



# Pitch influences sensorimotor synchronization to auditory rhythms

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Current models of rhythm perception propose that humans track musical beats using the phase, period, and amplitude of sound patterns. However, a growing body of evidence suggests that pitch can also influence the perceived timing of auditory signals. We recently discovered an inverted U-shaped relation between pitch and subjective ratings of tempo (Pazdera & Trainor, 2024), with subjective tempo increasing with pitch between A2 (110 Hz) and A4 (440 Hz), reaching a peak somewhere between A4 and A6 (1760 Hz), and declining again before reaching A7 (3520 Hz). In the present study, we conducted experiments to investigate whether pitch also affects sensorimotor synchronization timing. To do so, we asked participants to synchronize with a repeating tone, whose pitch on each trial was drawn from the same set as in our previous subjective rating experiments. In Experiment 1, we observed U-shaped patterns in both mean asynchrony and continuation tapping rates, with participants tapping earliest and fastest when synchronizing to the same moderately high pitches that produced the fastest subjective tempo in our previous study. In Experiment 2, we found that extremely high pitches still produced slower timing than moderately high pitches when participants were exposed to an exclusively high-pitched context. We advocate for the incorporation of pitch into models of rhythm perception, and we discuss the possibility that there may exist two pitch-based influences on perceived tempo: a top-down learned correlation between higher pitches and faster timing, and a bottom-up U-shaped effect of stimulus fundamental frequency on neural dynamics.

*Keywords:* auditory, continuation tapping, perceptual bias, pitch, sensorimotor, synchronization, tempo

**Significance statement:** The present study suggests that pitch height exerts a U-shaped effect on sensorimotor timing. Both low and extremely high pitches produced later and slower tapping than moderately high pitches, which may be attributed either to pitch-induced biases in tempo perception or to middle pitches producing the weakest auditory-motor synchronization. Our results support the incorporation of pitch into current models of rhythm perception.

In the field of music perception, there are several dominant models of how humans synchronize their movements to rhythmic sounds (Large et al., 2023; Palmer & Demos, 2022). *Rhythm* refers to a series of events that are predictably organized across time, and humans—as well as some non-human animals (Gámez et al., 2018; Patel, Iversen, Bregman, & Schulz, 2009a, 2009b)—are able to extract a sense of underlying *pulse* or *beat* from these predictable event struc-

tures. Some models envision this process of perceiving and synchronizing to the beat as an emergent property of neural dynamics, in which the auditory and motor systems resonate when driven by rhythmic stimulation (Large & Snyder, 2009; Large, Almonte, & Velasco, 2010; Large, Herrera, & Velasco, 2015; Roman, Roman, Kim, & Large, 2023). Others conceptualize the brain as a Bayesian prediction engine that works to infer the structure underlying predictable patterns in time, in accordance with predictive coding theory (Cannon, 2021; Friston, 2010; Koelsch, Vuust, & Friston, 2019; Vuust & Witek, 2014). Still others propose biophysical pacemaker models that learn stimulus timing through error correction (Bose, Byrne, & Rinzel, 2019; Egger, Le, & Jazayeri, 2020).

Regardless of category, these established models track rhythms based on the phase, period, and amplitude of sound patterns, but not their pitch. However, there is a wealth of evidence to suggest that pitch affects the perceived tempo of a rhythm (Boltz, 2011; Collier & Hubbard, 1998; Pazdera & Trainor, 2024), as do the size (Ammirante, Thompson, & Russo, 2011; Ammirante & Thompson, 2012; Boasson & Granot, 2012; Boltz, 1998) and direction of pitch changes (Boasson & Granot, 2019; Gordon & Ataucusi, 2021; Herrmann, Henry, Grigutsch, & Obleser, 2013; Her-

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rmann, Henry, Scharinger, & Obleser, 2014). In the present study, we sought to identify whether previously identified effects of pitch height on subjective tempo ratings (Pazdera & Trainor, 2024) also influence the timing of sensorimotor synchrony. If they do, it would support the incorporation of pitch as a factor in models of rhythm perception, whether as an influence on neural dynamics or as an informative cue in a Bayesian prediction process.

### Integration of Pitch and Timing

The idea that pitch and time perception are integrated dates back decades, originating as an extension of research on the *kappa* effect, in which observing spatial movement distorts time perception (Cohen, Hansel, & Sylvester, 1953, 1954). This concept of integrality was formalized by Jones (1976), who proposed that the brain integrates pitch, time, and loudness into a shared representational space. She hypothesized that music is represented as a trajectory of movement through this multidimensional space, and lawful relations between movements along different dimensions guide musical expectancy. A similar idea underlies the auditory pitch-motion hypothesis of Henry and McAuley (2013), in which the movements of an auditory signal in frequency space guide the predicted timing of that signal. Boltz (2017) has further suggested that pitch and time share an integrated representation in memory, and our own lab has recently presented evidence that pitch and timing bidirectionally influence one another in auditory perception (Pazdera & Trainor, 2023).

In general, higher pitch has been associated with faster and earlier perceived timing (Boltz, 2011, 2017; Collier & Hubbard, 1998; Gordon & Ataucusi, 2021; Herrmann et al., 2013, 2014; Pazdera & Trainor, 2023). For example, Collier and Hubbard (1998) found that participants rated higher-pitched repeating tones and musical scales as faster and as speeding up more than those played in a lower octave. Similarly, Boltz (2011) found that participants tended to rate melodies as faster when played in a higher octave, compared to a lower one. Furthermore, they rated ascending melodies as faster than descending melodies. Herrmann et al. (2013, 2014) have since discovered neural correlates of this pitch-induced illusory tempo effect in both magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI). Most relevant to models of rhythm perception is their discovery that patterns of ascending and descending pitch patterns shift the phase of entrained neural activity in opposite directions relative to a rhythmic auditory stimulus, and improve neural tracking of tempo changes in the congruent direction (Herrmann et al., 2013).

### Nonmonotonicity of Pitch-Induced Timing

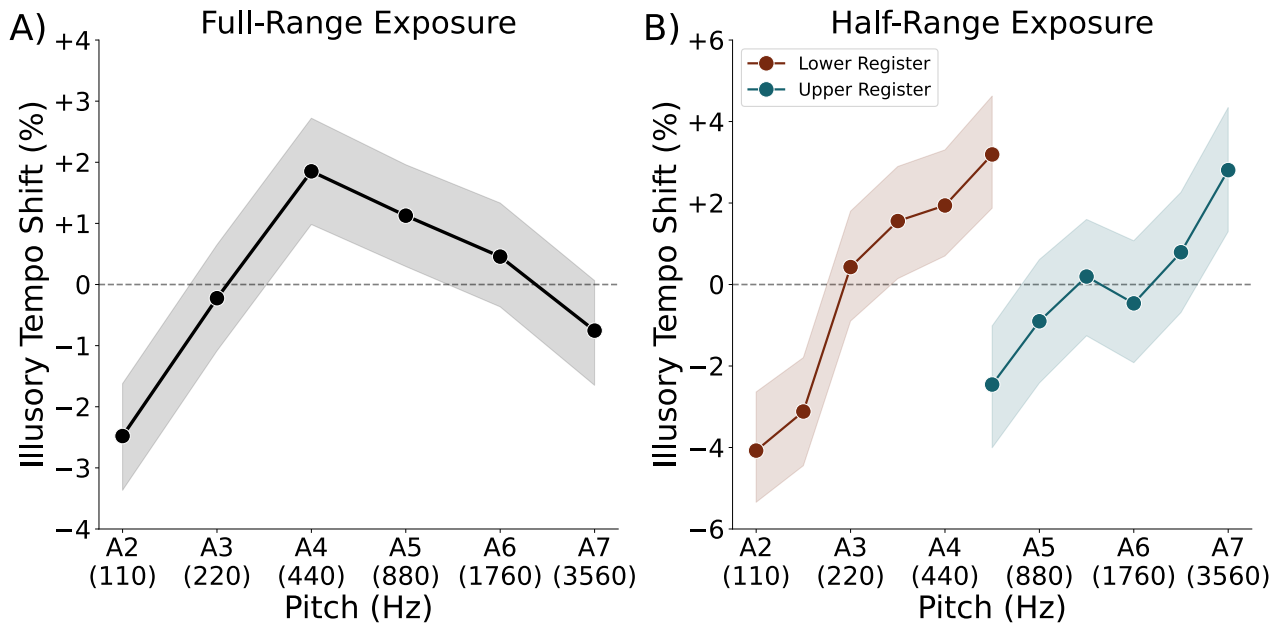
We recently conducted a study testing the generalizability of the aforementioned findings by Collier and Hubbard

(1998) and Boltz (2011) to a wider range of frequencies than previously tested (Pazdera & Trainor, 2024). Whereas the former compared the perceived timing of the pitches C4 (261.6 Hz), C5 (523.2 Hz), and C6 (1046.4 Hz) and the latter tested melodies starting on C3 (130.8 Hz) or C5 (523.2 Hz), we tested tempo perception across pitches as low as A2 (110 Hz; close to the average male speaking voice) to as high as A7 (3520 Hz; the fourth-highest note on a piano). In our study, we asked participants to rate how fast repeating tones were compared to a metronome. The metronome had the same tempo on every trial, acting as a standard reference, whereas the repeating tone varied in pitch and tempo across trials. Contrary to the generally accepted view that higher pitches are perceived as faster, we observed an inverted U-shaped relation between pitch and perceived tempo (Figure 1A). Between 110 Hz and 440 Hz, higher pitches were consistently perceived as faster; however, perceived tempo peaked somewhere between 440 Hz and 1760 Hz (varying across experiments), with 3520 Hz reliably perceived as slower than 440 Hz. These data suggest that the relation between pitch and perceived tempo is in fact nonmonotonic, and reverses direction at the upper octaves left untested by previous studies.

