



Trajectory formation during sensorimotor synchronization and syncopation to auditory and visual metronomes

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Abstract

Previous work on sensorimotor synchronization has investigated the dynamics of finger tapping and how individual movement trajectories contribute to timing accuracy via asymmetry in movement velocities. The present study investigated sensorimotor synchronization (in-phase) and syncopation (anti-phase) to both an auditory metronome and a visual flashing light at multiple frequencies to understand how individual movement phases contribute to the variability of timekeeping and error correction in different sensory modalities and with different task constraints. Results demonstrate that the proportional time spent in both the upward phase of movement and the holding phase of movement (time spent on the surface of the table) remain relatively invariant across both stimulus modalities and across tapping styles (syncopation and synchronization), but changes with interval duration, increasing as interval duration increases. The time spent in the downward phase of movement did significantly differ across stimulus modality and tapping style, increasing during both visuomotor timing and syncopation, accompanied by a significant decrease in flexion velocity during syncopation. Extension velocity and flexion time were found to be the main contributors to differences between visual and auditory timing, while flexion velocity and flexion time were found to be the main contributors to differences between synchronization and syncopation. No correlations were found between asynchrony and the upward, downward, or holding phases of movement, suggesting the existence of multiple error correction strategies.

Keywords Sensorimotor synchronization · Timing · Asynchrony · Syncopation · Motion capture

Introduction

Sensorimotor synchronization is the process by which humans coordinate their movements to a repetitive stimulus in the environment, most commonly investigated using a simple finger tapping paradigm (for an extensive review on sensorimotor synchronization, see Balasubramaniam 2005; Repp 2005; Repp and Su 2013; Ross and Balasubramaniam 2014; Comstock et al. 2018). Previous studies have focused on understanding the theoretical implications for neuro-entrainment and sensorimotor synchronization to various stimuli, diverging in opinion between the traditional information processing approach (Vorberg and Hambuch

1984; Vorberg and Wing 1996; Schulze and Vorberg 2002; Dumas and Wing 2007; Delignières et al. 2009) and more recent theory from the dynamical systems approach (Ross and Balasubramaniam 2014; Balasubramaniam 2005; Riley and Turvey 2002). Very few studies, however, have investigated the contribution of movement trajectories in the flexion, extension, and holding phases to error correction processes, or have compared these trajectories across visual and auditory modalities (Krause et al. 2010; Hove and Keller 2010 for visuomotor synchronization; Balasubramaniam et al. 2004 for auditory synchronization; Repp 2003; Kurgansky 2008; Hove et al. 2013; Lorås et al. 2012; Sugano et al. 2012). A visual depiction of the three phases of movement comprising a trajectory (flexion, extension, holding) in response to a stimulus is found in Fig. 1. Even fewer studies have clearly addressed differences between synchronization and syncopation, the action of tapping between beats in an isochronous metronome sequence, irrespective of stimulus modality (Balasubramaniam 2005; Mayville et al. 2001).

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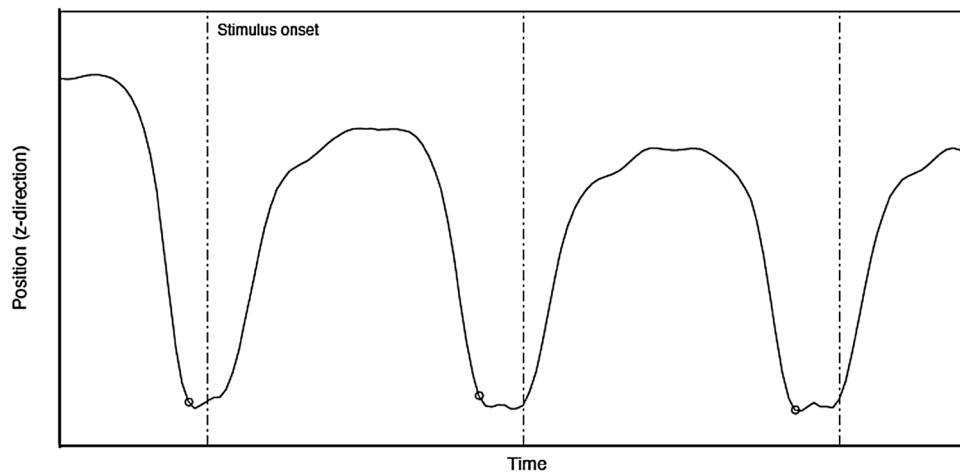


