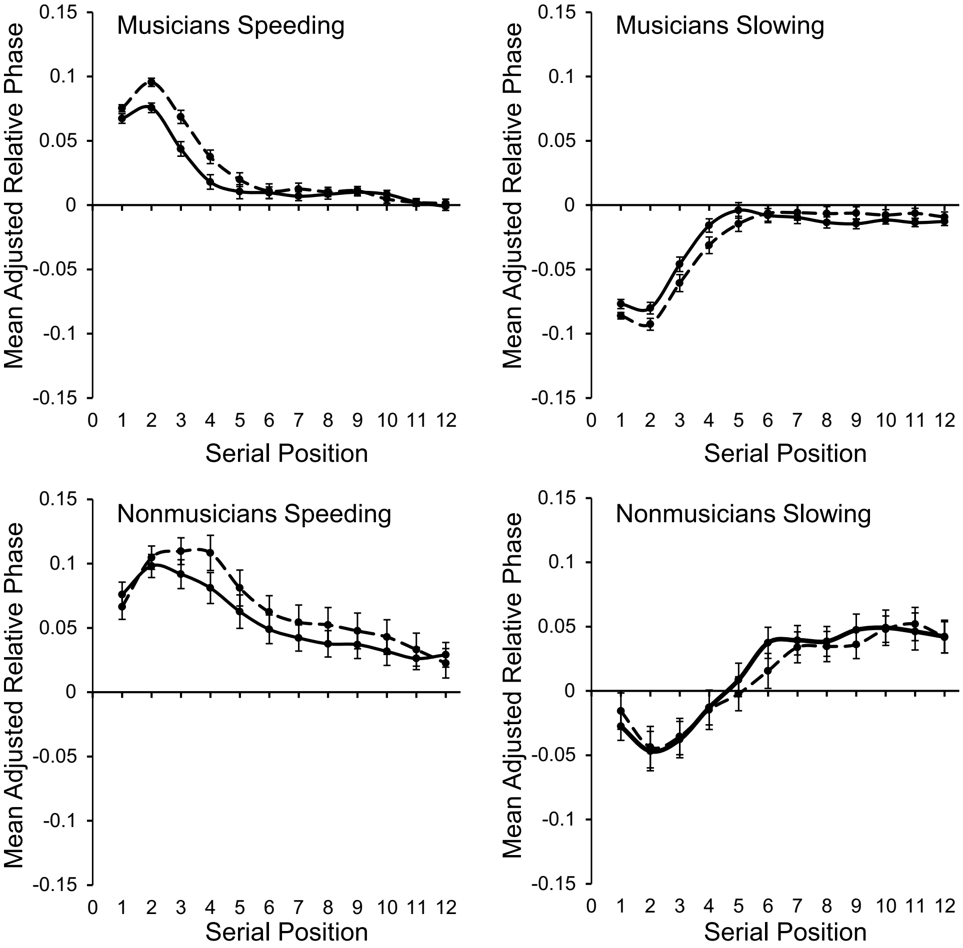

Fig. 4 Mean adjusted relative phase following perturbations by Group and Perturbation Type. Solid lines show responses that return to the Base rate, and dashed lines show responses that move away from the Base rate. Error bars represent standard error

for whether perturbations moved away from or toward the metronome base rate. Temporal adaptation did not show an effect of SPRs, but instead showed an effect of rate: adaptation was more effective at slower than faster base rates.

Musically trained participants showed greater synchronization accuracy than nonmusicians, consistent with previous findings (cf. Aschersleben 2002; Scheurich et al. 2018). The current study extends those findings to musicians' superior synchronization during both perturbed and unperturbed stimulus rates. The two participant groups did not differ in SPRs, and there was no advantage for synchronization accuracy when stimulus rates were set to participants' SPRs. It is possible that spontaneous production rates may represent an individual's optimal temporal range, rather than a single optimal rate. Had a wider range of stimulus rates been used, an advantage for synchronization accuracy at participants' SPRs might have been observed (Scheurich et al. 2018).