To address the possibility of a midpoint effect in which people perceive the middlemost pitches in any context as fastest, we next exposed one group of participants to pitches only between 110 Hz and 622.3 Hz and another group to pitches only between 622.3 Hz and 3520 Hz (Pazdera & Trainor, 2024, Experiment 5). If people perceive the average pitch in a context as fastest, we expected participants in both registers to show inverted U-shaped illusory tempo effects. If illusory tempo instead depends on absolute pitch, we expected participants assigned to the lower register to rate higher pitches as faster and participants in the upper register to rate higher pitches as slower. Unexpectedly, participants in both registers rated higher pitches as faster, eliminating the U-shaped effect entirely (Figure 1B). We interpreted this finding as an indication that illusory tempo depends on the pitch range within a context. Within a context spanning 2–3 octaves, higher pitches were consistently perceived as faster; however, pitches several octaves above baseline were instead perceived as slower, perhaps tying the effect to implicit knowledge about the span of human vocal ranges (Kuhn, Wachhaus, Moore, & Pantle, 1979).

### The Present Study

One limitation of a subjective rating paradigm like those previously used by ourselves and others (e.g., Boltz, 2011; Collier & Hubbard, 1998; Pazdera & Trainor, 2024) is that they cannot distinguish whether biases in people's ratings arise at the level of perception or decision making. That is, we cannot tell in Figure 1 whether participants rated certain tones as faster because they actually experienced them

**Figure 1***Effect of Pitch on Subjective Tempo (Pazdera & Trainor, 2024)*

*Note.* Subjective tempo ratings for isochronous repeating tones as a function of pitch, as observed when participants **A**) heard tones between 110 Hz and 3520 Hz (Pazdera & Trainor, 2024, Experiments 1–3), or **B**) heard tones from only the lower or upper half of that range (Pazdera & Trainor, 2024, Experiment 5). Shaded bands indicate 95% confidence intervals. Exposure to a five-octave range of frequencies produced an inverted U-shaped relation between pitch and perceived tempo, whereas exposure to a 2.5-octave range produced a bias to perceive higher pitches as faster regardless of absolute pitch.

as faster in real-time while listening to them, or because they implicitly (or explicitly) used pitch as evidence for how fast the tones likely were. To address this limitation, we designed the present study to test the perceived tempo of the same pitches as Pazdera and Trainor (2024) in the absence of an explicit decision-making task. If our previously-observed effects are preserved in the absence of decision-making, then it would provide evidence for a perceptual origin of pitch-induced illusory tempo.

Outside of subjective ratings, the most common measurement of human timing is through sensorimotor tasks, usually involving tapping (Repp, 2005; Repp & Su, 2013). Both synchronization (Boasson & Granot, 2012, 2019) and continuation (Ammirante & Thompson, 2010, 2012; Ammirante et al., 2011) tapping tasks have been used previously to study the effects of pitch distance, pitch direction, and contour changes on perceived tempo. We therefore adopted a synchronization-continuation tapping task for the present study, to determine whether pitch height also influences sensorimotor timing.

In a synchronization-continuation task, participants first synchronize their movements to a metronome or other pac-

ing signal, and then try to continue moving at the same tempo even after the signal ends (e.g., Michon, 1967; Stevens, 1886; Wing & Kristofferson, 1973) or switches to the participant's control (e.g., Flach, 2005; Ammirante et al., 2011). If the pitch of the pacing signal biases the perception of its tempo, then participants should synchronize to different pitches as if they were played at different tempos. For example, participants might tap at an earlier phase when synchronizing to pitches they perceive as speeding up (Boasson & Granot, 2012, 2019), and may tap faster when asked to continue moving at the tempo of the pacing signal (Ammirante & Thompson, 2010, 2012; Ammirante et al., 2011). Therefore, if pitch biases timing at the level of perception, we should observe a greater negative mean asynchrony (the extent to which tapping anticipates the stimulus) and shorter inter-tap intervals for the same pitches that participants rated as fastest in the Pazdera and Trainor (2024) experiments.

In the present study, we conducted two experiments to test whether the same effects of pitch on subjective tempo ratings would carry over to sensorimotor timing in a synchronization-continuation task. In Experiment 1, we attempted to replicate the U-shaped effect from Pazdera and

Trainor (2024) Experiments 1–3 (Figure 1A) by exposing participants to pitches spanning a five-octave range from A2 (110 Hz) to A7 (3520 Hz). In Experiment 2, we attempted to replicate the simple higher-faster bias from Pazdera and Trainor (2024) Experiment 5 (Figure 1B) by exposing participants to tones from only the lower half or upper half of that range.

### Experiment 1

In Experiment 1, we tested whether the nonmonotonic relation between pitch and perceived timing (Pazdera & Trainor, 2024) persists in the absence of an explicit decision-making task. Specifically, we asked participants to synchronize with eight isochronous tones that varied in pitch across trials, ranging from A2 (110 Hz) to A7 (3520 Hz), and then to continue tapping at the same tempo for 16 additional beats. If pitch affects subjective tempo at the level of perception, we should observe a similar pattern of results to those in the subjective rating task by Pazdera and Trainor (2024). However, if pitch affects subjective tempo at a later stage of processing—such as during decision-making—we should not observe the same effect of pitch on sensorimotor timing.

### Methods

#### Participants

Data for Experiment 1 were collected between April 2022 and January 2023, under special COVID-19 safety protocols, including mask requirements for all participants and experimenters. Thirty-eight undergraduate students (31 female, 6 male, 1 unreported) from McMaster University completed the experiment for course credit. Ages ranged from 17–30 ( $M = 18.7$ ,  $SD = 2.2$ ). An additional three participants completed the experiment, but were excluded based on performance criteria (see Data Analysis for details).

#### Data Availability

We have made all data, code, and stimuli from both experiments publicly available on the Open Science Framework at <https://osf.io/7bptg/>, as well as on GitHub at <https://github.com/jpazdera/IllusoryMotor>.

#### Materials

All text used in the experiment was displayed in white, 72-point Arial font on a black background. All auditory stimuli were 250 ms complex tones, which we generated in Python by summing sine waves for the fundamental frequency and the first two overtones. We summed the sine waves with random phase, and reduced the amplitude of overtones by 6 dB per octave. We then applied a percussive amplitude envelope (Schutz & Vaisberg, 2012) by adding a 10 ms linear rise followed by a 240 ms exponential fade. We applied an

additional linear fade to the final 10 ms of the tone so that the amplitude ended at zero. Finally, we normalized the loudness of all tones to 75 dBA using Audacity. For Arduino compatibility, tones were saved as WAV files with a sampling rate of 22 kHz instead of the standard 44.1 kHz (see Apparatus). To account for the reduced sampling rate, we ensured that none of the frequencies used in our tone design (the highest being 10560 Hz, the second overtone of A7) exceeded the Nyquist frequency of our audio (11025 Hz).

#### Apparatus

We conducted audiometry using a Grason-Stadler GSI-61 Clinical Audiometer. During the main experimental task, an Arduino Uno running custom C++ code controlled auditory stimulus presentation and tap detection. The Arduino used two attachments: an Adafruit Wave Shield for audio presentation and an Ohmite FSR01CE force sensitive resistor (FSR) as a tapping pad (see Schultz & van Vugt, 2016). Stimuli were presented over Senheiser HD280 Pro headphones plugged into the Wave Shield, and participants tapped on the FSR. The Arduino communicated over USB with a Windows 7 computer running a Python (version 3.6) program that used the PsychoPy library (Peirce et al., 2019) to control the trial order and to log all data collected. The computer sent the Arduino instructions regarding which experimental condition to use on each trial, and the Arduino returned a timestamp for each stimulus onset, tap onset, and tap release. All text was displayed on a 19-inch Dell 1908FP monitor with a resolution of  $1280 \times 1024$  and a frame rate of 60 Hz.

#### Design

Experiment 1 followed a 6 (Pitch Height)  $\times$  2 (Interonset Interval; IOI) within-subjects design. The pitch of the stimulus varied randomly between trials, and was one of A2 (110 Hz), A3 (220 Hz), A4 (440 Hz), A5 (880 Hz), A6 (1760 Hz), or A7 (3520 Hz) on each trial. The IOI of the synchronization tones also varied randomly between trials, and was either 600 ms (100 BPM) or 400 ms (150 BPM).

#### Procedure

Prior to the main synchronization-continuation task, we collected an audiogram from each participant in a sound-attenuated booth adjacent to the main testing room. Hearing thresholds were tested for pure tones at the frequencies 125 Hz, 250 Hz, 500 Hz, 1000 Hz, 2000 Hz, 4000 Hz, 8000 Hz. We first tested frequencies in ascending order from 1000 Hz to 8000 Hz, then tested in descending order from 1000 Hz to 125 Hz. At each frequency, we measured hearing threshold via a staircase procedure that began at +30 dB HL, reduced by 10 dB for every correct detection (to a minimum of -10 dB HL), and increased by 5 dB for every miss. We averaged the two measurements taken at 1000 Hz to obtain a single threshold value for this frequency.

The participant then returned to the main testing room, and we measured their spontaneous motor tempo by asking them to tap on the FSR with their index finger "at the rate that feels most natural and comfortable" to them. A fixation cross appeared on the screen to indicate when they should begin tapping, and the measurement ended after 30 taps.