Fig. 1 A typical movement trajectory in response to a metronome, with the upward movement representing extension, the downward movement toward the beat (in synchronization) representing flexion, and the non-movement stabilization referring to the holding phase (the onset of which is marked with an open circle). A custom MATLAB program was built to identify the different trajectory phases of each trial and calculate the time spent in each trajectory. Holding

phase is calculated as the time spent in a non-movement phase when velocity reaches 9.5% of the maximum velocity achieved over the course of an individual trial. Extension is calculated as the time spent when the velocity is greater than the 9.5% minimum and the acceleration of the trajectory is positive. Flexion is calculated as the time spent when velocity is greater than 9.5% of the maximum velocity for that trial and the acceleration of the trajectory is negative

Torre and Balasubramaniam (2009) investigated the extent to which both information processing theory and dynamical systems theory represent timekeeping in the context of auditory sensorimotor synchronization, and if the two theories account for different aspects of timing and synchronization. One way to test this is to control the type of additional incoming sensory stimulation in the presence of an auditory metronome; Torre and Balasubramaniam (2009) compared kinematics between auditory–motor synchronization trials with intermittent haptic feedback (tapping) and auditory–motor trials with continuous haptic feedback (oscillations, i.e., circular finger movements with continuous finger-to-table contact). They showed significantly higher timing variability in synchronized oscillations than synchronized tapping, and suggested that this could be due to peripheral sensory feedback during finger tapping perpetuating consistent error correction processes. Asynchrony is defined as the arrival of the effector in response to a stimulus during timing tasks relative to the onset of the stimulus, and can be either negative or positive (see Repp 2005 for discussion on negative mean asynchrony). The three phases of the finger tap movement are disproportionately adjusted to optimize the trajectory of the finger in order to ensure that the tap occurs on time with the target stimulus. These three tap phases, therefore, are adjusted continuously in order to minimize timing asynchronies. Torre and Balasubramaniam (2009) observed a strong negative correlation between asynchrony and the duration of the immediately following extension cycle for synchronized finger tapping, which suggests that the late arrival of the finger is compensated by a shorter

return phase and conversely for early arrival. Thus, the duration of time spent in extension phase in repetitive timing tasks may help with requirements of precision and accuracy relative to a target event, but it is unknown how the holding phase of movement contributes to consistent error correction. Torre and Balasubramaniam (2009) and Balasubramaniam et al. (2004) both compared the extension and flexion phases of repetitive finger tapping and repetitive finger oscillations, whereas the current study aims to examine the error correction mechanisms involved in tapping synchronization and syncopation in both auditory and visual modalities. Our specific interest is in how the holding phase (i.e., period of non-movement between extension and flexion) contributes to reducing timing errors.

No studies have directly compared the kinematics of synchronization and syncopation across auditory and visual domains. The present study aimed to both replicate and test hypotheses. The first hypothesis was that we would replicate Hove et al. (2013) in the visual modality, supporting that an increase in positive mean asynchrony would be accompanied by a decrease in interval duration. Along with this replication, we expected a marked asymmetry in movement velocity between the flexion and extension phases in both modalities: greater flexion velocity than extension velocity (Balasubramaniam et al. 2004), and a Weber-like increase in variability with increased interval duration (Gibbon 1977). The second hypothesis was that we would find three novel effects: (1) the kinematics of movement would differ between auditory and visual timing because they likely reflect separate underlying neural processes (Comstock and

Balasubramaniam 2018); (2) that kinematics of synchronization and syncopation for visual and auditory metronomes would differ, reflecting separate neural pathways for synchronized and syncopated movements (Mayville et al. 2001); (3) auditory and visual metronome modality would effect correlations between relative asynchrony (the average asynchrony per trial subtracted from the raw asynchrony of each interval) and the three phases of movement. Negative correlations were expected to occur between relative asynchrony and the extension and holding phases with an auditory metronome. Weaker correlations were expected between relative asynchrony and all three phases of movement for visuomotor timing because of proposed weaker temporal coupling for the visuomotor system (Comstock and Balasubramaniam 2018).

Methods

Participants

Seventeen undergraduate participants (15 female, 2 male; aged 18–32 years) at the University of California, Merced, were recruited from the undergraduate subject pool and completed this experiment for course credit. The protocol was approved by the UC Merced Institutional Review Board (IRB) and informed consent was given prior to participation. None of the participants reported having any neurological or motor issues that would prevent them from completing the study. All participants reported normal or corrected vision and no auditory atypicalities. All participants reported being right-handed. Seven participants reported having some musical experience with a range of 2–4 years of experience (additive) with a wide range of instruments, including guitar (2 years), violin (1–2 years), clarinet (2–3 years), and piano (2 years). Musical experience was not found to have main effects on any of the dependent variables analyzed, and thus was not used for further analysis. Dance experience was collected on a pre-experiment questionnaire, but was also not used for further analysis due to large variability of experience across participants.

