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Temporal coordination and adaptation to rate change in music performance

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Abstract

People often coordinate their actions with sequences that exhibit temporal variability and unfold at multiple periodicities. We compared oscillator- and timekeeper-based accounts of temporal coordination by examining musicians' coordination of rhythmic musical sequences with a metronome that gradually changed rate at the end of a musical phrase (Experiment 1) or at the beginning of a phrase (Experiment 2). The rhythms contained events that occurred at the same periodic rate as the metronome and at half the period. Rate change consisted of a linear increase or decrease in intervals between metronome onsets. Musicians coordinated their performances better with a metronome that decreased than increased in tempo (as predicted by an oscillator model), at both beginnings and ends of musical phrases. Model performance was tested with an oscillator period or timekeeper interval set to the same period as the metronome (1:1 coordination) or half the metronome period (2:1 coordination). Only the oscillator model was able to predict musicians' coordination at both periods. These findings suggest that coordination is based on internal neural oscillations that entrain to external sequences.

Keywords: coordination, synchronization, oscillator model, timekeeper model, music performance

Temporal coordination and adaptation to rate change in music performance

Many behaviors, such as dancing, playing sports, and performing music, require people to coordinate their actions with external events. These external events are often temporally variable (as when dancing with music that changes tempo) and can happen at multiple periodicities (as when audience members clap to music at different rates). Coordination of actions with external events has often been studied by having people tap along with periodic auditory sequences ranging from simple isochronous tones (consisting of a single recurrent time interval) to complex musical rhythms (consisting of multiple, related time intervals that often contain temporal variability; see Repp, 2005, for a review). Although models have been developed to explain how people coordinate periodic actions such as tapping with both simple and complex rhythmic sequences (e.g., Large & Kolen, 1994; Large & Palmer, 2002; Mates, 1994; Vorberg & Wing, 1996), little research has examined how people coordinate complex rhythmic actions with periodic sequences. The current studies examined musicians' coordination of complex musical rhythms with periodic sequences that changed rate, in order to compare model predictions for adaptation to rate change and coordination at multiple periodicities.

Several studies have examined people's ability to adapt to temporal fluctuations in the sequences with which they coordinate their actions. Examples of temporal fluctuations include phase perturbations, such as shifting a single event onset to occur earlier or later than expected (Repp, 2002a, 2002b), and period perturbations, which change the rate (tempo) of the sequence (Large, Fink, & Kelso, 2002; Madison & Merker, 2005; Schulze, Cordes, & Vorberg, 2005).

This work has shown that whereas people quickly and automatically adjust to phase perturbations (Large et al., 2002; Repp, 2001a, 2002b), adjustment to period perturbations requires conscious awareness and attention (Repp, 2001b; Repp & Keller, 2004). Furthermore,

mathematical modeling has shown that both the phase (onset time relative to the stimulus) and the period (duration between successive onsets) of an internal oscillator (Large et al., 2002) or timekeeper (Schulze et al., 2005) must be adjusted in order to maintain coordination in the face of changes in the sequence tempo. For example, adaptation of an internal period occurs in response to abrupt changes from one tempo to another (Large et al., 2002) and to gradual changes in tempo (Schulze et al., 2005).

The mechanisms by which people adjust to tempo changes are particularly relevant for musical coordination, because musicians often use tempo change to convey their expressive intentions (Palmer, 1989, 1996). For example, rubato, in which musicians shorten or lengthen the durations of a series of produced tones, is common in music performance (Shaffer, 1981, 1984; see Palmer, 1997, for a review). In fact, musicians produce rubato even when they are asked to perform without temporal fluctuations (Palmer, 1989; Repp, 1999a). People can coordinate taps or claps with music performances that contain tempo changes, as evidenced by the ease with which people clap along with music in everyday life (Drake, Penel, & Bigand, 2000). Moreover, musicians are able to maintain coordination with each other despite tempo changes in each musician's performance (Goebl & Palmer, 2009; Shaffer, 1984). However, the mechanisms by which people coordinate rhythmic behaviors such as music with sequences that change tempo have yet to be directly examined, despite the fact that this is a common requirement of ensemble music performance and other coordinated rhythmic behaviors.

Another issue that has yet to be addressed is how people coordinate complex rhythmic behaviors, in which events occur at multiple periodicities, with periodic external sequences. Musical rhythms are ideal for examining this issue. Western music compositions specify event durations in terms of categories that typically form integer multiples or fractions of each other

(for example, *eighth notes* are half the duration of *quarter notes*, which are half the duration of *half notes*). Performers do not produce event durations perfectly categorically, in part because of expressive tempo fluctuations. Nonetheless, listeners typically perceive a regular period, called the pulse, corresponding to the most salient duration category (London, 2004), as well as other periodicities at simple integer ratios (e.g., 1:2, 3:1) of the pulse period (Barnes & Jones, 2000; Palmer & Krumhansl, 1990; Pfordresher & Palmer, 2002). The pulse and other periodicities correspond, respectively, to the different rates at which people can tap along with a given musical performance. Thus, performers produce and listeners perceive events at multiple periods in musical performances.

Listeners can coordinate their production of periodic actions such as taps or claps with the multiple periodicities contained in musical rhythms. Researchers have assessed people's preferred tapping rates in a wide variety of musical styles (van Noorden & Moelants, 1999), determined the range of periodicities (falling at integer ratios of the pulse) with which people can coordinate their taps (Drake, Jones, & Baruch, 2000; Drake, Penel et al., 2000), and examined the accuracy with which people can tap along with the different periodicities in complex rhythms (Rankin, Large, & Fink, 2009; Toiviainen & Snyder, 2003). Few studies, however, have examined how people coordinate the production of rhythms requiring actions at multiple periodicities with periodic external sequences (Repp, 1999b). There is some evidence to suggest that coordinating musical rhythms with periodic sequences may be different from coordinating periodic tapping with musical rhythms. For example, producing taps at half the period of a stimulus sequence (2:1 coordination) reduces tap-tone asynchronies relative to producing taps at the same period as the stimulus sequence (1:1 coordination; Pressing, 1998a). In contrast, 2:1

coordination in rhythmic music performance increases keystroke-tone asynchronies relative to 1:1 coordination (Loehr & Palmer, 2009).

Models of temporal coordination

Two theoretical approaches that explain the processes by which people coordinate their actions with periodic sequences currently dominate the literature on temporal coordination. First, a dynamic approach assumes that an external rhythmic signal evokes intrinsic neural oscillations that entrain to the periodicities in the rhythmic sequence (Large, 2000, 2008). Entrainment is the process by which two oscillating systems, which have different periods when they function independently, assume the same period, or integer-ratio related periods, when they interact. According to the dynamic approach, rhythmic motor behavior arises from one or more oscillations, which can be modeled by nonlinear differential equations (Kelso, Delcolle, & Schöner, 1990; Large, 2000). Models based on the dynamics of neural oscillation have been termed intrinsic timing models, because they assert that time is inherent in neural dynamics (Ivry & Schlerf, 2008). Mathematical analysis of neural oscillation shows that under certain assumptions, neural oscillators share a set of universal properties that are independent of physiological details (Hoppensteadt & Izhikevich, 1997). We focus here on a temporally discrete *oscillator* model, which is a mathematical simplification that retains certain universal properties of neural oscillation including entrainment at multiple periodicities (deGuzman & Kelso, 1991; Large & Kolen, 1994).

The second approach, an information-processing approach, focuses on specifying psychological processes based on underlying computations and makes predictions about statistical properties of time series data. One popular model assumes that a central *timekeeper* measures temporal intervals by counting pulses generated by neural processes (Gibbon & Allen,

1977; Wing & Kristofferson, 1973). It is assumed that the timekeeper can generate motor commands (such as taps) and, with the addition of linear error correction mechanisms, can synchronize to an external stimulus sequence (Vorberg & Schulze, 2002; Vorberg & Wing, 1996). This timekeeper model can be considered a dedicated timing model, as it proposes a mechanism specifically devoted to representing temporal relationships between events (Ivry & Schlerf, 2008). Dedicated timing models are generally viewed as specific to particular neural structures (Fiala, Grossberg, & Bullock, 1996; Ivry & Schlerf, 2008; Miall, 1989).

It has been argued that oscillator and timekeeper models are intimately related, because both can be regarded as variants of a general control equation for referential behavior (Pressing, 1998b, 1999). Because of mathematical similarities between them, linear timekeeper models are sometimes treated as simplifications of nonlinear oscillator models, providing a tractable approximation in the vicinity of stable states (see, e.g., Repp, 2005). Despite the fact that the two theoretical approaches are based on very different assumptions about the nature of the neural processes underlying timing, they yield mathematically similar predictions for certain types of behavior. Here, we focus on behavior that might distinguish between the two models: the coordination of complex rhythms, which require actions produced at multiple periodicities, with stimulus sequences that change rate.

In the following sections, we compare an intrinsic *oscillator* model and a dedicated *timekeeper* model of temporal coordination. First, we describe the basics of each model in some detail. Although the models appear to differ considerably, the most obvious mathematical difference between them is that they are described in terms of different variables: The oscillator model works in terms of relative phase, a circular variable that reflects the intrinsic periodicity of neural oscillation (Large, 2008; Pikovsky, Rosenblum, & Kurths, 2001), whereas

the timekeeper model works in terms of absolute time, a linear variable that is not intrinsically periodic. We next explore similarities and differences between the two models by performing simple transformations by which the timekeeper model's predictions can be described in terms of relative phase, and the oscillator model's predictions in terms of absolute time (ms). Finally, we show model simulations that reveal differences in the behavior predicted by each model, and we describe the results of two experiments on musicians' temporal coordination with a metronome that illustrate these differences.