We then introduced the participant to the synchronization-continuation task. We informed them that they would hear several tones playing at a steady pace on each trial, and that after several beats they would gain control of the tones so that their tapping would cause the tones to play. We emphasized to the participant that their goals were to first synchronize their taps so that their finger "lands exactly when the next tone will begin", and then to "keep the tones playing at the same steady pace throughout the trial by continuing to tap at the same rate" even after gaining control of the tones.

Each trial consisted of 24 repetitions of a tone, which varied in pitch across trial. A fixation cross preceded the first tone of the trial by a uniformly jittered 1000 to 1500 ms. The first eight tones of the trial (the "synchronization tones") then played at an isochronous IOI of either 600 ms or 400 ms. The remaining 16 tones (the "continuation tones") were instead initiated by the participant's tapping. Continuation tones played 20 ms after the participants' taps, a delay which we introduced in order to help stabilize the transition from synchronization to continuation (Flach, 2005). If the participant tapped while the previous tone was still playing, no new tone would be generated until the participant lifted their finger off the FSR and tapped again. Immediately after the final continuation tone finished playing, the fixation cross disappeared and participants were shown the standard deviation (in milliseconds) of their continuation-phase inter-tap intervals alongside instructions to keep this score as low as possible by tapping steadily (Ammirante et al., 2011). This score remained onscreen for 2 s, after which a blank screen was displayed for 2 s before the next trial began.

Participants completed six practice trials and 120 experimental trials of the synchronization-continuation task. All practice trials used an IOI of 500 ms, and each used a different one of the six pitch height conditions, randomly ordered. The experimental trials were divided into five blocks of 24. Each block contained two trials of each pitch height and IOI combination, randomly ordered. Self-paced breaks were intended to be administered between blocks, but due to a software error were instead administered after the 12<sup>th</sup>, 24<sup>th</sup>, 36<sup>th</sup>, and 48<sup>th</sup> trials.

### *Data Analysis*

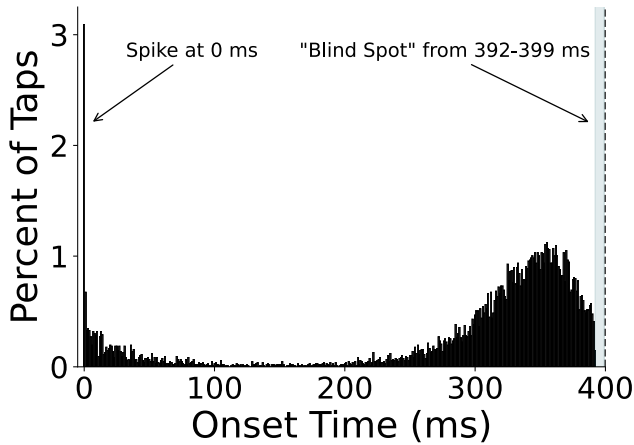
**Tap Debouncing.** To pre-process our tapping data, we first removed any falsely-detected taps through a debouncing procedure. The force sensitive resistor sometimes erroneously detected multiple onsets from a single tap if the participant's finger bounced upon landing, or if the tap pressure

fluctuated above and below the minimum detection threshold during initial contact. To avoid analyzing these false taps and releases, we programmed the Arduino to automatically ignore any below-threshold pressure reading within 20 ms of a tap onset, treating the participant's finger as remaining on the FSR. Similar pressure fluctuations could also occur as the participant lifted their finger off of the resistor; therefore, the Arduino also ignored any above-threshold pressure reading within 80 ms of the previous tap's release, as if the participant's finger remained off the FSR. A review of our tap duration data suggested that some additional false releases occurred up to 30 ms after tap onset, and so were not automatically rejected by the Arduino. Any time the participant's finger remained on the FSR for longer than the 80 ms debounce period, a false tap onset was detected exactly 80 ms after these false releases. We therefore excluded from further analysis any tap that began 80 ms after a tap whose recorded duration was 30 ms or less.

After applying these debouncing methods, we separated taps into synchronization taps and continuation taps. We categorized any tap occurring between the third and ninth tone as a synchronization tap (including the tap that triggered the ninth tone), and any tap occurring after the ninth tone as a continuation tap. We excluded taps before the third tone, as a review of the data suggested that synchronization tended to stabilize during the third inter-stimulus interval.

**Synchronization Tap Processing.** For each synchronization tap, we identified the pair of tones between which it occurred, and calculated the fraction of the stimulus IOI that had elapsed before the tap occurred. We then converted this fraction to a phase value relative to the preceding tone, from 0 to  $2\pi$ . If the tap that generated the first continuation tone occurred later than one IOI after the eighth synchronization tone (i.e., a relative phase greater than  $2\pi$ ), we excluded it from further analysis.

Because the Arduino can only perform one process at a time, it can only read from the FSR in between other operations. As such, longer operations can create "blind spots" in tap detection. In particular, we identified two operations lasting longer than 1 ms: loading an audio file from the Wave Shield's SD card took approximately 6 ms, and initializing audio playback took approximately 2 ms. In Experiment 1, file loading occurred immediately before playback; therefore, whenever the participant tapped within the 8 ms prior to a tone onset, the Arduino would instead detect the tap immediately after tone onset, producing an apparent relative phase of 0. To illustrate, Figure 2 shows the distribution of synchronization tap onset times relative to the preceding tone across all trials with an IOI of 400 ms. A review of this distribution suggests that the majority of taps recorded as occurring at the same millisecond as a tone were actually taps initiated during the preceding blind spot. We therefore excluded from further analysis all synchronization taps with

**Figure 2***Illustration of the Arduino's Pre-Stimulus "Blind Spot"*

*Note.* Distribution of synchronization taps recorded across all trials with an interonset interval of 400 ms. Onset time indicates the number of milliseconds that a tap was detected after the start of the most recent synchronization tone. Recorded taps across most onset times follow a circular-normal distribution; however, the inability of the Arduino to record taps while initializing the next stimulus results in an 8 ms gap (shaded region) leading up to the next tone (dashed line). All taps that begin during this "blind spot" are instead recorded immediately after the next tone begins, resulting in the spike at 0 ms post-stimulus. In Experiment 2, we reduced the pre-stimulus blind spot to 2 ms (see Experiment 2 Apparatus).

an apparent relative phase of 0.

We next converted each tap's phase within its inter-stimulus interval into an asynchrony relative to the tone at which it was most likely targeted. Figure 3 illustrates this conversion process in one example participant. For each participant,  $i$ , we first calculated the circular mean of their tapping phases,  $\mu_i$ , as well as the anti-phase of their average tap,  $\mu_i - \pi$  (the dashed and dotted lines in Figure 3A, respectively). Our conversion method next relies on two assumptions: 1) taps at the mean phase were made in anticipation of the subsequent tone (as participants were instructed), and 2) each person's tap timing is symmetrically distributed around the mean. Under these two assumptions, any taps with a relative phase in the range  $[\mu_i - \pi, 2\pi)$  (i.e., taps to the right of the dotted line in Figure 3A) were most likely targeted at the subsequent tone, and any taps with a relative phase in the range  $(0, \mu_i - \pi)$  (those to the left of the dotted line) were most likely targeted at the preceding tone. To ensure that the first assumption held, we excluded one participant whose mean phase fell closer to the preceding tone than to the subsequent tone and two additional participants with a mean resultant vector length less than 0.45 (indicating poor

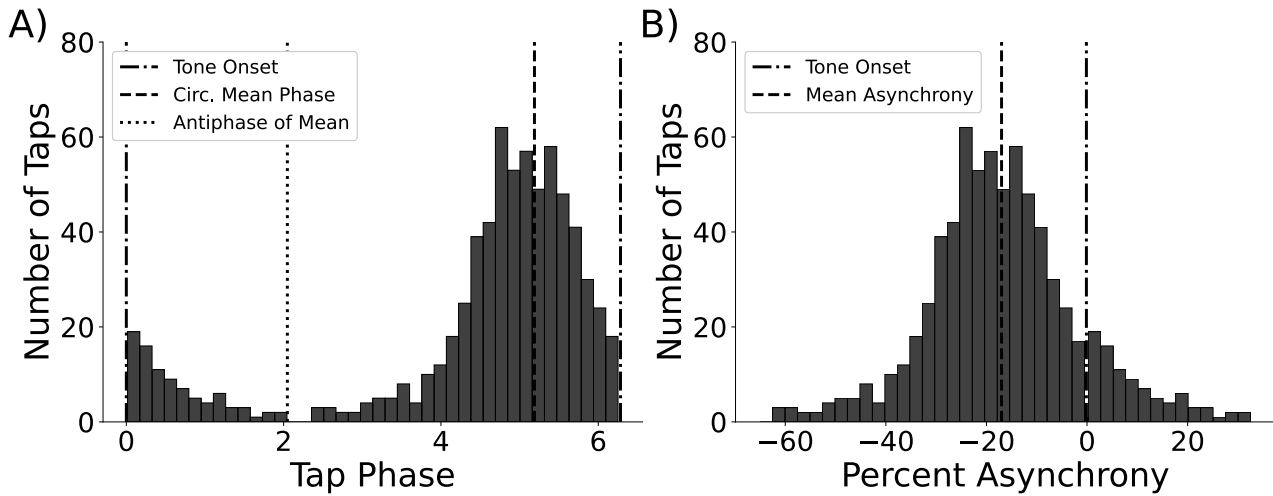
synchronization). Having aligned taps with the tones they most likely targeted, we concluded by calculating the percent of an interonset interval that each tap occurred before or after its target. This produced a percent asynchrony for each tap (Figure 3B), where a negative asynchrony indicates that the tap preceded its target tone and a positive asynchrony indicates the tap occurred after its target.