Procedure

A VICON™ motion capture system with eight Bonita B10 cameras was used for data collection. Data were collected at a sampling rate of 100 Hz. Participants were instructed to sit down at a (740 mm) high table in the center of the recording space. After obtaining informed consent, participants were briefed on the experimental procedures, and were asked to place their right hand on the table in a comfortable position. Participants were outfitted with four Vicon 14 mm reflective markers on their right hand. Markers were

placed on the left ulnar projection of the wrist, the right radial projection of the wrist, and the medial metacarpal for stabilization, and another marker was placed on the distal phalanx of the index finger. Participants were told that they would hear a series of beats, and they would be instructed to either tap along to the beat or tap in between every beat. Participants were also instructed to tap along to the beat of a flashing light or in between flashes. Tapping movements in these visual and auditory conditions were captured in two separate counterbalanced blocks, and the trials within these blocks were randomized by tapping style (i.e., synchronization or syncopation with the stimulus) and interval duration (500, 750, 1000 ms). There were five trials per condition (12 conditions total) with 30 cycles per trial (60 trials total). Participants practiced syncopating and synchronizing with each interval duration for both auditory and visual condition types until they were comfortable with performing the task in all conditions. Our factors for statistical analyses were stimulus modality (auditory vs. visual), musical experience (having two or more years of musical experience vs. having no musical experience), tapping style (synchronization and syncopation), and interval duration (500, 750, and 1000 ms intervals). The experimenter prompted the participant on the correct tapping style before the start of every trial. After the experiment, participants were asked to complete a brief survey collecting demographic information, including musical experience, dance experience, and languages spoken.

Stimuli

Participants were instructed to perform repetitive tapping movements with the right index finger that either synchronized or syncopated with the following stimuli: an auditory metronome or flashing light, delivered at inter-onset intervals of 1000 ms (1 Hz), 750 ms (1.33 Hz) or 500 ms (2 Hz). A 20-ms sine wave metronome with no ramp was created using Sound Studio 4.5.4.7z software and transformed into .wav files (16 bit 44,000 Hz). A period of silence equivalent to the stimulus IOI preceded presentation of the first tone of each auditory stimulus, and then used to space the subsequent tones for a total of 30 tones per trial. Participants listened to the metronome sequences through Sennheiser HD 280pro headphones. The volume of the headphones was set to 70 dB. One participant complained about the volume of the auditory stimuli, and their headphone volume was lowered to a comfortable level (65 dB). They were not excluded from the analysis. Visual stimuli were produced through Arduino 1.8.4 software and delivered to a circuit containing a 10-mm white LED, flashing for 20 ms at intervals of 500, 750, and 1000 ms. Participants completed the visual tapping block in semi-darkness with the light from the LED and the computer screen being the only light sources. 5 V were delivered to the LED and had a luminance of 18–20 cd,