Comparisons between models

The entrainment of a nonlinear oscillation to an external stimulus sequence can be qualitatively described using a *circle map* (Glass & Mackey, 1988; Pikovsky et al., 2001). A circle map produces a series of relative phase values representing the phase of an oscillation at which an external stimulus event occurs. The relative phase of the next onset in the series, ϕ_{n+1} , is determined by the phase of the current onset, ϕ_n , and the ratio of the current stimulus period to the oscillator period, p (see Appendix A for a list of symbols). If the stimulus period changes over the sequence, it is measured as $IOI_n = t_{n+1} - t_n$, where t_n is the onset time of event n (Large & Kolen, 1994). A coupling term describes the phase entrainment of the oscillation to the stimulus sequence, and is periodic, reflecting the periodicity of the oscillation. The simplest possible periodic coupling term is a sinusoidal one, $-\frac{\alpha}{2\pi} \sin 2\pi\phi_n$, and when this is chosen the map is called a *sine circle map*. The parameter α represents the strength of the coupling between the oscillator and the stimulus sequence. Other periodic coupling terms are also possible, depending on the underlying model of neural oscillation (cf. deGuzman & Kelso, 1991; Large & Kolen, 1994; Large & Palmer, 2002).

$$\phi_{n+1} = \phi_n + \frac{IOI_n}{p} - \frac{\alpha}{2\pi} \sin 2\pi\phi_n \quad (\text{mod}_{-.5,.5} 1) \quad (1)$$

The expression ($\text{mod}_{-.5,.5} 1$) indicates that phase is taken modulo 1 and normalized to the range $-0.5 < \phi_n < 0.5$. Relative phase arises from the periodicity of the underlying oscillation, and it is measured as a proportion of the cycle. In this formulation, negative values indicate that a stimulus event occurred early relative to the oscillator's temporal prediction and positive values indicate that a stimulus event occurred late. Because the model above was originally conceived as model of temporal expectancy, relative phase is taken from the point of view of the model (i.e., when stimulus events occur relative to expectancies). To make predictions about the relative phase of tapping data (i.e., the time at which taps occur relative to stimulus events), we invert relative phase, $-\phi_n$.

In order to maintain coordination when tempo fluctuations are large, period adaptation must also occur (Large & Jones, 1999; Large & Kolen, 1994; McAuley, 1995). The period of the next event in the series, p_{n+1} , is modeled as

$$p_{n+1} = p_n + \frac{p_n \beta}{2\pi} \sin 2\pi\phi_n \quad (2)$$

The coupling function is the same as that for phase, but the parameter β , representing the strength of the period coupling, is independent of the phase coupling strength parameter α . Thus, two parameters capture the behavior of the oscillator: phase coupling strength, α , and period adaptation strength, β , both of which are functions of the relative phase of the current onset.

The timekeeper model considered here is based on absolute time (tap–event asynchronies, in ms) rather than on relative phase. The timekeeper model also relies on two independent parameters, representing the strength of timing adjustments as well as adaptation of the timekeeper interval, to capture the behavior of a timekeeper that synchronizes to an external

stimulus sequence (Schulze et al., 2005; Vorberg & Schulze, 2002; Vorberg & Wing, 1996). The original model is a stochastic model whose internal timekeeper interval, T_n , varies randomly about a fixed mean, τ_n , and it also takes into account variable motor delays in the tapping task, M . The asynchrony between the next tap and stimulus event in the sequence, A_{n+1} , is adjusted by some proportion, α , of the current asynchrony between tap and stimulus event, A_n ,

$$A_{n+1} = T_n - C_n + (1 - \alpha)A_n + M_{n+1} - M_n,$$

where C_n is the current stimulus period. For simplicity we will work with a deterministic variant of the timekeeper model, which means that we ignore variability of the timekeeper interval (i.e., $T_n = \tau$), and we ignore motor delays. Under these assumptions, rearranging the terms of the above equation, we find

$$A_{n+1} = A_n + \tau - C_n - \alpha A_n \quad (3)$$

Adaptation of the central timekeeper interval is also a proportion, β , of the preceding asynchrony (Schulze et al., 2005)

$$\tau_{n+1} = \tau_n - \beta A_n \quad (4)$$

Although the models appear different on the surface, there is an underlying similarity that can be seen by noting that relative phase is equal to asynchrony divided by timekeeper interval ($\phi = A/\tau$), and, equivalently, asynchrony is equal to phase times oscillator period ($A = p\phi$). In Appendix B the models are transformed into similar terms (see also Pressing, 1999). This transformation reveals the main differences between the two models: Coupling between the oscillator and the stimulus sequence is nonlinear and periodic, whereas coupling between the timekeeper and the stimulus sequence is linear and nonperiodic. Figure 1 shows the relationship between the oscillator coupling function (solid line) and the timekeeper coupling function

(dashed line) by plotting the amount of adaptation, $F(\phi)$, that occurs as a function of the relative phase of a given onset, ϕ . The two coupling functions are shaped differently, although there is a region (within about $\pm 10\%$ of the cycle) where the nonlinear rule is approximately linear. Within this region, the error correction rule of Equation 3 could be thought of as a linearization of the oscillator phase coupling in Equation 1, and the timekeeper adaptation rule of Equation 4 as a linearization of the oscillator period adaptation in Equation 2.

Insert Figure 1 here

Within the region in which the nonlinear rule is approximately linear (i.e., when the oscillator period or timekeeper interval is close to the stimulus period), the two models make similar predictions with respect to adaptation to tempo changes. Even within this region, however, the different shapes of the two coupling functions result in small differences in the models' predictions concerning adaptation to linear changes in stimulus interval duration (interonset interval; IOI). These predictions are illustrated in Figure 2, which shows the two models' predicted asynchronies when the stimulus tempo increases or decreases by a constant number of ms (either 1% or 3% of the original IOI) on each beat (beginning at beat 9 in the figure). The timekeeper model always produces a symmetrical result with respect to tempo increases and decreases: Speeding up and slowing down produce adaptations of precisely the same magnitude when measured in terms of asynchrony (Figure 2, dashed lines). However, the oscillator model produces an asymmetric result when measured in terms of asynchrony (Figure 2, solid lines): Sequences that slow down (decrease in tempo) are handled more efficiently than sequences that speed up. This asymmetry arises due to the nonlinearity of the period adaptation function (compare Equations 2 and 4), and it increases as the size of the tempo change increases,

as illustrated in Figure 2. Thus, the linearity versus nonlinearity of the two models' coupling functions yields different behavioral predictions for people's adaptation to linear changes in stimulus interonset intervals.

Insert Figure 2 here

A second difference between the two models is that due to the intrinsic periodicity of neural oscillation (Large, 2008; Pikovsky et al., 2001), the nonlinear coupling function is periodic, whereas the linear coupling function is not intrinsically periodic. This has an important functional consequence when the oscillator period or timekeeper interval is not close to the stimulus period (for example, half the period of the stimulus). The nonperiodic coupling in the timekeeper model means that the timekeeper interval adjusts until it *synchronizes* with the stimulus sequence, producing one tap for every stimulus event (1:1 coordination). The model thus produces a 1:1 correspondence between taps and stimulus events, whether or not the events are periodic. In contrast, the periodic coupling in the oscillator model allows the oscillator to *entrain* to the stimulus sequence (Glass, 2001; Glass & Mackey, 1988; Pikovsky et al., 2001), in this example producing two taps for every stimulus event (referred to here as 2:1 coordination). The difference is illustrated in Figure 3, which shows the predicted phase and period for each model's coordination with an isochronous stimulus sequence (empty squares) that is twice the oscillator period or timekeeper interval (i.e., when an oscillator or timekeeper with a period/interval of 250 ms coordinates with a stimulus sequence set at 500 ms per interonset interval). Only the oscillator model predicts the coordination of periodicities related by integer multiples that is typical of the rhythms that musicians must produce (e.g., quarter notes and eighth notes).

Insert Figure 3 here

We next describe two experiments that address the different predictions of the oscillator and timekeeper models outlined above. In each experiment, musicians performed rhythmic musical sequences along with a metronome that gradually changed tempo. Tempo change was implemented as a linear increase or decrease in the interval between metronome onsets, such that the interval changed by a constant ms value on each of eight beats. This allowed us to test for the predicted (a)symmetry when musicians coordinated their performances with a metronome that increased versus decreased in tempo. The musical rhythms contained event durations corresponding to two periods (quarter notes and eighth notes); pianists coordinated these rhythms with a single-period metronome (sounded at the quarter-note level). We compared the models' ability to predict participants' coordination with the metronome period when the oscillator period or timekeeper interval was set to each of the two periods present in the musical rhythms: the same period as the metronome (1:1 coordination) or half the period of the metronome (2:1 coordination). We also manipulated the location of the tempo change such that it occurred at the end of a musical phrase in Experiment 1 and at the beginning of a musical phrase in Experiment 2. Performers typically slow down at the ends of musical phrases and speed up at the beginnings of phrases (Palmer, 1989). Manipulating the location of the tempo change therefore allowed us to test an alternative prediction based on music performance conventions: Pianists may be better at coordinating their performances with a decreasing tempo when tempo change occurs at the end of a phrase but not when it occurs at the beginning of a phrase.