**Continuation Tap Processing.** For each continuation tap, we calculated the preceding inter-tap interval as the number of milliseconds elapsed since the onset of the previous tap. We then divided the inter-tap interval by the IOI of the synchronization tones on that trial to obtain a score we will refer to as the *relative inter-tap interval*. A relative inter-tap interval of 1 would indicate perfectly accurate continuation tap timing, with the inter-tap interval being equal to the IOI. Scores greater than 1 indicate that the participant tapped slower than the synchronization tones, whereas scores less than 1 indicate faster tapping. To eliminate intervals where the participant paused or tapped excessively quickly, we excluded from further analysis any continuation tap with a relative inter-tap interval greater than 2 or less than 1/2, respectively.

**Audiometry.** As the frequencies tested during the audiogram did not match the fundamental frequencies of our stimuli, we used a cubic spline procedure to interpolate or extrapolate hearing thresholds for each stimulus frequency. To account for the log-linear perception of frequency, we fit the cubic spline to hearing thresholds as a function of the log of frequency, rather than frequency in Hz.

**Statistical Analysis.** We analyzed the effect of pitch on sensorimotor timing using a pair of linear mixed models, one to predict percent asynchrony and one to predict relative inter-tap interval. Each model contained fixed slopes for interonset interval, the linear and quadratic effects of pitch height, as well as the interaction between pitch height and IOI. We fit random participant-level intercepts and slopes for interonset interval, under the assumption that participants would differ in their ability to synchronize with and maintain different tempos.

Each model also included hearing threshold as a covariate, as determined from the participant's audiogram. Although we calibrated all tones to be equally loud for participants with normal hearing, individual hearing loss may still cause some pitches to be perceived as quieter than others. As there is some evidence that loudness can influence perceived tempo, with increasing loudness associated with a faster tempo (Boltz, 2011), differences in perceived loudness across our stimuli introduce a potential confound. For example, the prevalence of high frequency hearing loss may cause extremely high pitches to be perceived as quieter, and therefore slower, than other stimuli. By accounting for any hearing loss in our participants, we can separate the effects of pitch and loudness on sensorimotor timing.

**Figure 3***Example Asynchrony Calculation for One Participant*

*Note.* **A)** The distribution of synchronization tap phases, relative to the preceding tone onset, from one example participant. The dashed line denotes their circular mean tapping phase, while the dotted line indicates the antiphase of their tapping. We treated all tap times that were closer to the preceding stimulus than to the participant's mean tapping phase (i.e., all taps to the left of the antiphase line) as positive asynchronies targeted at the preceding tone. We treated all other tap times as negative asynchronies made in anticipation of the next tone. **B)** The resulting asynchrony values, expressed as a percent of the interonset interval of the stimulus.

To evaluate the significance of all fixed effects, we performed  $F$ -tests using the `lmerTest` package (Kuznetsova, Brockhoff, & Christensen, 2017). In cases where we observed a significant effect of pitch height, we determined whether the linear and/or quadratic terms were significant by using `lmerTest` to perform post-hoc  $t$ -tests with Holm-Bonferroni correction on the slope estimates.

## Results

We begin by discussing the effect of pitch on mean asynchrony during synchronization tapping, and then discuss its effect on the tempo of continuation tapping.

### Synchronization Tapping

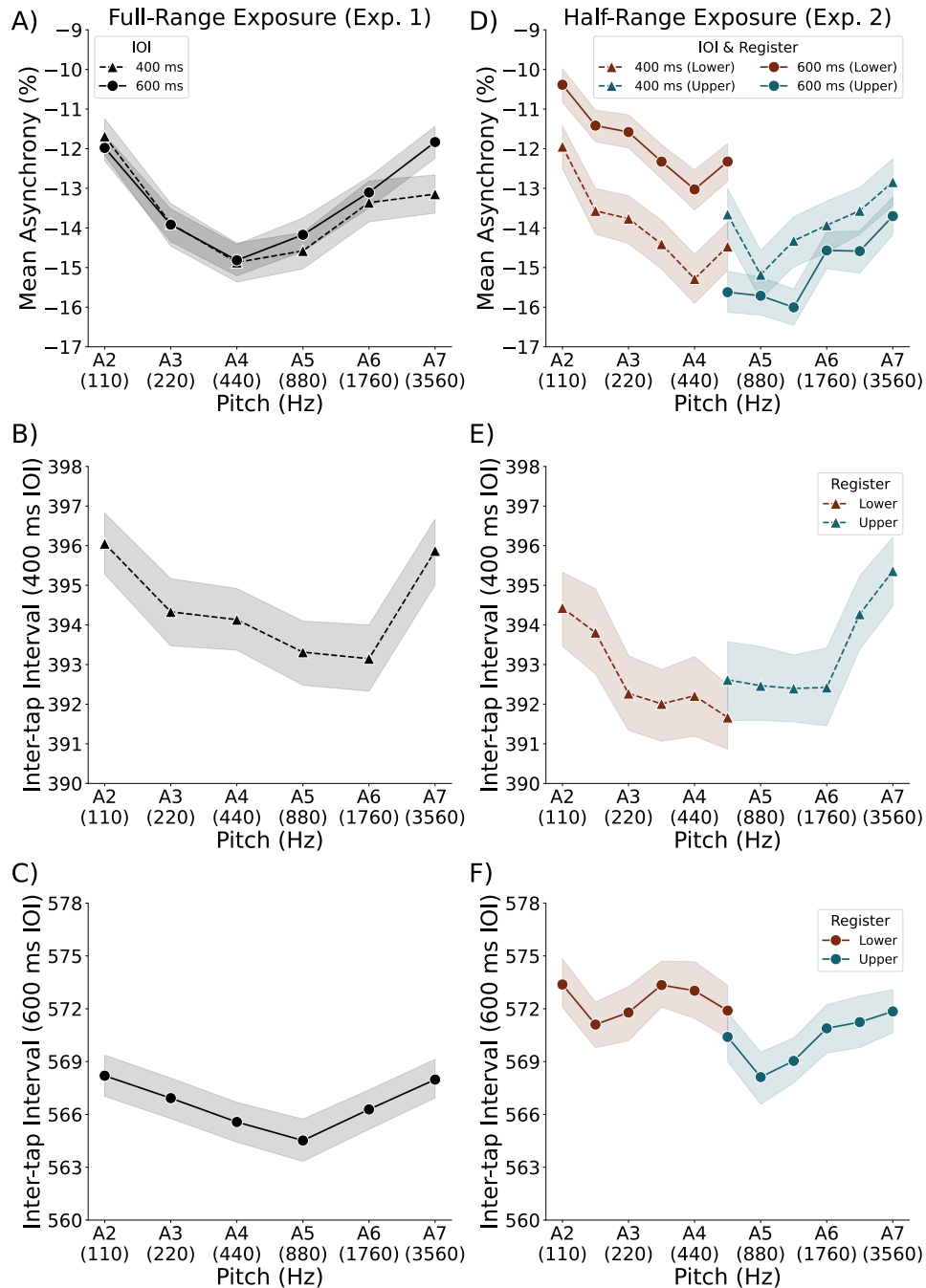
Figure 4A shows mean asynchronies for synchronization tapping to isochronous tones of each combination of pitch and interonset interval, expressed as a percent of that IOI. Larger negative asynchronies indicate earlier tapping relative to the tone being anticipating. Participants tapped earliest when synchronizing to A4 (440 Hz) or A5 (880 Hz) and latest when synchronizing to A2 (110 Hz) or A7 (3520 Hz). Our linear mixed model analysis confirmed that pitch height significantly affected the percent asynchrony of synchronization taps,  $F(2, 381.6) = 35.28$ ,  $p < .001$ . The effect of pitch was characterized by a significant positive quadratic slope,  $t(380.1) = 8.35$ ,  $p_{adj} < .001$ , and a nonsignificant

linear slope,  $t(383.2) = 0.50$ ,  $p_{adj} = .619$ , consistent with the mostly symmetrical U-shape of the data in Figure 4A. The main effect of IOI was nonsignificant,  $F(1, 38.0) = 0.35$ ,  $p = .559$ , suggesting that participants tapped at a consistent percent asynchrony regardless of the IOI of the stimulus. The interaction between IOI and pitch was also nonsignificant,  $F(2, 380.0) = 1.18$ ,  $p = .310$ , indicating that pitch did not differentially affect sensorimotor synchronization at different tempos. Higher (worse) hearing thresholds predicted later tapping on average ( $\beta = 0.034$ ,  $SE = 0.029$ ), but not significantly so,  $F(1, 391.9) = 1.35$ ,  $p = .246$ .

### Continuation Tapping

Figures 4B–C show average inter-tap intervals during continuation tapping that followed synchronization to tones played at 400 ms or 600 ms intervals, respectively. Note that, although we show raw inter-tap intervals in Figure 4 for interpretability, our statistical analysis focused on the ratio between the inter-tap interval and the target IOI. At both tempos, participants tapped slowest after synchronizing to A2 (110 Hz) or A7 (3520 Hz), and fastest after synchronizing to pitches between A4 (440 Hz) and A6 (1760 Hz). Our analysis confirmed that pitch height significantly affected relative inter-tap intervals during continuation tapping,  $F(2, 381.4) = 5.71$ ,  $p = .004$ . Similar to our asynchrony results, the effect of pitch was characterized by a significant positive quadratic

Figure 4

*Effect of Pitch on Sensorimotor Timing*

*Note.* Pitch height exerted a U-shaped effect on sensorimotor timing across the frequency range of 110–3520 Hz, regardless of whether participants heard the full five-octave range (Experiment 1; **A–C**) or tones from only one half of the full range (Experiment 2; **D–F**). **A & D**) Mean asynchrony as a function of the pitch and interonset interval (IOI) of the synchronization tones, expressed as a percent of that IOI. **B & E**) Average number of milliseconds between continuation taps, following synchronization to a 400 ms IOI. **C & F**) Average number of milliseconds between continuation taps, following synchronization to a 600 ms IOI. Shaded bands indicate 95% confidence intervals.



slope,  $t(380.1) = 3.37$ ,  $p_{adj} = .002$ , and a nonsignificant linear slope  $t(382.8) = 0.40$ ,  $p_{adj} = .968$ . Participants tapped slowest after synchronizing to low and extremely high pitches. IOI also significantly affected relative inter-tap interval,  $F(1, 38.0) = 45.16$ ,  $p < .001$ . Participants tapped faster than the synchronization tones at both tempos, but underestimated the IOI more when asked to match the slower, 600 ms IOI. The interaction between IOI and pitch was not significant,  $F(2, 380.0) = 0.10$ ,  $p = .907$ . Higher hearing thresholds predicted slower tapping on average ( $\beta = 2.3 \times 10^{-4}$ ,  $SE = 1.6 \times 10^{-4}$ ), but not significantly so,  $F(1, 390.6) = 2.04$ ,  $p = .154$ .