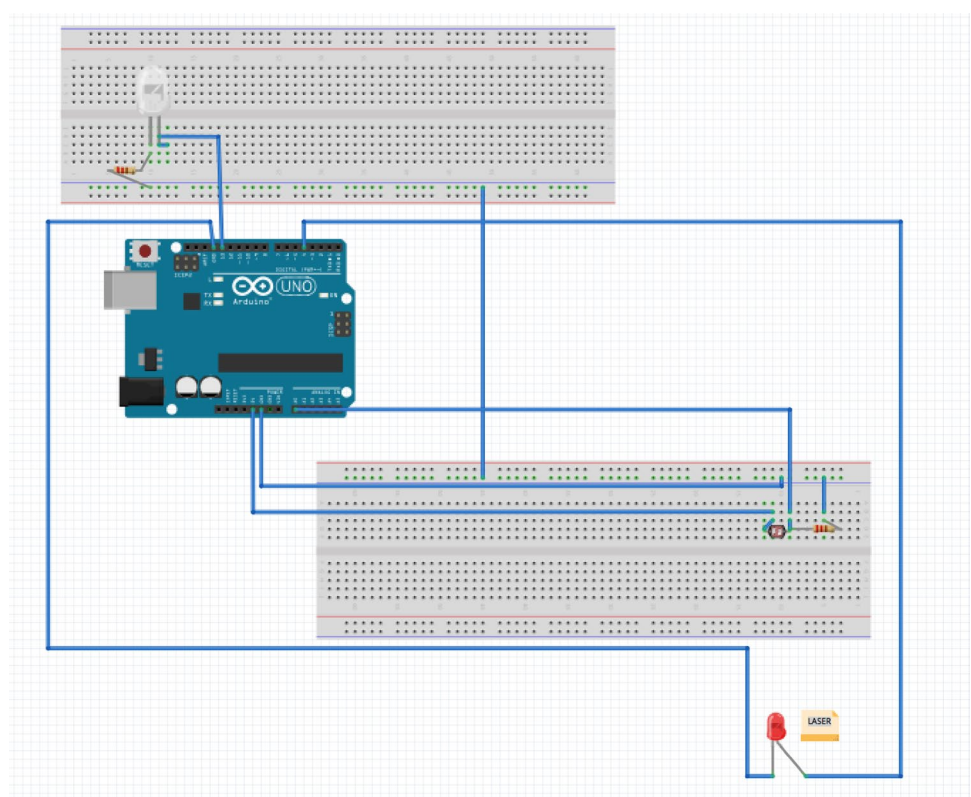
which was visible enough for participants to verbally confirm that they could focus and see the stimulus. No subjects indicated that they could not see the visual stimulus. The flash of light was delivered 30 times per trial. A custom laser tripwire was created so that the LED began flashing when the laser beam was crossed at the z-threshold. A diagram of this visual metronome generator is depicted in Fig. 2. Both auditory and visual stimuli were delivered through the Vicon Nexus software and time-locked with the motion capture recording using a z-threshold trigger matching the LED stimulus tripwire.

Analysis

Vertical movement trajectories were extracted and analyzed using a custom MATLAB R2015b (Mathworks, Natick, Mass., USA) script. Data was filtered using a fifth-order Savitzky–Golay filter (frame size 13 samples), and then velocity and acceleration were calculated. The movement phases of each tap were extension (up), followed by flexion (down), and the subsequent holding phase (dwell, on the surface of the table), shown in Fig. 1. Each finger tap movement cycle time was calculated by combining the time spent in flexion, extension, and holding phases for each respective tap. Holding phase was calculated by measuring the time spent when the finger trajectory velocity was less than or equal to 9.5% of the maximum velocity

per trial, using the procedure outlined in Balasubramaniam et al. (2004). Flexion and extension were calculated by using negative and positive velocity as identifiers, because we decelerate during flexion and accelerate during extension. Trials were visually inspected individually; any trial missing 5 taps was excluded from further analysis, and extra taps. It is important to underscore that these three-movement phases are defined in a functional manner using kinematic data, and do not necessarily correspond to muscular activation or biomechanical properties of finger flexion and extension. Asynchrony was calculated as the time from the beginning of the holding cycle to the onset of the stimulus, identified by the holding time that was closest to a metronome event. In the synchronization conditions, negative asynchrony indicates that the tap preceded the metronome event (beep/flash), while positive asynchrony indicates that the tap occurred after the metronome event. Measuring asynchrony in syncopation conditions was done in the same way, but instead of in reference to the metronome events was in reference to the halfway point between metronome events. Cross-correlations were calculated between relative asynchrony and the immediate subsequent extension time, flexion time, and holding time. Relative asynchrony was calculated as the mean asynchrony subtracted from each individual asynchrony per trial. A grand average correlation per condition was calculated by averaging the Fisher-transformed correlation

Fig. 2 A circuit diagram of the custom laser tripwire created to begin start the sequence of flashing lights in the visual conditions. An Arduino Uno R3 was supplied power via USB and was connected to a bread-board hosting a photoreceptor and additionally was connected to a laser-pointer. When the beam of light emitting from the laser that was pointed at the photoreceptor was broken, the Arduino sent a command to begin the sequence of flashes with the 10-mm LED at different interval durations. The photoreceptor and laser were placed at the same height as the trigger for the motion capture system to begin recording data, ensuring that the beginning of the visual sequence and the flashing lights were time-locked



scores of each individual trial and back-transforming the averages using the inverse of the Fisher function.