Experiment 1

Method

Participants. Two male and fourteen female pianists, ranging in age from 18 to 37 years ($M = 23.25$, $SD = 5.39$), were recruited from the Montreal community. All participants had at least 7 years of private piano lessons ($M = 12.41$, $SD = 2.39$), and all but one were right-handed. All subjects gave informed consent according to procedures reviewed by the Institutional Review Board of McGill University.

Stimulus Materials. Four five-measure melodies were created for the study; one melody is shown in the top panel of Figure 4. All melodies were written in 4/4 meter and contained a mixture of quarter notes (all of which were to be aligned with the metronome beats) and eighth notes (designed to be produced at half the metronome period). Notes that were to be aligned with the metronome are marked by Xs in the figure. Within the first two measures, across which the metronome tempo did not change, pairs of eighth notes occurred on any two of the beats. Within the third and fourth measures, across which the metronome tempo could change, pairs of eighth notes were evenly distributed across beats. Two of the melodies were notated in major keys, two were notated in minor keys, and all were performed with the right hand.

Insert Figure 4 here

Equipment. Melodies were performed on a Roland RD-700SX (Roland Corporation, Los Angeles, CA, USA) weighted-key digital piano. Presentation of metronome pulses and auditory feedback, as well as MIDI data acquisition, was implemented via the FTAP software program (Finney, 2001). Timbres were generated by an Edirol StudioCanvas SD-80, using a piano timbre from the Contemporary bank (Rock Piano, Instrument #002) for performances and the metronome click timbre from the Classical bank (Standard Set, Note 33) for the metronome

pulses. The participants heard the metronome pulses and performances over AKG K271S headphones. The volume was adjusted to a comfortable level for each participant.

Design and Procedure. Participants performed the melodies under five tempo change conditions in a within-subjects design. In the control condition, the metronome was set at 500 ms per quarter-note beat. In the remaining four conditions, the metronome sounded at 500 ms per beat for the first two measures (8 beats) of the melody and then its interonset intervals (IOIs) either increased or decreased linearly by 1% or 3% of the original tempo (5 or 15 ms per beat) on each of the remaining beats. The metronome period (IOI, in ms) for each beat in the five tempo change conditions is shown in the bottom panel of Figure 4. Tempo changes began on the ninth beat of the melody and the tenth beat was the first beat with a shortened or lengthened period.

Participants were presented with the four melodies on a single sheet of paper, which stayed in front of them during the experiment. They first practiced all four melodies until they could produce them without error, and they then completed 10 practice trials containing all five tempo change conditions. Each trial began with an auditory cue consisting of one to four drum sounds (also notated next to the melodies), indicating which melody was to be performed on that trial. After a delay of three seconds, eight metronome beats were sounded. Participants began performing the melody along with the ninth metronome beat, and continued until they had performed the entire melody. The next trial began when the participant indicated that he or she was ready. Participants were informed that the metronome would change tempo on some trials and were instructed to synchronize with the metronome, sounded at the quarter-note level, as accurately as possible. Participants performed five blocks of 20 trials (4 melodies x 5 tempo change conditions), for a total of 100 trials. Each block of trials contained all 20 melody x tempo change combinations presented in pseudorandom order such that the same melody never

occurred twice in a row. Participants also completed a questionnaire about their musical backgrounds. Participation in the experiment took approximately one hour, and participants received a nominal fee.

Analysis. We were primarily interested in participants' ability to coordinate with the metronome; the following analyses therefore focus on timing at the level of the quarter-note beats at which the metronome sounded. We first tested for asymmetry between tempo change conditions in the asynchrony data (observed keystroke onset time minus metronome onset time; negative values reflect tone onsets that preceded the metronome). We then fit the relative-phase-based formulations of the oscillator and timekeeper models to the observed relative phase data (asynchrony divided by preceding metronome interval)¹. Ninety-four trials (5.89%) contained pitch errors and were excluded from analysis.

Results

Asynchronies. Participants' mean asynchronies (observed keystroke onset minus metronome onset) on each beat within the five tempo change conditions are shown in Figure 5. The figure shows that after the first two to three beats, tone onsets preceded the metronome (negative asynchronies). The mean asynchrony over the first nine beats, during which there was no tempo change in any condition, differed significantly from zero ($M = -5.76$ ms, $SD = 12.78$, $F(1, 15) = 5.84$, $p < .03$) and is consistent with previous findings of a small negative asynchrony when rhythmic piano performances are coordinated with a metronome (Loehr & Palmer, 2009). Mean asynchronies remained significantly negative across all but the very last of the remaining beats in the isochronous control condition. Thus, a 'baseline' level of negative asynchrony ($M = -8.98$ ms across all beats) occurred in the absence of tempo change.

Insert Figure 5 here

To test for an asymmetry between tempo change conditions, we first adjusted for the baseline asynchrony by subtracting each performer's mean asynchrony on each beat in the control condition from their mean asynchrony on each beat of the tempo change conditions. We then conducted a three-factor repeated-measures ANOVA by tempo change type (speeding up, slowing down), percent change (1%, 3%), and beat (1-17) on the absolute values of the adjusted asynchronies. The ANOVA revealed significant main effects of tempo change type, $F(1,15) = 32.06, p < .001$, percent change, $F(1,15) = 32.80, p < .001$, and beat, $F(16, 240) = 22.18, p < .001$. All two-way interactions were significant, $p < .001$, as was the interaction between tempo change type, percent change, and beat, $F(16, 240) = 18.48, p < .001$. The absolute values of the adjusted asynchronies on the last five beats of the tempo change (beats 13-17) were larger when the metronome sped up ($M = 51.88$) than when it slowed down ($M = 27.57$), in the 3% change condition (Bonferroni-corrected $p < .0031$). Thus, there was a temporal asymmetry in performers' adjustment to tempo change, as predicted by the oscillator model: Pianists were better able to coordinate their production with a metronome that decreased rather than increased in tempo.

Model fits. We next fit the relative-phase-based formulations of the oscillator model (Equations 1 and 2) and timekeeper model (Equations B1 and B3) to the relative phase data. Parameter values were determined by choosing the estimates that minimized the sum of the squared error terms for the mean relative phase data for all 17 beats of all five tempo change conditions, for each participant separately. In addition to fitting the phase and period coupling parameters, α and β , for both models, a third parameter, ϕ_0 , was used to capture the baseline negative relative phase that occurred in the absence of tempo change. One explanation for this

negative relative phase is that an internal timekeeper interval differs from that of the metronome (Vorberg & Wing, 1996); this misestimation of the metronome period may be independent of phase and period adaptation (Schulze et al., 2005). The simplest way to account for this within the current modeling context is to add a period misestimation parameter to Equations 2 and B3 to accommodate the baseline relative phase:

$$p_{n+1} = p_n + p_n \frac{\beta}{2\pi} \sin 2\pi(\phi_n - \phi_0) \quad (7)$$

$$\tau_{n+1} = \tau_n - \beta \tau_n (\phi_n - \phi_0) \quad (8)$$

Thus, period adaptation was modeled as a function of both the phase of the current onset and misestimation of period. Note that negative values of ϕ_0 correspond to negative relative phase. The best-fitting model was determined using the Akaike Information Criterion (AIC; Akaike, 1973), an ordinal-scale measure in which lower (more negative) values indicate better fit².

We compared the oscillator and timekeeper models' ability to predict participants' relative phase at the level of the quarter-note beats at which the metronome sounded. We compared model performance under two conditions: first, with the initial oscillator period or timekeeper interval set to the prescribed quarter-note rate (500 ms/IOI, equivalent to the metronome period), and second, with the initial oscillator period or timekeeper interval set to the eighth-note rate (250 ms/IOI, half the metronome period). Thus, we examined each model's ability to generate predictions based on both 1:1 and 2:1 coordination with the metronome.

1:1 coordination. We first fit the oscillator and timekeeper models with the initial oscillator period or timekeeper interval set to the quarter-note rate (500 ms/IOI). The range of values used for the phase coupling parameter, α , was 0 to 2.0 in increments of 0.025; for the period coupling parameter, β , was 0 to 2.0 in increments of 0.025; and for the period

misestimation parameter, ϕ_0 , was -0.05 to 0.02 in increments of 0.005. Table 1 shows parameter values and AIC calculated across all five tempo change conditions for the oscillator model (left half) and timekeeper model (right half), fit to each participant's data and to the mean data across all participants (bottom row). As predicted based on the mathematical similarities between the two models, both the parameter values and model fits across all five conditions were similar for the two models. AIC was lower (indicating better fit) for the oscillator model than for the timekeeper model for 10/16 participants, which did not significantly differ from chance, $p = .23$. We next calculated the AIC values separately for the speeding 3% condition, for which the difference between model predictions was largest (as shown in Figure 2). AIC values, shown in Table 2, were calculated for fits of both models that were based on average parameter values from the two optimized model fits described above. The oscillator model fit the data better than the timekeeper model for 14/16 participants, significantly more than would be expected by chance, $p < .003$. Together, these results demonstrate that although the two models are nearly equivalent, overall, when predicting 1:1 coordination, the oscillator model has a small advantage due to its prediction of an asymmetry between adaptation to increases and decreases in tempo³.