How quickly and closely participants returned to baseline synchronization following period perturbations were modulated by the base rate; participants tended to adapt more quickly and closer to baseline synchronization for slower base rates. Within a perturbation paradigm, slower rates may allow participants more time to respond to period perturbations, leading to greater adaptation (Peters 1989). Additionally, musicians but not nonmusicians tended to be more perturbed when period perturbations moved away from than when they returned to the base rate. Interestingly, we did not show an advantage of being perturbed toward the SPR. As previously discussed, a wider range of rates may have yielded an SPR advantage. Importantly, these findings were not a function of participants' biomechanical limits, confirmed with a condition in which participants were pushed to their maximal rates.

A damped harmonic oscillator model provided a better fit to relative phase measures than an exponential decay model that did not contain a periodic component (Pfordresher and Kulpa 2011). The greater number of parameters in the damped harmonic oscillator model did not account for the model's advantage. Fits to relative phase measures yielded larger damping coefficients for musicians than nonmusicians, suggesting that musicians adapted faster to period perturbations than nonmusicians as reported by Repp (2010). Additionally, musicians had smaller intercepts than nonmusicians, suggesting that musicians returned closer to

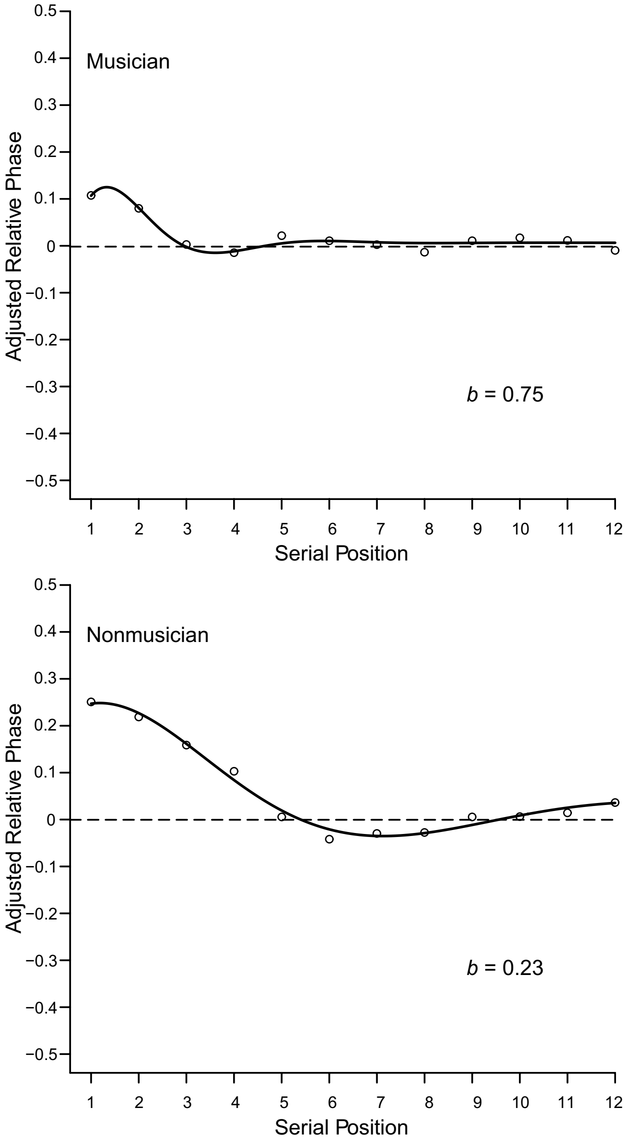

Fig. 5 Example damped harmonic oscillator model fits to data demonstrating *b* parameter differences between Musicians and Nonmusicians. Black lines represent model fits and markers represent data. Top: Musician's performance in 18% Slower Base rate condition (Speeding, Return to Base rate), demonstrating high *b* (faster dampening; $c = 0.01$ and $f = 0.22$). Bottom: Nonmusician's performance in 18% Slower Base rate condition (Speeding, Return to Base rate) demonstrating low *b* (slower dampening; $c = 0.02$ and $f = 0.08$)