Results

We analyzed the effects of stimulus modality (auditory vs. visual), tapping style (synchronization and syncopation), and interval duration (500, 750, and 1000 ms intervals) on extension time, flexion velocity and asynchrony with linear-mixed effects models. These same effects were also analyzed on flexion time, holding time, and extension velocity using linear-mixed effects models using the log-normal distribution of the data. In addition, the same analyses were calculated on the variance of each dependent variable, with linear-mixed effects models run on the variance of extension time and holding time, and linear-mixed effects models using the log-normal distribution of the data on the variance of flexion time, extension and flexion velocity, and asynchrony, a total of 12 linear models run. Results reported from linear-mixed effects models report the estimate and 95% confidence intervals. Values reported using the log-normal distribution of the data are using the back-transformed estimates and confidence intervals of the transformed data. Estimates and confidence intervals for significant effects on variance are reported as standard deviation. Both analyses used the *lmer4* package (Bates et al. 2015) in the R environment (R development core team 2015). In all models, participants and trial order were specified as random intercepts. Visual inspection of the residual plots did not reveal any obvious violations of homoscedasticity or normality. *p* values were obtained for the linear-mixed effects models through the *lmerTest* package in R (Kuznetsova et al. 2017). The significance threshold was set to 0.05.

Timing of movement trajectories

Linear-mixed effects modeling revealed that extension time did not differ across stimulus modality or tapping style, but did differ significantly across interval durations (see Fig. 3). Time spent in extension phase during 750-ms interval durations compared to the time spent in extension phase during 500-ms interval durations significantly increased by 150.61 ms [95% CI (104.03, 197.20), $p < .001$]. Additionally, time spent in extension phase during 1000-ms interval durations compared to the time spent in extension phase during 500-ms interval durations significantly increased by 339.37 ms [95% CI (293.50, 385.24), $p < .001$]. No significant interaction effects were found for extension time. No significant main effects or interactions occurred for the variance of extension time.

Linear-mixed effects models revealed that flexion time differed across both stimulus modality and tapping style,

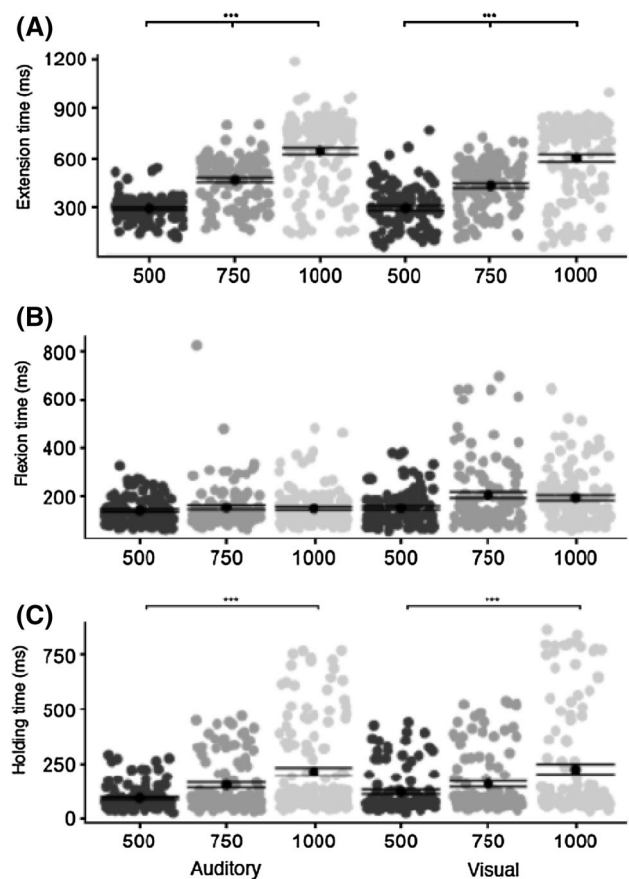


Fig. 3 Time spent in the extension, flexion, and holding phases across auditory and visual tapping conditions with error bars depicting standard error of the mean. Extension time and holding time were found to significantly differ across interval duration, demonstrating that both the upward phase of movement and the holding phase are used for error correction despite changes in tapping style or stimulus modality. Flexion time was found to significantly differ across both stimulus modality and tapping style but not interval duration, serving as a co-contributor to error correction