Insert Tables 1 and 2 here

2:1 coordination. We next tested the models' ability to generate accurate predictions based on 2:1 coordination by fitting each model with the initial oscillator period or timekeeper interval set to the eighth-note rate (250 ms/eighth note, half the metronome period) to the events produced on the quarter-note beats (i.e., only the events that were aligned with the metronome period, the same as in the analysis of 1:1 coordination). The maximum values for the phase and period coupling parameters were increased to 2.5 because stronger coupling is required to

maintain phase coordination in the 2:1 regime. The range of values for the period misestimation parameter, which does not reflect coupling, remained unchanged. Table 3 shows parameter values and AIC for the oscillator model (left half) and the timekeeper model (right half) fit to each participant's data and to the mean data across all participants. The AIC was lower (indicating better fit) for the oscillator model than for the timekeeper model for all 16 participants; no participants produced the large fluctuations in relative phase predicted when a timekeeper with half the interval of the stimulus sequence synchronizes with that sequence. Thus, fits to the relative phase data favored the oscillator model over the timekeeper model when the models' initial period or interval reflected 2:1 coordination.

Insert Table 3 here

Individual differences. Finally, we examined individual differences in participants' performance data and best-fitting parameter values from the 1:1 oscillator model fits. The top three panels of Figure 6 show the predicted values (lines with small markers) and obtained data (large markers) for three of the 16 participants, who represent a range of coordination behaviors and model fits. The bottom panel shows the parameter values fit to the mean obtained data. Participant 12 (first panel) maintained relatively close coordination with the metronome, as evidenced by small relative phase values across the tempo change conditions and high phase and period coupling values. The parameter values for Participant 1 (second panel) represent near-optimal values for this model (values for which coupling strengths are as high as possible without producing unstable behavior and overcorrection; Large & Palmer, 2002). These values fall near the middle of the range of parameter values obtained in Experiment 1, and reflect the moderate relative phase values displayed by this participant. Finally, Participant 8 (third panel)

showed an atypical pattern of coordination consisting of relative phase values that were considerably larger than those for other participants. This participant was less able to adapt to the changing tempo, and the relatively low coupling parameter values reflect this inability.

Insert Figure 6 here

We compared the model's parameter estimates with individual differences in adaptation to tempo change (timing error) and musical background (years of performing experience and hours of weekly practice). Individual pianists' phase and period coupling strength (as fit by the 1:1 oscillator model) correlated significantly with timing error (absolute value of observed – expected IOIs, averaged across the eight beats over which tempo change could occur in all conditions, $M = 21.58$, $SE = 0.42$). Pianists who exhibited lower timing error (i.e., who were more closely coordinated with the metronome) had higher estimates of phase coupling ($r = -.71$, $p < .05$) and period coupling ($r = -.62$, $p < .05$). Increased coupling strength was also associated with greater amounts of performing experience, for both phase ($r = .49$, $p = .054$) and period ($r = .58$, $p < .05$). These findings suggest that the model's coupling parameters accounted for timing error associated with individual differences in pianists' musical backgrounds.

Discussion

Musicians' coordination of complex rhythms with auditory sequences that changed tempo favored the predictions of an oscillator model over those of a timekeeper model in two ways. First, musicians' timing patterns revealed an asymmetry in their coordination performance: Musicians were better able to coordinate their performances with a metronome that decreased rather than increased in tempo. Asymmetry between tempo conditions was predicted only by the oscillator model. Second, the oscillator model provided a better fit to the data when

the initial period was set to the eighth-note production rate (2:1 coordination); the oscillator model thus predicted coordination based on multiple periodicities, whereas the timekeeper model did not.

In Experiment 1, the tempo change was always introduced toward the end of the musical phrase. It is possible that musicians were better able to adapt to a decreasing tempo than to an increasing tempo because they have more experience with slowing down than with speeding up at the end of the phrase, as slowing down at phrase endings is typical in expressive music performance. Therefore, Experiment 2 introduced tempo changes at the beginning of the musical phrase, where slowing down is less likely to occur (Palmer, 1989). This allowed us to determine whether similar patterns of adaptation would occur regardless of the location of the tempo change within the musical structure.

Experiment 2

In Experiment 2, musicians produced longer melodies that permitted coordination with a metronome that changed tempo at the start of a musical phrase. The tempo change consisted of a linear increase or decrease in metronome IOIs over eight beats of the melody, as in Experiment 1. However, the tempo change began on the seventeenth beat in Experiment 2, which marked the beginning of the second phrase of the melody, and the metronome resumed a final fixed tempo for the final eight beats of the melody. Participants were told to synchronize their performances with the metronome, as in Experiment 1. Examining adaptation to tempo change at the beginning of a musical phrase allowed us to separate the predictions of the oscillator and timekeeper models from predictions based on music performance conventions concerning slowing tempo at the end of a musical phrase.

Method

Participants. Three male and thirteen female pianists, ranging in age from 18 to 35 years ($M = 22.19$, $SD = 4.14$), were recruited from the Montreal community. All participants had at least 8 years of private piano lessons ($M = 11.28$, $SD = 2.77$), all but one were right-handed, and none had participated in Experiment 1.

Stimulus Materials and Equipment. In order to implement the tempo change at the beginning of a phrase while maintaining an initial section with no tempo change, we lengthened each melody from Experiment 1 by adding a repetition of the 4-measure melody (now considered the first phrase) to form the second phrase in a new 9-measure melody. The fourth measure of each new melody was altered so that the second phrase was not an exact repetition of the first. One melody is shown in the top panel of Figure 7. The equipment used for Experiment 2 was the same as for Experiment 1.

Insert Figure 7 here

Design and Procedure. Participants performed the melodies under five tempo change conditions in a within-subjects design. As in Experiment 1, the control condition consisted of an isochronous metronome set at 500 ms per quarter-note beat. The remaining four conditions consisted of a metronome sounded at 500 ms per beat for the first phrase (beats 1-17), followed by a change in tempo over each beat in the first half of the second phrase (beats 18-25), and finally continuing at the fixed final tempo for the remainder of the phrase (beats 26-33). The metronome period (IOI, in ms) for each stimulus beat in the five tempo change conditions is shown in the bottom panel of Figure 7. Tempo change was again implemented by either increasing or decreasing the metronome IOIs linearly by 1% or 3% of the original tempo on each beat. As in Experiment 1, participants performed five blocks of 20 trials (4 melodies x 5 tempo

change conditions). The procedure remained the same with the exception that only four metronome beats were sounded before participants began synchronizing with the metronome (to decrease the length of each trial).

Analysis. As in Experiment 1, we were primarily interested in participants' ability to coordinate with the metronome. The following analyses therefore focus on timing at the level of the quarter-note beats at which the metronome sounded. Eighty-five trials (5.31%) contained pitch errors and were excluded from analysis.

Results

Asynchronies. The mean asynchrony for each beat within the five tempo change conditions is shown in Figure 8 (in which the vertical line marks the end of the tempo change). The mean asynchrony over the first 17 beats, during which there was no tempo change in any condition, differed significantly from zero ($M = -7.79$ ms, $SD = 12.09$, $F(1, 15) = 9.21, p < .01$). Mean asynchronies remained significantly negative across all but the very last of the remaining beats in the control condition. Thus, as in Experiment 1, a baseline level of negative asynchrony ($M = -7.59$ ms across all beats) occurred in the absence of tempo change.

Insert Figure 8 here

To test for an asymmetry between tempo change conditions, we adjusted for the baseline asynchrony by subtracting each performer's mean asynchrony on each beat in the control condition from their mean asynchrony on each beat of the tempo change conditions. We then conducted an ANOVA by tempo change type (speeding up, slowing down), percent change (1%, 3%), and beat (1-33) on the absolute values of the adjusted asynchronies. The ANOVA revealed significant main effects of percent change, $F(1, 15) = 150.06, p < .001$, and beat, $F(32, 480) =$

57.71, $p < .001$. All two-way interactions were significant, $ps < .001$, as was the interaction between tempo change type, percent change, and beat, $F(32, 480) = 9.03, p < .001$. The absolute values of the adjusted asynchronies on the last three beats of the tempo change and the first two beats after the tempo change (beats 23-27) were larger when the metronome sped up ($M = 28.81$) than when it slowed down ($M = 16.36$), in the 3% change condition (Bonferroni-corrected $p < .0016$). In addition, the absolute adjusted asynchrony on the final beat of the sequence (beat 33) was larger when the metronome slowed down ($M = 16.73$) than when it sped up ($M = 10.30$), in the 3% change condition. Thus, there was an asymmetry in performers' adjustment to tempo change, as predicted by the oscillator model: Pianists were better able to coordinate their production with a metronome that decreased rather than increased in tempo.

Model fits. As in Experiment 1, the models were fit to the relative phase data separately for each participant. Parameter values were determined by choosing the estimate that minimized the sum of the squared error term for the mean relative phase data for all 33 beats of all five tempo change conditions, using the same ranges of parameter values as in Experiment 1. The best-fitting model was again determined using the Akaike Information Criterion (AIC). Model performance was compared when the initial oscillator period or timekeeper interval was set to the prescribed quarter-note rate (500 ms/IOI, equivalent to the metronome period; 1:1 coordination), and when the initial oscillator period or timekeeper interval was set to the eighth-note rate (250 ms/IOI, half the metronome period; 2:1 coordination).