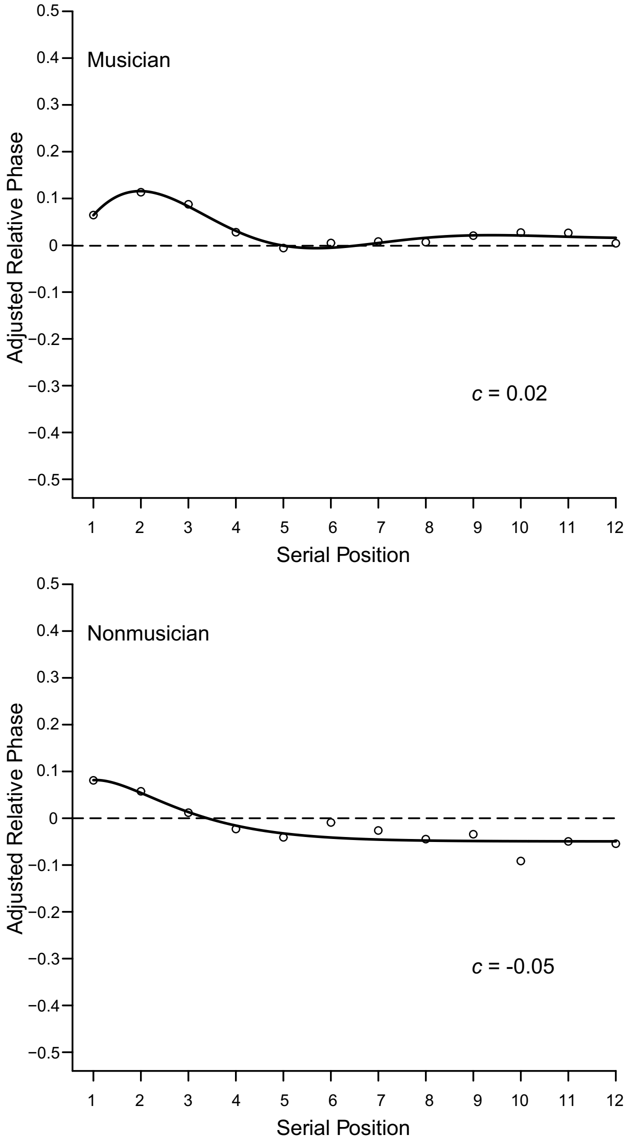

Fig. 6 Example damped harmonic oscillator model fits to data demonstrating *c* parameter differences between Musicians and Nonmusicians. Black lines represent model fits and markers represent data. Top: Musician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate), demonstrating small *c* (intercept values near 0; $b = 0.40$ and $f = 0.14$). Bottom: Nonmusician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate) demonstrating large *c* (intercept values far from 0; $b = 0.89$ and $f = 0.01$)

baseline synchronization following period perturbations than nonmusicians. Finally, musicians had larger oscillation frequencies than nonmusicians. The more oscillatory behaviour of musicians may reflect greater responsiveness or sensitivity to period perturbations, as has been shown perceptually (Repp 2010). Future research could further investigate this finding with a wider range of period perturbations.

One limitation of the current study is that only a single isochronous version of a familiar melody was used. Future research could examine more rhythmically complex stimuli while also providing simple to complex auditory feedback. Although the melody was familiar to all participants, the rhythmic structure was adjusted to be isochronous so as to create an easier task for musically untrained participants to perform. Future work could extend this paradigm to examine adaptation to unfamiliar melodies. Additionally, some participants did not tap at their fastest possible rate in the