and only the 1000-ms interval duration (see Fig. 3). Time spent in flexion phase while tapping to a visual stimulus compared to tapping to an auditory stimulus increased by 1.18 ms [95% CI (1.02, 1.36), $p = .02$]. Additionally, tapping in syncopation with a stimulus compared to tapping in synchronization with a stimulus increased time spent in the flexion phase by 1.39 ms [95% CI (1.18, 1.62), $p < .001$]. Compared to 500-ms interval durations, tapping at 1000-ms interval durations increased flexion time significantly by 1.15 ms [95% CI (1.01, 1.32), $p = .04$], and no main effect of interval duration was found 750 ms intervals. A significant interaction between tapping style and stimulus modality was found on flexion time, with flexion time significantly decreasing by 2.34 ms [95% CI (−1.67, −1.08), $p = .009$] during syncopation with visual flashes compared to synchronization with auditory tones. Main effects of stimulus modality, tapping style, and interval duration were found on

the variance of flexion time. Flexion time variance increased during visuomotor timing compared to auditory timing by 1.99 ms [95% CI (1.40, 2.83), $p < .001$]. Compared to synchronization, syncopation increased flexion time variance by 2.80 ms [95% CI (1.92, 4.10), $p < .001$]. Tapping at 750-ms interval durations compared to 500-ms interval durations increased flexion time variance by 1.45 ms [95% CI (1.03, 2.03), $p = .03$], and tapping at 1000-ms interval durations compared to 500-ms interval durations increased flexion time variance by 1.63 ms [95% CI (1.17, 2.28), $p = .004$]. A significant interaction was observed for flexion time variance between tapping style and stimulus modality: flexion time variance significantly decreased during visuomotor syncopation compared to audiomotor synchronization by 2.97 ms [95% CI (−5.07, −1.73), $p < .001$].

For holding time, a main effect of interval duration was observed. Tapping at 750-ms interval durations compared to 500-ms interval durations increased time spent in the holding phase by 1.62 ms [95% CI (1.33, 1.97), $p < .001$]. Tapping at 1000-ms interval durations compared to 500-ms interval durations also increased holding time by 1.89 ms [95% CI (1.55, 2.30), $p < .001$]. No significant interactions were observed with holding time. Interval duration had a main effect on the variance of holding time, with variance

increasing when tapping to a 1000-ms metronome by 80.50 ms [95% CI (50.73, 101.92), $p = .001$].

Analysis of velocity profiles

For extension velocity, main effects were observed across interval duration, shown in Fig. 4. Compared to tapping at a frequency of 500 ms, tapping at an interval duration of 750 ms significantly decreased velocity by 1.42 mm/s [95% CI (−1.63, −1.24), $p < .001$], while tapping at a frequency of 1000 ms decreased extension velocity by 1.99 mm/s [95% CI (−2.27, −1.74), $p < .001$]. No significant interactions were observed for extension velocity. Main effects of tapping style, stimulus modality, and interval duration were found on the variance of extension velocity. During syncopation, the variance of extension velocity increased by 1.57 mm/s [95% CI (1.25, 1.98), $p < .001$] compared to tapping in synchronization with stimuli. Visuomotor timing compared to audiomotor timing increased the variance of extension velocity by 1.48 mm/s [95% CI (1.20, 1.82), $p < .001$]. Compared to tapping at an interval duration of 500 ms, tapping at 1000-ms interval durations decreased extension velocity variance by 1.48 mm/s [95% CI (−1.80, −1.21), $p < .001$], however this same decrease in variance