1:1 coordination. We first fit the oscillator and timekeeper models with the initial oscillator period or timekeeper interval set to the quarter-note rate (500 ms/IOI). Table 4 shows parameter values and AIC calculated across all five tempo change conditions for the oscillator model (left half) and timekeeper model (right half), fit to each participant's data and to the mean

data across all participants (bottom row). As in Experiment 1, both the parameter values and model fits across all five conditions were similar for the two models. AIC was lower (indicating better fit) for the oscillator model than for the timekeeper model for 11/16 participants, which did not significantly differ from chance, $p = .11$. We next calculated the AIC values separately for the speeding 3% condition, for which the difference between model predictions was largest (see Figure 2). AIC values, shown in Table 5, were calculated for fits of both models that were based on average parameter values from the two optimized model fits described above. As in Experiment 1, the oscillator model fit the data better than the timekeeper model for 13/16 participants, significantly more than would be expected by chance, $p < .02$. Together, these results demonstrate that although the two models are nearly equivalent when predicting 1:1 coordination, the oscillator model has a small advantage due to its prediction of an asymmetry between adaptation to increases and decreases in tempo.

Insert Tables 4 and 5 here

2:1 coordination. We next tested the models' ability to generate accurate predictions based on 2:1 coordination by fitting each model with the initial oscillator period or timekeeper interval set to the eighth-note rate (250 ms/eighth note) to the events produced on the quarter-note beats (those aligned with the metronome period, the same as in the analysis of 1:1 coordination). Table 6 shows model parameters and AIC for the oscillator model (left half) and the timekeeper model (right half), fit to each participant's data and to the mean data across all participants. The AIC was lower (indicating better fit) for the oscillator model than for the timekeeper model for all 16 participants; no participants produced the large fluctuations in relative phase predicted when a timekeeper with half the interval of the stimulus sequence

synchronizes with that sequence. Thus, as in Experiment 1, fits to the relative phase data favored the oscillator model over the timekeeper model when the models' initial period or interval reflected 2:1 coordination.

Insert Table 6 here

Individual differences. We next examined individual differences in participants' performance data and best-fitting parameter values from the 1:1 oscillator model fits. Figure 9 shows the predicted values (lines with small markers) and obtained data (large markers) for three participants (top six panels) and for the mean data (bottom two panels). For clarity of display, the control and 3% tempo change conditions are shown in the left half of the figure, the 1% tempo change conditions are shown in the right half, and only the four beats before the onset of the tempo change are shown for all conditions. The participants whose data are shown in Figure 9 represent a similar range of parameter and fit values as those participants whose data were shown for Experiment 1. Participant 9 (first panel) showed a pattern of over-adaptation to both initial and final tempo changes, which is reflected in relatively high period coupling. Participant 6's data (second panel) were fit with moderate parameter values that were close to optimal for this model (Large & Palmer, 2002). Participant 13 (third panel) showed less adaptation to tempo change, reflected in splayed relative phase values and a relatively low period coupling value.

Insert Figure 9 here

As in Experiment 1, we compared estimates of individual pianists' phase and period coupling strength (as fit by the 1:1 oscillator model) with individual differences in adaptation to

tempo change (timing error, computed as in Experiment 1, $M = 18.02$, $SE = 0.27$) and musical background (years of performing experience and hours of weekly practice). Lower timing error (better coordination with the metronome) was marginally associated with higher phase coupling ($r = -.44$, $p < .10$). Lower timing error was also associated with increased musical experience (hours of weekly practice: $r = -.55$, $p < .05$). Together, these findings suggest that the model's coupling parameters accounted for timing error associated with pianists' musical experience.

Discussion

The findings of Experiment 2 again favored an oscillator model over a timekeeper model in two ways. First, as in Experiment 1, musicians were better able to coordinate their performances with a metronome that decreased rather than increased in tempo, as predicted by the oscillator model. Importantly, musicians' performances showed the predicted asymmetry even when the tempo change occurred at the beginning of a musical phrase, thus dissociating the asymmetry from music performance conventions concerning expressive tempo change. Also as in Experiment 1, the oscillator model provided a better fit to the data when the initial period was set to the eighth-note production rate (2:1 coordination). In contrast, the timekeeper model captured musicians' performances only when the timekeeper's initial interval was set to the quarter-note rate. Thus, the oscillator model was able to predict coordination based on multiple periodicities, whereas the timekeeper model was not.

General Discussion

Musicians coordinated their performances of rhythmic musical sequences with a metronome that gradually changed tempo in two experiments. Musicians' coordination patterns were used to compare the predictions of an oscillator model (Large, 2000, 2008; Large & Jones, 1999; Large & Palmer, 2002) and a timekeeper model (Schulze et al., 2005; Vorberg & Wing,

1996; Wing & Kristofferson, 1973). First, we tested for an asymmetry in musicians' ability to coordinate with a metronome that decreased versus increased in tempo. As predicted by the oscillator model, musicians were better able to coordinate with sequences that decreased in tempo than with sequences that increased in tempo, regardless of whether the tempo change occurred at the beginning or the end of a musical phrase. Second, we compared the oscillator and timekeeper models' ability to predict musicians' coordination performance when the initial model periods or intervals were set to the two rates at which performers were instructed to produce tones (quarter-note and eighth-note interonset intervals). Although the two models' predictions were nearly equivalent at the quarter-note rate (1:1 coordination with the metronome), the oscillator model showed a small advantage because it predicted the asymmetry between adaptation to increases and decreases in tempo. Furthermore, only the oscillator model was able to predict coordination at the eighth note time scale, i.e., when the initial period was set to half the metronome rate (2:1 coordination). Together, these findings provide stronger support for the oscillator model than for the timekeeper model.

Coordinating actions with sequences that change tempo

To our knowledge, this is the first study to systematically manipulate the tempo changes with which participants must coordinate complex rhythmic behavior. Two studies, which examined 1:1 coordination of finger taps with stimulus sequences that changed tempo, provide a close comparison. Madison and Merker (2005) had participants tap along with sequences whose interonset intervals (IOIs) linearly increased or decreased, and Schulze et al. (2005) had participants tap along with sequences whose IOIs increased or decreased according to a sigmoidal function, which is more consistent with the tempo changes typical of expressive music performance (Todd, 1985). In both studies, participants' taps initially lagged behind the

sequence's onsets when the sequence sped up and preceded its onsets when it slowed down. Madison and Merker (2005) found that participants' asynchronies tended to fluctuate pseudo-periodically across the 90 events over which the tempo changed; Schulze et al. (2005) also showed that participants' asynchronies fluctuated as they caught up to the metronome and over-adjusted twice during the 16 events over which tempo changed. In the current study, participants coordinated rhythmic musical sequences with an auditory sequence whose IOIs changed linearly. Consistent with the findings described above, participants' keystrokes initially lagged behind the sequence events when the sequence sped up and preceded the sequence events when it slowed down. Participants' asynchronies also fluctuated over the eight beats over which tempo changed. However, direct comparisons between increasing and decreasing tempo conditions revealed an asymmetry: Participants caught up with the metronome by the end of the eight beats of tempo change, but only when the metronome slowed down. The current findings thus suggest that similar patterns of coordination can occur across types of tempo change (linear and sigmoidal) and rhythmicities of the coordinated actions, but also highlight differences between coordinating with sequences that slow down versus speed up.

The asymmetry in coordination abilities between decreasing and increasing tempi was evident regardless of whether the tempo change occurred at the end of a musical phrase (Experiment 1), where slowing is typical in expressive music performance, or at the beginning of a phrase (Experiment 2), where slowing is atypical. Musicians have considerable experience with performance conventions concerning tempo change, as evidenced by the systematic timing patterns they produce when asked to perform music without tempo change of any kind (Palmer, 1989; Repp, 1999a) or to tap along with music that has been produced by a computer without tempo change (Repp, 1999a). An experience-based account therefore predicts that musicians

would be better at coordinating with a metronome that decreased tempo when the tempo change occurred at the end of a musical phrase, but not when the tempo change occurred at the beginning of a musical phrase. Such an account was not supported by the current findings. Instead, the asymmetry between tempo change conditions was dissociated from musical conventions concerning typical tempo change.

Musical experience did affect model estimates of the degree to which participants adapted to tempo changes in the sequences with which they coordinated their performances. Musicians' temporal coordination was modeled with parameter values for phase and period coupling in both experiments. In Experiment 1, smaller timing error was associated with larger parameter values reflecting stronger phase and period coupling, which in turn were associated with increased musical experience (years of pianists' training). In Experiment 2, smaller timing error was again associated with increased phase coupling strength, as well as with increased musical experience (hours of weekly practice). These findings suggest that the phase and period coupling parameters may reflect long-term adjustments that occur over years of musical experiences. Although these are correlational relationships, they suggest further that the model's parameters capture underlying individual differences in coordination abilities, which change with musical experience.

Oscillator versus timekeeper models

The current study addressed two differences between the oscillator and timekeeper models. The first difference concerned linear versus nonlinear coupling between the timekeeper or oscillator and the stimulus sequence. The linear coupling of the timekeeper model predicted that participants' adaptation to a metronome that decreased in tempo should have been of precisely the same magnitude as their adaptation to a metronome that increased in tempo, when

measured in terms of asynchrony. In contrast, the nonlinear coupling of the oscillator model predicted that participants should have been better able to adapt to sequences that decreased rather than increased in tempo. The current findings provide evidence for the latter prediction, as participants were better able to coordinate with a metronome that slowed down than with a metronome that sped up, regardless of musical conventions concerning tempo changes in expressive performance. Thus, musicians' coordination with a metronome that changed tempo favored an oscillator-based account over a timekeeper- or experience-based account.