## Discussion

Experiment 1 successfully replicated the findings of Experiments 1–3 from Pazdera and Trainor (2024) in a synchronization-continuation tapping task. Pitches A2 (110 Hz) and A7 (3520 Hz) produced both the latest synchronization tapping (i.e., smallest negative mean asynchrony; Figure 4A) and the slowest continuation tapping (i.e., largest inter-tap intervals; Figure 4B–C). Meanwhile, A4 (440 Hz) produced the earliest synchronization tapping, and A5–A6 (880–1760 Hz) produced the fastest continuation tapping. Similarly, Pazdera and Trainor (2024) observed that participants perceived A2 and A7 as subjectively slowest (Figure 1A), while the subjectively fastest pitch varied between A4 and A6 across experiments. Observing the same U-shaped relation between pitch and timing in the absence of an explicit decision-making task suggests that pitch biases timing at the level of perception, rather than decision-making—a distinction that could not be made from our previous study.

## Experiment 2

In Experiment 1, we demonstrated that the U-shaped effect of pitch on perceived tempo observed by Pazdera and Trainor (2024) also applies to sensorimotor timing. In Experiment 2, we examined whether the linear increase in perceived tempo with increased pitch, previously seen under conditions where only the lower or upper range of pitches were included (Pazdera & Trainor, 2024, Experiment 5; see Figure 1B), would also be observed for sensorimotor responses. Specifically, we presented each participant with pitches from only the lower half or only the upper half of the full 110–3520 Hz range used in Experiment 1.

## Methods

### Participants

Data for Experiment 2 were collected between May and October 2023, with the COVID-19 safety protocols from Experiment 1 remaining in place for all participants collected before August. Forty-six undergraduate students (34 female,

12 male) from McMaster University completed the experiment for course credit. Ages ranged from 17–24 ( $M = 18.3$ ,  $SD = 1.1$ ). Twenty-two participants (14 female) were randomly assigned to hear lower-register tones only, while the remaining 24 (20 female) were assigned to hear upper-register tones only. An additional six participants completed the experiment, but were excluded (four in the lower-register condition and two in the upper-register condition; see Data Analysis).

### Materials

We generated all tones according to the same procedure used in Experiment 1, and all text was displayed in the same font as before.

### Apparatus

All hardware was identical to that used in Experiment 1. We updated the Arduino routine to pre-load each new tone immediately after the previous tone stopped playing, instead of immediately before playing the new tone. This change reduced the pre-stimulus "blind spot", during which the Arduino could not read from the tapping pad (see Experiment 1 Data Analysis), from approximately 8 ms to 2 ms. Although the blind spot cannot be eliminated entirely without a multiple-Arduino setup, its impact can be minimized by moving the majority of the audio processing time close to the offbeat, when participants are unlikely to tap. We also added the ability for the Arduino to send the computer information about the peak pressure of each tap and the timestamp of that peak pressure. Although we do not report on the tapping pressure data in the present manuscript, we have included these data in our open-access dataset.

### Design

Experiment 2 followed a 2 (Register)  $\times$  6 (Pitch Height)  $\times$  2 (Interonset Interval) mixed design. Participants were randomly assigned to hear six unique pitches from either the lower half or upper half of the pitch range used in Experiment 1. The pitch of the stimulus varied between trials, with participants assigned to the lower register hearing one of A2 (110 Hz), D#3 (155.6 Hz), A3 (220 Hz), D#4 (311.1 Hz), A4 (440 Hz), or D#5 (622.3 Hz) on each trial. Those assigned to the upper register instead heard one of D#5 (622.3 Hz), A5 (880 Hz), D#6 (1244.5 Hz), A6 (1760 Hz), D#7 (2489.0 Hz), or A7 (3520 Hz) on each trial. The IOI of the synchronization tones again varied between trials, and was either 600 ms (100 BPM) or 400 ms (150 BPM).

### Procedure

We again collected an audiogram from each participant via the same procedure as Experiment 1, with the exception that participants assigned to the lower register only received

the descending half of the audiogram (from 1000 Hz to 125 Hz) and participants assigned to the upper register only received the ascending half of the audiogram (from 1000 Hz to 8000 Hz). We collected only half of the audiogram in order to limit participants' exposure to stimuli from the register they were not assigned to. The spontaneous motor tempo and synchronization-continuation tasks followed identical procedures to those of Experiment 1, with two exceptions. First, participants heard a different set of six unique pitches across trials depending on which register they were assigned to (see Design). Second, we corrected the positioning of the self-paced breaks, such that there were always 24 trials between breaks.

### Data Analysis

We processed our tapping and audiometry data using the same methods as Experiment 1. We excluded five participants for poor synchronization (mean resultant vector length less than .45), and one additional participant for rushing through the continuation tapping task. A further three participants showed anomalous synchronization or continuation tapping behavior for the first one to two blocks of the experiment, but performed the task correctly on all remaining blocks. For these participants, we excluded only the affected blocks. We performed the same statistical analyses as in Experiment 1, with the exception that we fit separate linear mixed models for each of the two register conditions, as each register used a unique set of pitch heights.

### Results

We present our synchronization tapping results first for participants assigned to each register, followed by our continuation tapping results for each group.

#### Synchronization Tapping

Figure 4D shows mean asynchronies for each combination of pitch and interonset interval in Experiment 2, when participants were exposed to tones from only one half of the full range of pitches used in Experiment 1. In general, participants assigned to the lower register (110 - 622.3 Hz) tapped earlier while synchronizing to higher pitches, whereas participants assigned to the upper register (622.3 Hz - 3520 Hz) tapped later while synchronizing to higher pitches. Looking across registers in Figure 4D, there appears to a reversal in direction just above A4 (440 Hz) or below A5 (880 Hz).

Among participants assigned to the lower register, pitch significantly affected the percent asynchrony of synchronization tapping,  $F(2, 220.7) = 20.53$ ,  $p < .001$ . The effect of pitch was characterized by both a significant negative linear slope,  $t(221.5) = -5.78$ ,  $p_{adj} < .001$ , and a significant positive quadratic slope,  $t(219.9) = 2.83$ ,  $p_{adj} = .005$ , matching the hook-like shape of the lower-register data. Unlike

in Experiment 1, tempo significantly affected percent asynchrony in the lower register,  $F(1, 22.0) = 5.24$ ,  $p = .032$ , such that participants tapped at an earlier phase when synchronizing to a 400 ms IOI, compared to a 600 ms IOI. However, the interaction between tempo and pitch was non-significant,  $F(2, 219.9) = 0.50$ ,  $p = .606$ , suggesting that pitch again affected percent asynchrony similarly across tempos. Higher hearing thresholds predicted later tapping on average ( $\beta = 0.029$ ,  $SE = 0.043$ ), but not significantly so,  $F(1, 229.4) = 0.46$ ,  $p = .497$ .

Among participants assigned to the upper register, pitch also significantly affected percent asynchrony,  $F(2, 240.4) = 12.37$ ,  $p < .001$ . The effect of pitch was characterized by both a significant positive linear slope,  $t(240.4) = 4.31$ ,  $p_{adj} < .001$ , and a significant positive quadratic slope,  $t(240.5) = 2.69$ ,  $p_{adj} = .008$ , consistent with the check-mark shape of the upper-register data. IOI did not significantly affect percent asynchrony,  $F(1, 24.0) = 1.37$ ,  $p = .253$ , and the interaction between IOI and pitch was not significant,  $F(2, 240.0) = 0.43$ ,  $p = .651$ . Higher hearing thresholds significantly predicted later tapping in the upper register ( $\beta = 0.093$ ,  $SE = 0.031$ ),  $F(1, 248.2) = 8.95$ ,  $p = .003$ .

#### Continuation Tapping

Figures 4E–F show average inter-tap intervals for 400 ms and 600 ms IOI trials, respectively, during Experiment 2. Similar to Experiment 1, participants tapped faster than the target tempo in both the 400 ms and 600 ms IOI conditions, but tapped closer to the correct tempo in the 400 ms IOI condition. Participants assigned to hear lower-register tones generally tapped faster after synchronizing to higher pitched tones, whereas participants assigned to the upper register generally tapped slower after synchronizing to higher pitched tones.