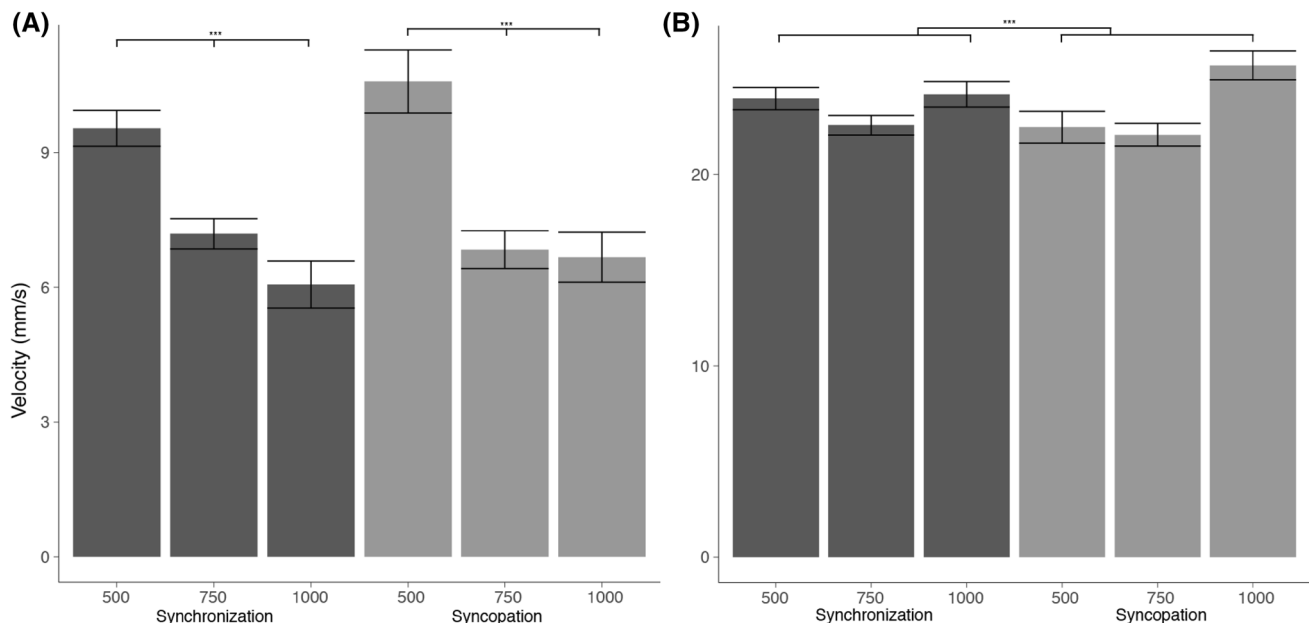


Fig. 4 **a** Extension velocity for the interval durations (500, 750, 1000 ms) for each tapping style (synchronization and syncopation) with error bars reflecting standard error of the mean. Extension velocity significantly differed across all three interval durations, decreasing as the interval duration increased. Extension velocity did not differ across tapping style or stimulus modality (auditory and visual stimuli). The variance of extension velocity significantly increased during visual timing and syncopation to stimuli. **b** The absolute value of flexion velocity for each interval duration (500, 750, and 1000 ms)

and each tapping style with error bars reflecting standard error of the mean. Flexion velocity differed as a function of tapping style, observing a decrease in velocity during syncopation compared to synchronization. The variance of flexion velocity significantly increased during visuomotor timing compared to auditory–motor timing, and also significantly increased during syncopation compared to synchronization. Both figures depict the marked asymmetry between flexion and extension velocity, with much more emphasis placed on flexion than on extension

was not observed for 750-ms interval durations. A significant interaction was found between stimulus modality and tapping style: tapping in syncopation with a visual stimulus compared to synchronizing with auditory tones decreased the variance of extension velocity decreased by 1.41 mm/s [95% CI (−1.94, −1.02), $p = .04$]. No other interaction effects were observed for the variance of extension velocity.

For flexion velocity, a main effect of tapping style was found. Tapping in syncopation with a stimulus compared to tapping in synchronization with a stimulus significantly decreased flexion velocity by −3.80 mm/s [95% CI (−5.99, −1.60), $p = .001$]. Significant interactions were observed between stimulus modality and tapping style, and additionally between tapping style and the 1000-ms interval duration. Compared to synchronization with an auditory metronome, syncopating to visual flashes significantly increased flexion velocity by 4.08 mm/s [95% CI (0.98, 7.18), $p = .01$]. When tapping in syncopation with a rhythm at 1000-ms interval duration, comparative to tapping in synchronization with a rhythm at 500-ms interval durations, flexion velocity significantly increased by 3.66 mm/s [95% CI (0.72, 6.61), $p = .02$]. No other significant interactions were observed for flexion velocity. Main effects of both stimulus modality and tapping style were observed on the variance of flexion velocity. Tapping to a visual flash as opposed to tapping to an auditory tone increased flexion velocity variance by 1.45 mm/s [95% CI (1.27, 1.66), $p < .001$]. Tapping in syncopation to a stimulus compared to tapping in synchronization with a stimulus also increased flexion velocity variance by 1.47 mm/s [95% CI (1.27, 1.70), $p < .001$]. An interaction effect between tapping style and stimulus modality was observed on the variance of flexion velocity; the variance decreased by 1.43 mm/s [95% CI (−1.76, −1.17), $p = .001$].