The second difference between the two models concerned nonperiodic versus periodic coupling between the timekeeper or oscillator and the stimulus sequence. The nonperiodic coupling of the timekeeper model means that when the timekeeper period is not close to the stimulus period, the timekeeper period adjusts until it *synchronizes* with the stimulus sequence (1:1 coordination). In contrast, the periodic coupling of the oscillator model means that when the oscillator period is not close to the stimulus period, the oscillator period *entrains* to the stimulus sequence, producing multiple taps for every stimulus event (e.g., 2:1 coordination). The current findings provide evidence for the latter account; participants' relative phase values better matched the relative phase values predicted when an oscillator set at half the stimulus period entrained to the stimulus sequence (maintaining 2:1 coordination across the sequence) than those predicted when a timekeeper set at half the stimulus interval came into synchrony with the stimulus sequence (eventually reaching 1:1 coordination toward the end of the sequence).

These experiments illustrate, by theoretical argument and empirical demonstration, that the hypothesis of intrinsic dynamic oscillation provides a more realistic model for coordination of complex musical rhythms with periodic, tempo-changing stimuli than does the hypothesis of a dedicated timekeeper mechanism with linear phase and period correction. The crux of the

theoretical argument is that intrinsic properties of neural oscillation, which are not present in dedicated information-processing mechanisms, capture important aspects of temporal coordination. For example, the periodic, nonlinear coupling function of the oscillator model is derived from the intrinsic dynamics of neural systems. In contrast, the linear error correction function is not an intrinsic prediction of dedicated timing models, but rather an ad hoc mechanism added to enable application to synchronization tasks. It could be argued that a fairer comparison between an oscillator and a timekeeper model would be obtained by implementing a different type of error correction in the timekeeper model. Piecewise linear, periodic (i.e., sawtooth) error-correction functions could be implemented to capture the periodic nature of the stimulus sequences. Alternatively, specific nonlinear error correction functions could be implemented based on empirical findings showing nonlinear error correction in some 1:1 synchronization tasks (Engbert et al., 1997; Repp, 2002a, 2002c). However, these studies suggest a timekeeper model whose coupling term is nonlinear and/or periodic, properties that are intrinsically present in oscillator models that are derived from neural dynamics. Moreover, an empirical approach to deriving error-correction functions would necessarily lead to different coupling functions for different stimuli and tasks (Engbert et al., 1997; Repp, 2002a, 2002c), underscoring the need for theoretical predictions about how stimuli and tasks can lead to different coordination behavior.

Intrinsic properties also allow a single neural oscillation to produce a complex structure of nonlinear resonances, which captures the coordination of multiple periodicities that occur in music performance and other complex tasks. In contrast, multiple timekeepers are required to produce complex structures (e.g., Engbert et al., 1997; Jagacinski, Marshburn, Klapp, & Jones, 1988; Pressing, 1999; Vorberg & Wing, 1996). For example, the 2:1 coordination task described

here would typically be fit with a two-level timekeeper hierarchy, with initial timekeeper intervals of 500 ms and 250 ms. This hierarchy is essential for a timekeeper to capture performance on both the 250 and 500 ms levels. Thus, the timekeeper structure *must* be equal in complexity to the structure of the task, whereas entrainment at multiple periodicities is a universal property of single neural oscillations (Glass & Mackey, 1988; Large, 2008; Pikovsky et al., 2001). Furthermore, more complex dynamic models that include multiple oscillations with amplitude and phase (Hoppensteadt & Izhikevich, 1997; Large, 2000; Large & Jones, 1999) make intrinsic predictions regarding which oscillations will arise in response to a particular stimulus (Large, 2000, 2008). In contrast, timekeeper hierarchies must be configured specifically for specific stimuli and/or tasks (Vorberg & Wing, 1996). Finally, oscillator models with amplitude and phase dimensions also make predictions about the dependence of frequency (inverse of period) on amplitude, and thus can capture the notion of period misestimation in a parsimonious way (Large, 2008). Thus, intrinsic properties of neural oscillation capture multiple aspects of temporal coordination that dedicated information-processing mechanisms must be specifically configured to address.

Conclusions

Musicians' coordination of rhythmic musical sequences with temporally varying auditory sequences favored an oscillator-based account of coordination performance over timekeeper- and experience-based accounts. Musicians' timing patterns revealed that they were better able to coordinate their performances with a metronome that decreased than increased in tempo. Asymmetry in temporal adaptation between tempo conditions was predicted only by the oscillator model. This was true regardless of whether the tempo change occurred at the end of a musical phrase (where slowing is typical) or the beginning of a musical phrase (where slowing is

less typical). The oscillator model was also able to predict coordination based on multiple periods, and to account for experience-based individual differences in coordination performance. Together, these findings support the hypothesis that coordination is based on internal neural oscillations that entrain to an external sequence.

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Appendix A

List of Symbols:

ϕ_n – relative phase at event n

p_n – oscillator period at event n

t_n – time of stimulus event onset n

$IOI_n = C_n = t_n - t_{n-1}$ – metronome interval at event n

α – phase coupling parameter

β – period coupling parameter

τ_n – timekeeper mean at event n (equivalent to period)

A_n – asynchrony between tap and stimulus at event n

Appendix B

Under a certain set of assumptions, the timekeeper model can be translated into a form similar to the oscillator model. For simplicity we chose to work with a deterministic variant of the timekeeper model (meaning that $T_n = \tau$), and we ignore motor delays. Under these assumptions, the asynchrony between the next tap and stimulus event in the sequence is determined by the equation

$$A_{n+1} = A_n + \tau - C_n - \alpha A_n$$

Asynchrony can be transformed to relative phase using the relation $\phi = A/\tau$

$$\begin{aligned} \frac{A_{n+1}}{\tau} &= \frac{A_n}{\tau} + \frac{\tau}{\tau} - \frac{C_n}{\tau} - \alpha \frac{A_n}{\tau} \\ \phi_{n+1} &= \phi_n + 1 - \frac{C_n}{\tau} - \alpha \phi_n \end{aligned} \quad (\text{B1})$$

The result is a timekeeper model described in terms of relative phase.

Similarly, it is possible to describe the neural oscillator model in terms of asynchrony, with some assumptions. We begin with the equation for the phase at which the next stimulus event occurs

$$\phi_{n+1} = \phi_n + \frac{IOI_n}{p} - \frac{\alpha}{2\pi} \sin 2\pi\phi_n \quad (\text{mod}_{-5,5} 1)$$

We first subtract one from the right hand side, which is allowable because the result is taken modulo one. Next, the modulo operator can be eliminated; because \sin is a periodic function, phase can grow without bound and timing adjustments will still be periodic. Subtracting one keeps phase near zero under the assumption of 1:1 coordination.

$$\phi_{n+1} = \phi_n + \frac{IOI_n}{p} - 1 - \frac{\alpha}{2\pi} \sin 2\pi\phi_n$$

Next, relative phase can be transformed to asynchrony using the relation $A = p\phi$

$$\begin{aligned} p\phi_{n+1} &= p\phi_n + IOI_n - p - \frac{p\alpha}{2\pi} \sin 2\pi\phi_n \\ A_{n+1} &= A_n + IOI_n - p - \frac{p\alpha}{2\pi} \sin \frac{2\pi}{p} A_n \end{aligned} \quad (B2)$$

Finally, transformation of the interval and period adaptation rules involve only transforming asynchrony to phase and vice versa. Therefore, the timekeeper model's interval adaptation rule,

$$\tau_{n+1} = \tau_n - \beta A_n ,$$

becomes

$$\tau_{n+1} = \tau_n - \beta \phi_n \tau_n \quad (B3)$$

when described in terms of phase, while the oscillator model's period adaptation rule,

$$p_{n+1} = p_n + \frac{p_n \beta}{2\pi} \sin 2\pi\phi_n ,$$

becomes

$$p_{n+1} = p_n + \frac{p_n \beta}{2\pi} \sin \frac{2\pi}{p} A_n \quad (B4)$$

when described in terms of asynchrony.

Table B1 shows how the phase (asynchrony) equations for each model compare when both models are written in comparable terms (phase in the left panel and asynchrony in the right panel); Table B2 shows how the period (timekeeper interval) adaptation equations compare. Note that IOI_n and C_n are equivalent variables, indicating the changing stimulus time intervals, and p and τ are also equivalent variables, representing oscillator period and timekeeper interval, respectively. Furthermore, in the phase-based formulation of the timekeeper model the term '+ 1'

performs a similar job to $(\text{mod}_{-.5,.5} 1)$, keeping the phase near zero under the assumption of 1:1 coordination¹. Together, these equations highlight the main difference between the two models: Coupling between the oscillator and the stimulus is periodic and nonlinear, whereas coupling between the timekeeper and the stimulus is nonperiodic and linear.