Among participants assigned to the lower register, our linear mixed modeling analysis indicated that pitch significantly affected relative inter-tap intervals during continuation tapping,  $F(2, 220.5) = 5.11$ ,  $p = .007$ . The effect of pitch was characterized by a significant negative linear slope,  $t(221.1) = -3.13$ ,  $p_{adj} = .004$ , and a nonsignificant positive quadratic slope  $t(220.0) = 0.69$ ,  $p_{adj} = .494$ . Within the lower register, participants tapped significantly faster after synchronizing to higher pitches. Tempo also significantly affected relative inter-tap interval,  $F(1, 22.0) = 21.00$ ,  $p < .001$ , with participants underestimating 600 ms IOIs to a greater extent than 400 ms ones. Although Figures 4E–F suggest a clearer effect of pitch at 400 ms than at 600 ms, the interaction between tempo and pitch was not significant,  $F(2, 220.0) = 1.94$ ,  $p = .146$ . Lastly, higher hearing thresholds predicted significantly faster tapping on average ( $\beta = -8.2 \times 10^{-4}$ ,  $SE = 2.3 \times 10^{-4}$ ),  $F(1, 226.8) = 12.49$ ,  $p < .001$ .

Among participants assigned to the upper register,

pitch also significantly affected relative inter-tap intervals,  $F(2, 240.1) = 6.17, p = .002$ . The effect of pitch was characterized by a significant positive linear slope,  $t(240.1) = 3.05, p_{adj} = .005$ , and a nonsignificant positive quadratic slope  $t(240.1) = 1.90, p_{adj} = .058$ . Opposite to the pattern observed among participants in the lower register, participants in the upper register tapped slower after synchronizing to higher pitches. Tempo again significantly affected relative inter-tap interval,  $F(1, 24.0) = 50.51, p < .001$ , in a pattern consistent with that of participants in the lower register. The interaction between tempo and pitch was nonsignificant,  $F(2, 240.0) = 0.39, p = .680$ . Hearing thresholds did not significantly predict relative inter-tap interval among participants in the upper register ( $\beta = 4.0 \times 10^{-5}, SE = 1.3 \times 10^{-4}$ ),  $F(1, 243.1) = 0.10, p = .752$ .

## Discussion

Unlike in Experiment 5 of our previous subjective rating study (Pazdera & Trainor, 2024; Figure 1B), exposing participants to tones from only the upper half of the full 110–3520 Hz pitch range did not cause extremely high pitches to be perceived as fast; rather, they were perceived as slower than medium pitches (Figure 4D–F). Within the lower register, participants tapped earlier and faster to higher pitches, as expected. Within the upper register, however, participants tapped later and slower to higher pitches, consistent with Experiment 1 (Figure 4A–C). Asynchrony also showed significant positive quadratic effects of pitch in both registers, as the relation between pitch and sensorimotor timing reversed direction above 440 Hz in the lower register and below 880 Hz in the upper register. The significant quadratic term further highlights the failure to eliminate the overall U-shaped relation between pitch and perceived timing by restricting the pitch range. The effects of pitch were even similar in scale to those observed in Experiment 1, with mean asynchrony differing across pitches by about 3% of the interonset interval and inter-tap intervals differing by less than 1%.

Whatever factor previously caused the change in subjective tempo ratings for extremely high pitches in exclusively upper-octave contexts (Pazdera & Trainor, 2024) does not appear to carry over to sensorimotor timing. Accordingly, we conclude that the U-shaped relation between pitch and timing operates at the level of perception and depends on absolute pitch height, rather than relative pitch height within a context.

## General Discussion

Across two synchronization-continuation tapping experiments, we investigated how the pitch of a rhythmic auditory stimulus influences sensorimotor timing. Testing the same five-octave range of pitches as in the perception study of Pazdera and Trainor (2024), we found the same U-shaped relation between pitch and timing. We observed the earliest

and fastest sensorimotor timing for the same range of pitches (between 440–1760 Hz) that a separate group of participants rated as subjectively fastest in our previous study. Below this range, higher pitches were consistently associated with faster perceived timing; above this range, higher pitches were consistently associated with slower perceived timing.

We previously argued based on Pazdera and Trainor (2024) Experiment 5 that the U-shaped relation depends on pitch height relative to the lowest pitches in a context. We suggested that pitch might be positively correlated with perceived tempo within a range of two to three octaves of baseline—perhaps tied to human vocal ranges (Kuhn et al., 1979)—before reversing direction after exceeding that range. Experiment 2 of the present experiment instead supports the hypothesis that the U-shaped relation between pitch and tempo perception depends on absolute pitch. Given that we have now observed slow timing at A7 (3520 Hz) in six experiments, the simplest explanation is that the U-shaped effect does depend on absolute pitch, and that the unusual effects in our previous subjective rating study (Figure 1B) resulted from another unidentified factor. Further work is needed to determine why we observed a qualitatively different effect in Pazdera and Trainor (2024) Experiment 5 compared to all six other experiments.

## Attenuated Effects on Continuation Tapping

Although pitch significantly affected both mean asynchrony and continuation tapping tempo, we found a larger effect of pitch on the former in both experiments. Mean asynchrony varied across octaves by approximately 3% of the interonset interval of the pacing signal, whereas inter-tap intervals varied by less than 1%. For comparison, our previous subjective rating study found that perceived tempo varied across octaves by about 4–5% (Figure 1A; Pazdera & Trainor, 2024), similar to the scale of the effect on asynchrony in the present study. This pattern of results suggests that one or more factors attenuated the effect of pitch during continuation tapping.

One possible explanation is that providing auditory feedback allowed participants to recognize their own incorrect timing and correct for the majority of the pitch-induced bias. Specifically, when the initial transition from synchronization to continuation happens, the participant can hear the stimulus sequence suddenly change tempo. As the task instructions emphasized keeping the stimuli playing "at the same steady pace," participants should respond by adjusting their taps in such a way as to undo their initial bias.

For example, if a participant perceived a particular 600 ms stimulus as 3% faster than it truly is due to pitch-induced bias, they might begin tapping at 582 ms intervals to match their internal representation of the tempo. However, this will cause the stimulus sequence to speed up from a 600 ms IOI to a 582 ms IOI, which—with a +3% tempo bias—will be

perceived as a shift from 582 to 565 ms. If participants are able to recognize this shift as a result of their own timing error, we might expect them to correct the majority of this error over the next few beats (Mates, 1994b, 1994a; Michon, 1967), leaving relatively little effect of pitch on their inter-tap intervals. Accordingly, we may have observed a larger effect during continuation tapping if performed in the absence of auditory feedback. Without feedback, we might expect the participant to simply continue trying to maintain the 582 ms interval they originally perceived, perhaps while also drifting towards their spontaneous motor tempo (Roman et al., 2023; Zamm, Wang, & Palmer, 2018).

Alternatively, our data may indicate that pitch affects the relative phase of neural entrainment to the beat more than its tempo. During an MEG study investigating the effect of pitch change on neural entrainment, Herrmann et al. (2013) found that pitch shifted the relative phase of entrained oscillations, without significantly changing the frequency of those oscillations. Furthermore, a classification analysis they conducted found that pitch-induced phase shifts predicted subjective ratings of tempo change, potentially bridging the gap between neural dynamics and subjective tempo; however, it remains an open question why a shift in neural phase without a change in frequency would be consciously experienced as a faster tempo. Regardless, if we assume that sensorimotor timing reflects underlying neural dynamics, our data might be interpreted as a behavioral consequence of pitch altering the phase of neural entrainment, shifting asynchrony while only slightly altering inter-tap intervals.

Herrmann et al. (2013) proposed that this shift in the relative phase of entrainment is consistent with the brain recruiting oscillators with different spontaneous frequencies to track stimuli with different pitches. A subsequent dynamical systems analysis by Kim and Large (2015) supports the plausibility of this account. Their simulations reveal that when a neural oscillator entrains to a frequency that differs from its own natural frequency, the difference between these two frequencies biases the relative phase of entrainment. Therefore, if the pitch of a rhythmic stimulus affected which neurons in a gradient frequency network (Large et al., 2010, 2015) responded to it, the phase of entrainment might vary with pitch, even though the network remained frequency-locked to the true stimulus tempo. One simulation by Large (2000) tested such a model, in which lower-pitched stimuli were more strongly coupled to neural oscillators with slower natural frequencies. He found that such a model better predicted human synchronization to music than a model in which all pitches were coupled to all oscillators equally. A similar modeling approach may be able to account for the results of the present study, and we believe that future work should focus on incorporating pitch into rhythm perception modeling.

### Slower Timing or Better Timing?

One limitation of our study is that our sensorimotor task cannot differentiate slower timing from more accurate timing. This confound arises because humans exhibit a general tendency to tap with a negative mean asynchrony and speed up during continuation tapping (Flach, 2005; Repp, 2005), and these same patterns arise in our data (see Figure 4). Therefore, later synchronization tapping also means that participants' taps landed closer to the stimulus onsets. Similarly, slower continuation tapping means that participants deviated less from the target tempo. There has been considerable attention in previous literature regarding a possible superiority of lower pitches for rhythm perception (Hove, Keller, & Krumhansl, 2007; Hove, Marie, Bruce, & Trainor, 2014; Lenc, Keller, Varlet, & Nozaradan, 2018; Repp, 2003) and for inducing spontaneous entrained movement or the urge to move (Cameron et al., 2022; Stupacher, Hove, & Janata, 2016; Varlet, Williams, & Keller, 2020). If this superiority exists, slower timing for A2 (110 Hz) in our study could be due to improved timing accuracy rather than biased timing.<sup>1</sup>

Such an account of our results leaves open the question of why, within the upper register we tested (622.3–3520 Hz), timing was slower/more accurate at higher pitches, rather than lower pitches. If we assume our results were an effect of some pitches producing better timing accuracy than others, it would imply that frequencies as high as 3520 Hz produce synchronization as strong as low frequencies near 110 Hz. At least one simulation study has supported this possibility: Zuk, Carney, and Lalor (2018) used a model of the auditory nerve and midbrain to simulate neural synchrony in response to a variety of periodic sounds. In a supplementary analysis, they found a U-shaped relation between stimulus frequency and synchronization strength. Simulated neural synchrony was weakest for tones between 500–1000 Hz, and strongest for tones below 250 Hz or above 2000 Hz (see Zuk et al., 2018, Supplementary Figure 3), which closely aligns with the pattern in our data. We (Pazdera & Trainor, 2024) previously discounted the strength of neural synchrony as an explanation for the effect of pitch on subjective tempo, due to the elimination of the U-shaped relation when participants only heard tones from the upper register (Figure 1B). However, given the persistence of the U-shaped effect on sensorimotor timing under similar conditions in the present study (Figure 4D–F), the Zuk et al. (2018) simulation would provide a parsimonious account of our data. One possible explanation for the difference between Experiment 2 of the present study and Experiment 5 of the Pazdera and Trainor (2024) study is that there are multiple processes by which pitch af-

<sup>1</sup>However, see Wojtczak, Mehta, and Oxenham (2017) for a counter-argument that the proposed low-pitch superiority for rhythm might be due to a timing bias, rather than improved accuracy.

fects perceived timing. Specifically, a top-down, learned correlation between higher pitches and faster timing may influence decision making, while a bottom-up U-shaped effect influences rhythmic entrainment.