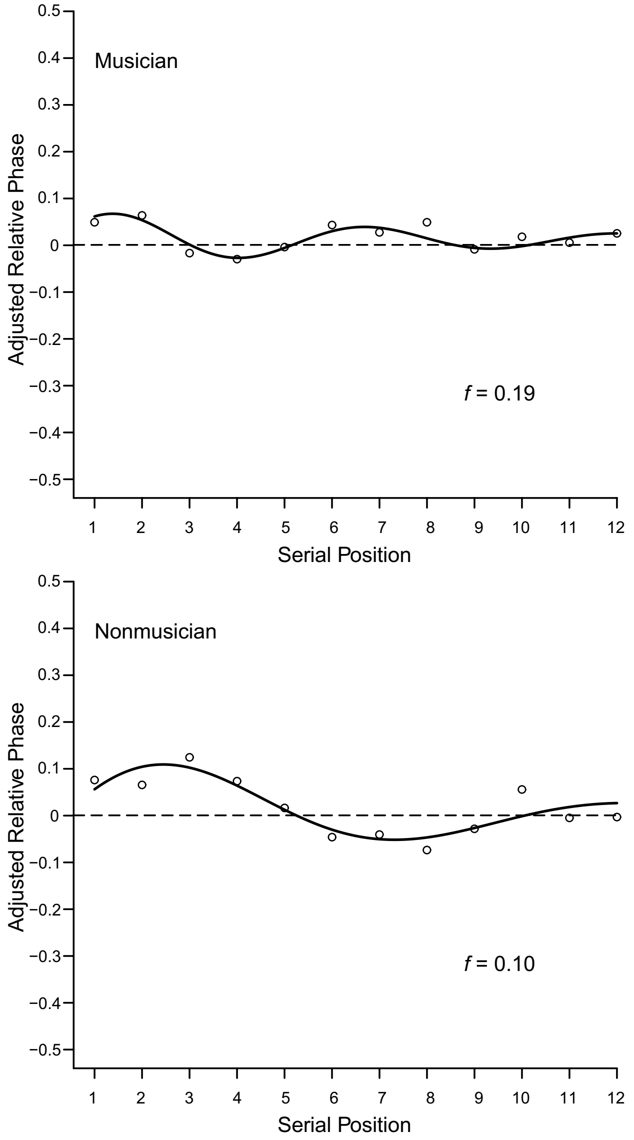

Fig. 7 Example damped harmonic oscillator model fits to data demonstrating f parameter differences between Musicians and Nonmusicians. Black lines represent model fits and markers represent data. Top: Musician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate), demonstrating high f (faster oscillation frequency; $b = 0.13$ and $c = 0.01$). Bottom: Nonmusician's performance in 18% Faster Base rate condition (Speeding, Return to Base rate), demonstrating low f (slower oscillation frequency; $b = 0.15$ and $c = 0.001$)

maximal rate task; that is, their performance in the synchronization-perturbation task was faster than their maximal rate performance. Future research could measure maximal rates with isochronous finger tapping in the absence of melody feedback. Participants could also be given more practice with the task to improve maximal rate measures.

In sum, musical training influenced temporal adaptation to period perturbations under conditions in which individual differences in SPRs were taken into account. Musicians synchronized more accurately and adapted more quickly to period perturbations than nonmusicians. Musicians also appeared to be more responsive or sensitive to period perturbations than nonmusicians. These findings were further supported by damped harmonic oscillator model fits, which better accounted for temporal adaptation than an exponential decay model through parameters reflecting adaptation time, achieved adaptation, and oscillation frequency. Together, these findings suggest that musical training enhances temporal flexibility and adaptability critical for achieving successful auditory-motor coordination.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrox BN, Caski F (eds) 2nd Int. Symp. information theory. Akademiai Kiado, Budapest, pp 267–281

Aschersleben G (2002) Temporal control of movements in sensorimotor synchronization. Brain Cogn 48(1):66–79

Elzhov TV, Mullen KM, Spiess A-N, Bolker B (2016) minpack.lm: R interface to the Levenberg-Marquardt nonlinear least squares algorithm found in MINPACK, plus support for bounds. R Package Version 1.2-1. https://cran.r-project.org/web/packages/minpack.lm/minpack.lm.pdf. Accessed 21 Nov 2018

Finney SA (2001) FTAP: a Linux-based program for tapping and music experiments. Behav Res Methods Instrum Comput 33(1):65–72