Table B1. Comparable phase (asynchrony) equations for the two models.

| Model | Variable | |
|--|---|--|
| | Phase | Asynchrony |
| Dynamic (oscillator) | $\phi_{n+1} = \phi_n + \frac{IOI_n}{p} - \frac{\alpha}{2\pi} \sin 2\pi\phi_n \quad (\text{mod}_{-.5,.5} 1)$ | $A_{n+1} = A_n + IOI_n - p - \frac{p\alpha}{2\pi} \sin \frac{2\pi}{p} A_n$ |
| Information-processing (timekeeper) | $\phi_{n+1} = \phi_n + 1 - \frac{C_n}{\tau_n} - \alpha\phi_n$ | $A_{n+1} = A_n + \tau - C_n - \alpha A_n$ |

Table B2. Comparable period (interval) adaptation equations for the two models.

| Model | Variable | |
|--|---|---|
| | Phase | Asynchrony |
| Dynamic (oscillator) | $p_{n+1} = p_n + \frac{p_n\beta}{2\pi} \sin 2\pi\phi_n$ | $p_{n+1} = p_n + \frac{p_n\beta}{2\pi} \sin \frac{2\pi}{p} A_n$ |
| Information-processing (timekeeper) | $\tau_{n+1} = \tau_n - \beta\phi_n\tau_n$ | $\tau_{n+1} = \tau_n - \beta A_n$ |

Footnote

¹The timekeeper model assumes 1:1 coordination regardless of whether it is based on synchrony or relative phase. In contrast, the oscillator model does not assume 1:1 coordination; only the transformation from relative phase to synchrony requires this assumption. Thus, it is

legitimate to compare the two models in relative phase units because transforming the timekeeper model into relative phase units requires fewer additional assumptions than transforming the oscillator model into asynchrony units. In addition, it is possible to derive an oscillator model based on absolute time (from which asynchronies can be calculated) that predicts the coordination of multiple periodicities, including 2:1 coordination (see Large & Kolen, 1994). In contrast, the timekeeper model's assumption of linear error correction precludes the coordination of multiple periodicities, regardless of whether the model is based on relative phase or asynchrony units.

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Footnotes

¹Relative-phase-based versions of the two models were fit to the relative phase data because transforming the timekeeper model into relative phase requires fewer assumptions than transforming the oscillator model into asynchrony (as discussed in Appendix B).

²AIC was estimated using the equation $AIC = n * \ln SSE + 2 * k$, where $SSE = \text{sum of squared errors}$, $n = \text{number of observations}$ (Experiment 1: 5 tempo change conditions \times 17 beats = 85 observations; Experiment 2: 5 tempo change conditions \times 33 beats = 165 observations), and $k = \text{number of free parameters}$ (3 for both models). AIC values are interpretable only as relative differences, with smaller values indicating better fit (Myung & Pitt, 1998).

³We also fit asynchrony-based formulations of the oscillator model (Equations B2 and B4) and timekeeper model (Equations 3 and 4) to the asynchrony data (for 1:1 coordination only; see Appendix B). For both Experiments 1 and 2, the patterns of results were nearly identical to those based on relative phase, indicating that the oscillator model's advantage was not due to the use of relative phase as the dependent variable.

Table 1.

Parameter values and AIC for 1:1 oscillator (left) and timekeeper (right) model fits to Experiment 1 data.

| Participant | Oscillator model | | | | Timekeeper model | | | |
|-------------|------------------|---------|----------|---------|------------------|---------|----------|---------|
| | α | β | ϕ_0 | AIC | α | β | ϕ_0 | AIC |
| 1 | 1.075 | 0.525 | -0.015 | -199.44 | 1.050 | 0.500 | -0.015 | -199.94 |
| 2 | 0.775 | 0.675 | -0.015 | -170.80 | 0.750 | 0.650 | -0.015 | -169.40 |
| 3 | 0.750 | 0.400 | -0.025 | -118.54 | 0.700 | 0.350 | -0.025 | -120.64 |
| 4 | 0.775 | 0.600 | -0.030 | -100.17 | 0.725 | 0.575 | -0.030 | -96.77 |
| 5 | 0.400 | 0.450 | 0.020 | 32.61 | 0.875 | 0.300 | 0.020 | 39.14 |
| 6 | 0.950 | 0.700 | 0 | -232.99 | 0.925 | 0.700 | 0 | -233.74 |
| 7 | 0.875 | 0.450 | -0.050 | -119.04 | 0.750 | 0.400 | -0.050 | -122.92 |
| 8 | 0.250 | 0.250 | -0.020 | -38.01 | 0.250 | 0.150 | -0.020 | 5.40 |
| 9 | 0.800 | 0.375 | 0.005 | -73.56 | 0.800 | 0.350 | 0.005 | -70.62 |
| 10 | 0.800 | 0.600 | -0.005 | -184.37 | 0.775 | 0.575 | -0.005 | -186.31 |
| 11 | 0.975 | 0.600 | -0.030 | -95.92 | 0.900 | 0.575 | -0.030 | -94.65 |
| 12 | 1.625 | 1.200 | 0.010 | -231.98 | 1.625 | 1.200 | 0.010 | -231.86 |
| 13 | 0.800 | 0.475 | 0.015 | -63.38 | 0.750 | 0.450 | 0.015 | -63.57 |
| 14 | 0.975 | 0.450 | -0.010 | -54.29 | 0.950 | 0.425 | -0.010 | -53.73 |
| 15 | 1.425 | 0.450 | 0.020 | -75.40 | 1.300 | 0.475 | 0.020 | -74.02 |
| 16 | 0.750 | 0.475 | -0.015 | -136.44 | 0.700 | 0.450 | -0.015 | -136.37 |
| Mean Data | 0.875 | 0.450 | -0.010 | -146.51 | 0.850 | 0.425 | -0.010 | -145.82 |

Table 2.

Parameter values and AIC for 1:1 oscillator and timekeeper fits to the speeding 3% condition in Experiment 1.

| Participant | α | β | ϕ_0 | AIC | |
|-------------|----------|---------|----------|------------------|------------------|
| | | | | Oscillator Model | Timekeeper Model |
| 1 | 1.0625 | 0.5125 | -0.015 | -73.57 | -71.19 |
| 2 | 0.7625 | 0.6625 | -0.015 | -57.16 | -56.07 |
| 3 | 0.7250 | 0.3750 | -0.025 | -57.08 | -47.78 |
| 4 | 0.7500 | 0.5875 | -0.030 | -58.15 | -55.96 |
| 5 | 0.6375 | 0.3750 | 0.020 | -16.05 | -10.20 |
| 6 | 0.9375 | 0.7000 | 0 | -75.04 | -75.93 |
| 7 | 0.8125 | 0.425 | -0.050 | -53.54 | -51.39 |
| 8 | 0.2500 | 0.2000 | -0.020 | 34.76 | -2.61 |
| 9 | 0.8000 | 0.3625 | 0.005 | -37.49 | -31.29 |
| 10 | 0.7875 | 0.5875 | -0.005 | -73.15 | -71.98 |
| 11 | 0.9375 | 0.5875 | -0.030 | -38.04 | -37.13 |
| 12 | 1.6250 | 1.2000 | 0.010 | -86.68 | -86.28 |
| 13 | 0.7750 | 0.4625 | 0.015 | -40.65 | -38.88 |
| 14 | 0.9625 | 0.4375 | -0.010 | -28.16 | -26.41 |
| 15 | 1.3625 | 0.4625 | 0.020 | -40.55 | -38.48 |
| 16 | 0.7250 | 0.4625 | -0.015 | -58.19 | -52.72 |
| Mean Data | 0.8625 | 0.4375 | -0.010 | -50.24 | -45.91 |

Table 3.

Parameter values and AIC for 2:1 oscillator (left) and timekeeper (right) model fits to Experiment 1 data.

| Participant | Oscillator model | | | | Timekeeper model | | | |
|-------------|------------------|-------|----------|---------|------------------|---------|----------|--------|
| | α | B | ϕ_0 | AIC | α | β | ϕ_0 | AIC |
| 1 | 2.000 | 0.475 | -0.015 | -185.03 | 2.025 | 1.025 | -0.015 | 306.05 |
| 2 | 1.975 | 0.600 | -0.015 | -125.12 | 2.000 | 0.925 | -0.010 | 306.31 |
| 3 | 1.250 | 0.325 | -0.025 | -117.25 | 2.000 | 0.925 | -0.020 | 310.76 |
| 4 | 1.125 | 0.375 | -0.035 | -79.08 | 2.025 | 0.925 | -0.035 | 306.56 |
| 5 | 1.575 | 0.275 | 0.020 | 31.99 | 1.975 | 0.950 | 0.020 | 320.40 |
| 6 | 2.250 | 0.650 | 0 | -186.07 | 2.000 | 1.000 | 0 | 308.02 |
| 7 | 1.375 | 0.350 | -0.050 | -112.62 | 2.050 | 0.925 | -0.050 | 304.92 |
| 8 | 1.225 | 0.150 | -0.005 | -22.35 | 1.950 | 0.750 | -0.010 | 317.25 |
| 9 | 1.575 | 0.325 | 0.005 | -73.49 | 1.950 | 0.850 | 0.010 | 307.97 |
| 10 | 1.725 | 0.500 | -0.005 | -143.01 | 2.000 | 0.950 | -0.005 | 310.75 |
| 11 | 1.875 | 0.500 | -0.030 | -82.63 | 2.025 | 0.950 | -0.030 | 304.74 |
| 12 | 2.500 | 0.900 | 0.010 | -191.04 | 1.975 | 0.975 | 0.015 | 308.87 |
| 13 | 1.300 | 0.400 | 0.015 | -68.34 | 2.025 | 1.125 | 0.015 | 316.05 |
| 14 | 1.550 | 0.400 | -0.010 | -55.61 | 2.000 | 0.925 | -0.005 | 309.50 |
| 15 | 2.400 | 0.450 | 0.020 | -74.44 | 1.950 | 0.875 | 0.020 | 310.68 |
| 16 | 1.250 | 0.375 | -0.020 | -126.23 | 1.975 | 0.850 | -0.010 | 305.26 |
| Mean Data | 1.500 | 0.400 | -0.010 | -142.58 | 2.000 | 0.950 | -0.005 | 308.78 |

Table 4.