In order to differentiate a learned tempo bias from an intrinsic property of neural dynamics, future research might test whether new correlations between pitch and timing can be learned through novel musical exposure. Boltz (1998, 2011) favored an imputed timing hypothesis, in which the brain learns real-world correlations between pitch and tempo and imposes this expected timing onto the rhythms we hear, similar to a Bayesian prior (e.g., Cannon, 2021; Vuust & Witek, 2014). Previous research suggests that humans implicitly learn both the melodic (Bharucha, 1987; Krumhansl & Kessler, 1982; Trainor & Trehub, 1992, 1994) and rhythmic structure (Jacoby & McDermott, 2017; Jacoby et al., 2024) underlying their native musical culture, and that they can learn a new musical grammar even within a short period of exposure (Loui, Wessel, & Kam, 2010; Loui, 2012; Rohrmeier, Rebuschat, & Cross, 2011). However, the learning of cross-dimensional priors has received little investigation. Therefore, it would be useful to perform a direct test of whether people can learn—and have their timing biased by—novel pitch-timing correlations.

Real-world correlations between pitch and timing in music also require more exploration. One corpus analysis found that ordinally lower parts in polyphonic Western music tend to have fewer notes than the higher parts they accompany, and that higher-pitched instruments tend to play faster during solos than lower-pitched instruments (Broze & Huron, 2013). However, further analysis of cross-cultural corpora would be useful for determining whether the correlations between pitch and timing vary across cultures, and whether there exists either a monotonic or U-shaped relation between pitch and timing that might explain the biases we have observed (Pazdera & Trainor, 2023, 2024).

### Conclusion

Regardless of whether the effect of pitch on perceived timing derives from a learned perceptual bias or variability in synchronization strength, the present study makes it clear that pitch affects sensorimotor synchronization, and that models of rhythm perception should be extended to account for the influence of pitch.

### Declarations

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#### Conflicts of interest

The authors have no conflicting financial or non-financial interests to disclose.

#### Ethics approval

This study was performed in line with the principles of the Declaration of Helsinki. Approval for the present research was granted by the McMaster Research Ethics Board (No. 2609).

#### Consent to participate

All participants provided informed consent prior to their participation in our study.

#### Open practices statement

All data, code, and stimuli from our experiments are publicly available on the Open Science Framework at <https://osf.io/7bptg/>, as well as on GitHub at <https://github.com/jpazdera/IllusoryMotor>.

#### Author Contributions

**Conceptualization:** JKP, LJT

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**Formal analysis:** JKP

**Funding acquisition:** LJT

**Investigation:** JKP

**Methodology:** JKP, LJT

**Project administration:** JKP, LJT

**Resources:** LJT

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**Supervision:** LJT

**Visualization:** JKP

**Writing – original draft:** JKP

**Writing – review & editing:** JKP, LJT

#### References

- Ammirante, P., & Thompson, W. F. (2010). Melodic accent as an emergent property of tonal motion. *Empirical Musicology Review*, 5(3), 94–107. doi: 10.18061/1811/47559
- Ammirante, P., & Thompson, W. F. (2012). Continuation tapping to triggered melodies: Motor resonance effects of melodic motion. *Experimental Brain Research*, 216(1), 51–60. doi: 10.1007/s00221-011-2907-5

- Ammirante, P., Thompson, W. F., & Russo, F. A. (2011). Ideomotor effects of pitch on continuation tapping. *Quarterly Journal of Experimental Psychology*, *64*(2), 381–393. doi: 10.1080/17470218.2010.495408
- Bharucha, J. J. (1987). Music cognition and perceptual facilitation: A connectionist framework. *Music Perception*, *5*(1), 1–30. doi: 10.2307/40285384
- Boasson, A., & Granot, R. (2012). Melodic direction's effect on tapping. In *Proceedings of the 12th International Conference on Music Perception and Cognition and the 8th Triennial Conference of the European Society for the Cognitive Sciences of Music* (pp. 110–119). Thessaloniki, Greece.
- Boasson, A., & Granot, R. (2019). Short latency effects of auditory frequency change on human motor behavior. *Auditory Perception & Cognition*, *2*(1–2), 98–128. doi: 10.1080/25742442.2019.1698264
- Boltz, M. G. (1998). Tempo discrimination of musical patterns: Effects due to pitch and rhythmic structure. *Perception & Psychophysics*, *60*(8), 1357–1373. doi: 10.3758/bf03207998
- Boltz, M. G. (2011). Illusory tempo changes due to musical characteristics. *Music Perception*, *28*(4), 367–386. doi: 10.1525/mp.2011.28.4.367
- Boltz, M. G. (2017). Memory for vocal tempo and pitch. *Memory*, *25*(10), 1309–1326. doi: 10.1080/09658211.2017.1298808
- Bose, A., Byrne, Á., & Rinzel, J. (2019). A neuromechanistic model for rhythmic beat generation. *PLOS Computational Biology*, *15*(5), e1006450. doi: 10.1371/journal.pcbi.1006450
- Broze, Y., & Huron, D. (2013). Is higher music faster? Pitch–speed relationships in Western compositions. *Music Perception*, *31*(1), 19–31. doi: 10.1525/mp.2013.31.1.19
- Cameron, D. J., Dotov, D., Flaten, E., Bosnyak, D., Hove, M. J., & Trainor, L. J. (2022). Undetectable very-low frequency sound increases dancing at a live concert. *Current Biology*, *32*(21), R1222–R1223. doi: 10.1016/j.cub.2022.09.035
- Cannon, J. (2021). Expectancy-based rhythmic entrainment as continuous Bayesian inference. *PLOS Computational Biology*, *17*(6), e1009025. doi: 10.1371/journal.pcbi.1009025
- Cohen, J., Hansel, C. E. M., & Sylvester, J. D. (1953). A new phenomenon in time judgment. *Nature*, *172*(4385), 901–901. doi: 10.1038/172901a0
- Cohen, J., Hansel, C. E. M., & Sylvester, J. D. (1954). Interdependence of temporal and auditory judgments. *Nature*, *174*(4431), 642–644. doi: 10.1038/174642a0
- Collier, W. G., & Hubbard, T. L. (1998). Judgments of happiness, brightness, speed and tempo change of auditory stimuli varying in pitch and tempo. *Psychomusicology: A Journal of Research in Music Cognition*, *17*(1–2), 36–55. doi: 10.1037/h0094060
- Egger, S. W., Le, N. M., & Jazayeri, M. (2020). A neural circuit model for human sensorimotor timing. *Nature Communications*, *11*(1), 1–14. doi: 10.1038/s41467-020-16999-8
- Flach, R. (2005). The transition from synchronization to continuation tapping. *Human Movement Science*, *24*(4), 465–483. doi: 10.1016/j.humov.2005.09.005
- Friston, K. (2010). The free-energy principle: A unified brain theory? *Nature Reviews Neuroscience*, *11*(2), 127–138. doi: 10.1038/nrn2787
- Gordon, M. S., & Ataucusi, A. (2021). Continuous sliding frequency shifts produce an illusory tempo drift. *JASA Express Letters*, *1*(5), 053202. doi: 10.1121/10.0005001
- Gámez, J., Yc, K., Ayala, Y. A., Dotov, D., Prado, L., & Merchant, H. (2018). Predictive rhythmic tapping to isochronous and tempo changing metronomes in the nonhuman primate. *Annals of the New York Academy of Sciences*, *1423*(1), 396–414. doi: 10.1111/nyas.13671
- Henry, M. J., & McAuley, J. D. (2013). Perceptual distortions in pitch and time reveal active prediction and support for an auditory pitch-motion hypothesis. *PLoS ONE*, *8*(8), e70646. doi: 10.1371/journal.pone.0070646
- Herrmann, B., Henry, M. J., Grigutsch, M., & Obleser, J. (2013). Oscillatory phase dynamics in neural entrainment underpin illusory percepts of time. *Journal of Neuroscience*, *33*(40), 15799–15809. doi: 10.1523/jneurosci.1434-13.2013
- Herrmann, B., Henry, M. J., Scharinger, M., & Obleser, J. (2014). Supplementary motor area activations predict individual differences in temporal-change sensitivity and its illusory distortions. *NeuroImage*, *101*, 370–379. doi: 10.1016/j.neuroimage.2014.07.026
- Hove, M. J., Keller, P. E., & Krumhansl, C. L. (2007). Sensorimotor synchronization with chords containing tone-onset asynchronies. *Perception & Psychophysics*, *69*(5), 699–708. doi: 10.3758/bf03193772
- Hove, M. J., Marie, C., Bruce, I. C., & Trainor, L. J. (2014). Superior time perception for lower musical pitch explains why bass-ranged instruments lay down musical rhythms. *Proceedings of the National Academy of Sciences*, *111*(28), 10383–10388. doi: 10.1073/pnas.1402039111
- Jacoby, N., & McDermott, J. H. (2017). Integer ratio priors on musical rhythm revealed cross-culturally by iterated reproduction. *Current Biology*, *27*(3), 359–370. doi: 10.1016/j.cub.2016.12.031
- Jacoby, N., Polak, R., Grahn, J. A., Cameron, D. J., Lee, K. M., Godoy, R., ... McDermott, J. H. (2024).