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6:65–70

Hoyt DF, Taylor R (1981) Gait and the energetics of locomotion in horses. Nature 292(5820):239–240

Krause V, Pollok B, Schnitzler A (2010) Perception in action: the impact of sensory information on sensorimotor synchronization in musicians and non-musicians. Acta Physiol (Oxf) 133(1):28–37

Large EW, Jones MR (1999) The dynamics of attending: how people track time-varying events. Psychol Rev 106(1):119–159

Large EW, Fink P, Kelso JAS (2002) Tracking simple and complex sequences. Psychol Res 66:3–17

Loehr JD, Palmer C (2011) Temporal coordination between performing musicians. Q J Exp Psychol 64(11):2153–2167

Loehr JD, Large EW, Palmer C (2011) Temporal coordination and adaptation to rate change in music performance. J Exp Psychol Hum Percept Perform 37(4):1292

MacKay DG (1982) The problems of flexibility, fluency, and speed-accuracy trade-off in skilled behavior. Psychol Rev 89(5):483–506

Madison G, Merker B (2004) Human sensorimotor tracking of continuous subliminal deviations from isochrony. Neurosci Lett 370:69–73

Palmer C, Zamm A (2017) Interactions in ensemble music performance: empirical and mathematical accounts. In: Lessaffre M, Leman M, Maes PJ (eds) The Routledge companion to embodied music interaction. Routledge, London, pp 370–379

Palmer C, Lidji P, Peretz I (2014) Losing the beat: deficits in temporal coordination. Philos Trans R Soc B 369:20130405

Palmer C, Spidle F, Koopmans E, Schubert P (2019) Ears, heads, and eyes: when singers synchronise. Q J Exp Psychol 72(9):2272–2287

Pecenka N, Keller PE (2011) The role of temporal prediction abilities in interpersonal sensorimotor synchronization. Exp Brain Res 211(3–4):505–515

Peretz I, Champod AS, Hyde K (2003) Varieties of musical disorders: the Montreal Battery of Evaluation of Amusia. Ann NY Acad Sci 999(1):58–75

Peters M (1989) The relationship between variability of intertap intervals and interval duration. Psychol Res 51(1):38–42

Pfordresher PQ, Kulpa JD (2011) The dynamics of disruption from altered auditory feedback: further evidence for a dissociation of sequencing and timing. J Exp Psychol Hum Percept Perform 37(3):949

Repp BH (2002) Phase correction in sensorimotor synchronization: nonlinearities in voluntary and involuntary responses to perturbations. Hum Mov Sci 21(1):1–37

Repp BH (2005) Sensorimotor synchronization: a review of the tapping literature. Psychon Bull Rev 12(6):969–992

Repp BH (2010) Sensorimotor synchronization and perception of timing: effects of music training and task experience. Hum Mov Sci 29(2):200–213

Repp BH, Su Y-H (2013) Sensorimotor synchronization: a review of recent research (2006-2012). Psychon Bull Rev 20(3):403–452

Scheurich R, Zamm A, Palmer C (2018) Tapping into rate flexibility: musical training facilitates synchronization around spontaneous production rates. Front Psychol 9:458

Strogatz SH, Stewart I (1993) Coupled oscillators and biological synchronization. Sci Am 269:102–109

R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 21 Nov 2018

Thaut MH, Miller RA, Schauer LM (1998) Multiple synchronization strategies in rhythmic sensorimotor tasks: phase vs period correction. Biol Cybern 79:241–250

Zamm A, Pfordresher PQ, Palmer C (2015) Temporal coordination in joint music performance: effects of endogenous rhythms and auditory feedback. Exp Brain Res 233(2):607–615

Zamm A, Wellman C, Palmer C (2016) Endogenous rhythms influence interpersonal synchrony. J Exp Psychol Hum Percept Perform 42(5):611

Zamm A, Wang Y, Palmer C (2018) Musicians' natural frequencies of performance display optimal temporal stability. J Biol Rhythm 33(4):432–440