Parameter values and AIC for 1:1 oscillator (left) and timekeeper (right) model fits to Experiment 2 data.

| Participant | Oscillator model | | | | Timekeeper model | | | |
|-------------|------------------|---------|----------|---------|------------------|---------|----------|---------|
| | α | β | ϕ_0 | AIC | α | β | ϕ_0 | AIC |
| 1 | 0.950 | 0.475 | -0.050 | -77.82 | 0.850 | 0.425 | -0.050 | -81.28 |
| 2 | 1.075 | 0.600 | -0.035 | -202.60 | 1.050 | 0.600 | -0.035 | -202.46 |
| 3 | 1.375 | 0.800 | -0.005 | -193.80 | 1.350 | 0.775 | -0.005 | -193.43 |
| 4 | 1.050 | 0.700 | -0.005 | -207.49 | 1.025 | 0.675 | -0.005 | -207.14 |
| 5 | 1.175 | 0.325 | -0.010 | -138.29 | 1.100 | 0.300 | -0.010 | -141.25 |
| 6 | 1.100 | 0.525 | -0.020 | -192.48 | 1.100 | 0.500 | -0.020 | -191.87 |
| 7 | 1.475 | 0.575 | -0.010 | -123.58 | 1.475 | 0.550 | -0.010 | -123.22 |
| 8 | 1.125 | 0.375 | 0.020 | -139.09 | 1.050 | 0.350 | 0.020 | -140.31 |
| 9 | 1.125 | 0.800 | -0.015 | -159.81 | 1.100 | 0.775 | -0.015 | -159.32 |
| 10 | 1.250 | 0.500 | 0.020 | -219.13 | 1.175 | 0.475 | 0.020 | -220.68 |
| 11 | 1.150 | 0.675 | -0.010 | -230.92 | 1.150 | 0.675 | -0.005 | -230.52 |
| 12 | 1.450 | 0.650 | -0.045 | -195.57 | 1.425 | 0.650 | -0.045 | -193.97 |
| 13 | 1.125 | 0.425 | -0.015 | -276.90 | 1.075 | 0.400 | -0.015 | -275.92 |
| 14 | 1.325 | 0.425 | -0.020 | -300.80 | 1.300 | 0.400 | -0.020 | -297.81 |
| 15 | 1.175 | 0.525 | -0.015 | -135.36 | 1.150 | 0.525 | -0.015 | -134.50 |
| 16 | 1.175 | 0.500 | -0.005 | -259.76 | 1.125 | 0.475 | -0.005 | -261.13 |
| Mean Data | 1.175 | 0.525 | -0.015 | -331.27 | 1.150 | 0.500 | -0.015 | -329.94 |

Table 5.

Parameter values and AIC for 1:1 oscillator and timekeeper fits to the speeding 3% condition in Experiment 2.

| Participant | α | B | ϕ_0 | AIC | |
|-------------|----------|--------|----------|------------------|------------------|
| | | | | Oscillator Model | Timekeeper Model |
| 1 | 0.9000 | 0.4500 | -0.0500 | -67.11 | -66.81 |
| 2 | 1.0625 | 0.6000 | -0.0350 | -95.93 | -96.19 |
| 3 | 1.3625 | 0.7875 | -0.0050 | -84.42 | -84.14 |
| 4 | 1.0375 | 0.6875 | -0.0050 | -94.47 | -95.81 |
| 5 | 1.1375 | 0.3125 | -0.0100 | -62.63 | -61.65 |
| 6 | 1.1000 | 0.5125 | -0.0200 | -90.02 | -87.59 |
| 7 | 1.4750 | 0.5625 | -0.0100 | -52.30 | -51.94 |
| 8 | 1.0875 | 0.3625 | 0.0200 | -72.40 | -71.85 |
| 9 | 1.1125 | 0.7875 | -0.0150 | -76.05 | -75.89 |
| 10 | 1.2125 | 0.4875 | 0.0200 | -85.96 | -85.62 |
| 11 | 1.1500 | 0.6750 | -0.0075 | -85.81 | -85.47 |
| 12 | 1.4375 | 0.6500 | -0.0450 | -90.37 | -89.64 |
| 13 | 1.1000 | 0.4125 | -0.0150 | -104.00 | -103.40 |
| 14 | 1.3125 | 0.4125 | -0.0200 | -104.29 | -100.15 |
| 15 | 1.1625 | 0.5250 | -0.0150 | -81.57 | -80.95 |
| 16 | 1.1500 | 0.4875 | -0.0050 | -106.65 | -107.22 |
| Mean Data | 1.1625 | 0.5125 | -0.0150 | -106.12 | -104.63 |

Table 6.

Parameters and AIC for 2:1 oscillator (left) and timekeeper (right) model fits to Experiment 2 data.

| Participant | Oscillator model | | | | Timekeeper model | | | |
|-------------|------------------|---------|----------|---------|------------------|---------|----------|--------|
| | α | β | ϕ_0 | AIC | α | β | ϕ_0 | AIC |
| 1 | 1.450 | 0.375 | -0.050 | -78.41 | 2.025 | 0.850 | -0.050 | 580.36 |
| 2 | 2.125 | 0.525 | -0.035 | -171.23 | 2.050 | 0.975 | -0.035 | 588.08 |
| 3 | 2.425 | 0.700 | -0.005 | -166.67 | 1.975 | 0.900 | 0 | 593.90 |
| 4 | 2.225 | 0.600 | -0.005 | -172.77 | 2.025 | 1.025 | -0.005 | 598.22 |
| 5 | 2.050 | 0.300 | -0.010 | -125.93 | 1.975 | 0.875 | -0.005 | 599.41 |
| 6 | 2.000 | 0.450 | -0.020 | -171.61 | 2.000 | 0.900 | -0.020 | 596.79 |
| 7 | 2.200 | 0.525 | -0.010 | -110.47 | 2.000 | 0.925 | -0.005 | 599.78 |
| 8 | 2.025 | 0.350 | 0.020 | -129.98 | 1.975 | 1.000 | 0.020 | 604.61 |
| 9 | 2.125 | 0.650 | -0.015 | -123.45 | 2.000 | 0.900 | -0.015 | 594.95 |
| 10 | 2.150 | 0.450 | 0.020 | -206.84 | 1.975 | 0.975 | 0.020 | 606.66 |
| 11 | 2.050 | 0.550 | -0.005 | -200.96 | 2.000 | 0.925 | -0.005 | 598.34 |
| 12 | 2.225 | 0.550 | -0.045 | -169.02 | 2.05 | 0.950 | -0.045 | 585.49 |
| 13 | 2.050 | 0.400 | -0.015 | -250.47 | 2.000 | 0.925 | -0.015 | 597.91 |
| 14 | 2.075 | 0.400 | -0.020 | -270.68 | 2.000 | 0.925 | -0.015 | 593.51 |
| 15 | 2.050 | 0.475 | -0.015 | -126.01 | 2.000 | 0.900 | -0.015 | 592.01 |
| 16 | 2.000 | 0.450 | -0.005 | -231.10 | 1.975 | 0.925 | 0 | 600.70 |
| Mean Data | 2.075 | 0.475 | -0.015 | -288.54 | 2.000 | 0.925 | -0.010 | 594.83 |

Figure Captions

Figure 1. Amount of adaptation, $F(\phi)$, as a function of relative phase, ϕ , for the oscillator model (solid line) and timekeeper model (dashed line).

Figure 2. Predicted asynchronies as a function of tempo change beginning at beat 9, for the oscillator model (solid lines) and timekeeper model (dashed lines).

Figure 3. Predicted relative phase (top panel) and period (bottom panel) for an oscillator (solid line) or timekeeper (dashed line) whose initial period is half the stimulus period (empty squares).

Figure 4. Top panel: One stimulus melody from Experiment 1. Xs mark notes that were aligned with the metronome beat. Bottom panel: Metronome period (interonset interval, ms) for each beat of the five tempo change conditions.

Figure 5. Mean asynchronies ($\pm SE$) for each beat of the five tempo change conditions in Experiment 1.

Figure 6. Obtained (large markers) and predicted (lines with small markers, based on 1:1 model fits) relative phase values for three participants (top three panels) and for the mean data (bottom panel) of Experiment 1.

Figure 7. Top panel: One stimulus melody from Experiment 2. Xs mark notes that were aligned with the metronome beat. Bottom panel: Metronome period (interonset interval, in ms) for each beat of the five tempo change conditions.

Figure 8. Mean asynchronies ($\pm SE$) for each beat of the five tempo change conditions in Experiment 2. The vertical line indicates the end of the tempo change.

Figure 9. Obtained (large markers) and predicted (lines with small markers, based on 1:1 model fits) relative phase values for three participants (top six panels) and for the mean data (bottom two panels) of Experiment 2. Left panels show the control and 3% tempo change conditions;

right panels show the 1% tempo change conditions. Vertical lines indicate the end of the tempo change.

