- Commonality and variation in mental representations of music revealed by a cross-cultural comparison of rhythm priors in 15 countries. *Nature Human Behaviour*. doi: 10.1038/s41562-023-01800-9
- Jones, M. R. (1976). Time, our lost dimension: Toward a new theory of perception, attention, and memory. *Psychological Review*, 83(5), 323–355. doi: 10.1037/0033-295x.83.5.323
- Kim, J. C., & Large, E. W. (2015). Signal processing in periodically forced gradient frequency neural networks. *Frontiers in Computational Neuroscience*, 9. doi: 10.3389/fncom.2015.00152
- Koelsch, S., Vuust, P., & Friston, K. (2019). Predictive processes and the peculiar case of music. *Trends in Cognitive Sciences*, 23(1), 63–77. doi: 10.1016/j.tics.2018.10.006
- Krumhansl, C. L., & Kessler, E. J. (1982). Tracing the dynamic changes in perceived tonal organization in a spatial representation of musical keys. *Psychological Review*, 89(4), 334–368. doi: 10.1037/0033-295x.89.4.334
- Kuhn, T. L., Wachhaus, G., Moore, R. S., & Pantle, J. E. (1979). Undergraduate nonmusic major vocal ranges. *Journal of Research in Music Education*, 27(2), 68–75. doi: 10.2307/3344893
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13). doi: 10.18637/jss.v082.i13
- Large, E. W. (2000). On synchronizing movements to music. *Human Movement Science*, 19(4), 527–566. doi: 10.1016/s0167-9457(00)00026-9
- Large, E. W., Almonte, F. V., & Velasco, M. J. (2010). A canonical model for gradient frequency neural networks. *Physica D: Nonlinear Phenomena*, 239(12), 905–911. doi: 10.1016/j.physd.2009.11.015
- Large, E. W., Herrera, J. A., & Velasco, M. J. (2015). Neural networks for beat perception in musical rhythm. *Frontiers in Systems Neuroscience*, 9, 159. doi: 10.3389/fnsys.2015.00159
- Large, E. W., Roman, I., Kim, J. C., Cannon, J., Pazdera, J. K., Trainor, L. J., ... Bose, A. (2023). Dynamic models for musical rhythm perception and coordination. *Frontiers in Computational Neuroscience*, 17. doi: 10.3389/fncom.2023.1151895
- Large, E. W., & Snyder, J. S. (2009). Pulse and meter as neural resonance. *Annals of the New York Academy of Sciences*, 1169(1), 46–57. doi: 10.1111/j.1749-6632.2009.04550.x
- Lenc, T., Keller, P. E., Varlet, M., & Nozaradan, S. (2018). Neural tracking of the musical beat is enhanced by low-frequency sounds. *Proceedings of the National Academy of Sciences*, 115(32), 8221–8226. doi: 10.1073/pnas.1801421115
- Loui, P. (2012). Learning and liking of melody and harmony: Further studies in artificial grammar learning. *Topics in Cognitive Science*, 4(4), 554–567. doi: 10.1111/j.1756-8765.2012.01208.x
- Loui, P., Wessel, D. L., & Kam, C. L. H. (2010). Humans rapidly learn grammatical structure in a new musical scale. *Music Perception*, 27(5), 377–388. doi: 10.1525/mp.2010.27.5.377
- Mates, J. (1994a). A model of synchronization of motor acts to a stimulus sequence: II. stability analysis, error estimation and simulations. *Biological Cybernetics*, 70(5), 475–484. doi: 10.1007/bf00203240
- Mates, J. (1994b). A model of synchronization of motor acts to a stimulus sequence: I. timing and error corrections. *Biological Cybernetics*, 70(5), 463–473. doi: 10.1007/bf00203239
- Michon, J. A. (1967). *Timing in temporal tracking*. Soesterberg, Netherlands: Institute for Perception RVO-TNO.
- Palmer, C., & Demos, A. P. (2022). Are we in time? How predictive coding and dynamical systems explain musical synchrony. *Current Directions in Psychological Science*, 31(2), 147–153. doi: 10.1177/09637214211053635
- Patel, A. D., Iversen, J. R., Bregman, M. R., & Schulz, I. (2009a). Experimental evidence for synchronization to a musical beat in a nonhuman animal. *Current Biology*, 19(10), 827–830. doi: 10.1016/j.cub.2009.03.038
- Patel, A. D., Iversen, J. R., Bregman, M. R., & Schulz, I. (2009b). Studying synchronization to a musical beat in nonhuman animals. *Annals of the New York Academy of Sciences*, 1169(1), 459–469. doi: 10.1111/j.1749-6632.2009.04581.x
- Pazdera, J. K., & Trainor, L. J. (2023). Bidirectional interactions of pitch and time. In *Proceedings of the 17th International Conference on Music Perception and Cognition* (pp. 301–306). Tokyo, Japan.
- Pazdera, J. K., & Trainor, L. J. (2024). Pitch-induced illusory percepts of time. *PsyArXiv*. doi: 10.31234/osf.io/6fx87
- Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., ... Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods*, 51(1), 195–203. doi: 10.3758/s13428-018-01193-y
- Repp, B. H. (2003). Phase attraction in sensorimotor synchronization with auditory sequences: Effects of single and periodic distractors on synchronization accuracy. *Journal of Experimental Psychology: Human Perception and Performance*, 29(2), 290–309. doi: 10.1037/0096-1523.29.2.290

- Repp, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin & Review*, *12*(6), 969–992. doi: 10.3758/bf03206433
- Repp, B. H., & Su, Y.-H. (2013). Sensorimotor synchronization: A review of recent research (2006–2012). *Psychonomic Bulletin & Review*, *20*(3), 403–452. doi: 10.3758/s13423-012-0371-2
- Rohrmeier, M., Rebuschat, P., & Cross, I. (2011). Incidental and online learning of melodic structure. *Consciousness and Cognition*, *20*(2), 214–222. doi: 10.1016/j.concog.2010.07.004
- Roman, I. R., Roman, A. S., Kim, J. C., & Large, E. W. (2023). Hebbian learning with elasticity explains how the spontaneous motor tempo affects music performance synchronization. *PLOS Computational Biology*, *19*(6), e1011154. doi: 10.1371/journal.pcbi.1011154
- Schultz, B. G., & van Vugt, F. T. (2016). Tap Arduino: An Arduino microcontroller for low-latency auditory feedback in sensorimotor synchronization experiments. *Behavior Research Methods*, *48*(4), 1591–1607. doi: 10.3758/s13428-015-0671-3
- Schutz, M., & Vaisberg, J. M. (2012). Surveying the temporal structure of sounds used in *Music Perception*. *Music Perception*, *31*(3), 288–296. doi: 10.1525/mp.2014.31.3.288
- Stevens, L. T. (1886). On the time-sense. *Mind*, *43*(11), 393–404.
- Stupacher, J., Hove, M. J., & Janata, P. (2016). Audio features underlying perceived groove and sensorimotor synchronization in music. *Music Perception*, *33*(5), 571–589. doi: 10.1525/mp.2016.33.5.571
- Trainor, L. J., & Trehub, S. E. (1992). A comparison of infants' and adults' sensitivity to Western musical structure. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(2), 394–402. doi: 10.1037/0096-1523.18.2.394
- Trainor, L. J., & Trehub, S. E. (1994). Key membership and implied harmony in Western tonal music: Developmental perspectives. *Perception & Psychophysics*, *56*(2), 125–132. doi: 10.3758/bf03213891
- Varlet, M., Williams, R., & Keller, P. E. (2020). Effects of pitch and tempo of auditory rhythms on spontaneous movement entrainment and stabilisation. *Psychological Research*, *84*, 568–584. doi: 10.1007/s00426-018-1074-8
- Vuust, P., & Witek, M. A. G. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Frontiers in Psychology*, *5*. doi: 10.3389/fpsyg.2014.01111
- Wing, A., & Kristofferson, A. (1973). The timing of interresponse intervals. *Perception & Psychophysics*, *13*(3), 455–460. doi: 10.3758/bf03205802
- Wojtczak, M., Mehta, A. H., & Oxenham, A. J. (2017). Rhythm judgments reveal a frequency asymmetry in the perception and neural coding of sound synchrony. *Proceedings of the National Academy of Sciences*, *114*(5), 1201–1206. doi: 10.1073/pnas.1615669114
- Zamm, A., Wang, Y., & Palmer, C. (2018). Musicians' natural frequencies of performance display optimal temporal stability. *Journal of Biological Rhythms*, *33*(4), 432–440. doi: 10.1177/0748730418783651
- Zuk, N. J., Carney, L. H., & Lalor, E. C. (2018). Preferred tempo and low-audio-frequency bias emerge from simulated sub-cortical processing of sounds with a musical beat. *Frontiers in Neuroscience*, *12*. doi: 10.3389/fnins.2018.00349