Analysis of asynchrony measurements

No main effects on asynchrony were observed across conditions, however significant two-way interactions were observed between modality and interval duration (see Fig. 5). When tapping to a visual metronome at 750 ms, compared to tapping to an auditory metronome at 500 ms, asynchrony significantly increased by 75.94 ms [95% CI (24.99, 126.88), $p = .004$]. Tapping to a visual metronome at 1000 ms, also compared to tapping to an auditory metronome at 500 ms, significantly increased asynchrony by 143.02 ms [95% CI (92, 194.03), $p < .001$]. Error correction becomes much more variable in the visual modality as the frequency of the metronome decreases. No other significant interactions were observed on asynchrony. Main effects of stimulus modality, tapping style, and interval duration were all found on the variance of asynchrony. Visuomotor timing, compared to audiomotor timing, increased the variance of asynchrony by 2.78 ms [95%

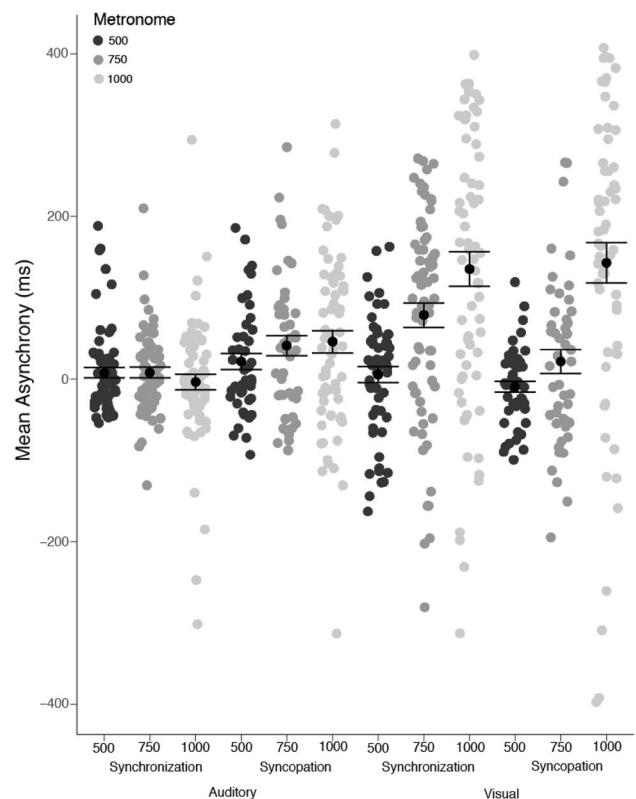


Fig. 5 Distribution of asynchronies for each condition with error bars depicting standard error of the mean. In general, asynchrony across all conditions grew larger as the interval durations increased, as predicted by Weber's law. The variance of asynchrony significantly increased during visuomotor timing compared to audiomotor timing, increased during syncopation compared to synchronization, and also increased as interval duration increased

CI (2.38, 3.45), $p < .001$]. Syncopation, compared to synchronization, also increased asynchrony variance by 3.42 ms [95% CI (2.80, 4.18), $p < .001$]. Interval duration also increased asynchrony variance: compared to tapping at 500-ms interval durations, tapping at 750 ms intervals increased variance by 1.55 ms [95% CI (1.30, 1.86), $p < .001$], and tapping during 1000 ms intervals increased asynchrony variance by 1.90 ms [95% CI (1.59, 2.27), $p < .001$]. Several interaction effects were observed across asynchrony variance. Visuomotor timing during syncopation as opposed to audiomotor timing during synchronization significantly decreased asynchrony variance by 2.88 ms [95% CI (−3.82, −2.17), $p < .001$]. Additionally, visuomotor timing during 1000-ms interval durations compared to audiomotor timing during 500-ms interval durations significantly decreased variance of asynchrony by 1.76 ms [95% CI (−2.28, −1.36), $p < .001$]. Tap style and interval duration also interacted: compared to synchronization at 500 ms intervals, syncopation during 750 ms intervals reduced the variance of asynchrony by 2.02 ms [95% CI (−2.68, −1.53), $p < .001$], and syncopation

during 1000 ms intervals reduced the variance of asynchrony by 2.29 ms [95% CI (− 2.99, − 1.75), $p < .001$].

No significant correlations between relative asynchrony and the immediate subsequent extension time, flexion time, or holding time were found in any conditions, indicating that variability surrounding asynchrony cannot be attributable to individual movement phases, but rather is spread across the entire tapping interval itself.

Discussion

The purpose of this study was to explore the contribution of kinematics to timing processes by investigating the differences between synchronization and syncopation to visual and auditory stimuli. We were specifically interested in how the holding phase involving haptic feedback (finger contact with the table surface) contributes to the error correction process in timing. We successfully replicated Balasubramaniam et al. (2004) in their finding of a marked asymmetry between extension and flexion velocity, with faster flexion than extension. This asymmetry between flexion and extension velocities is demonstrated in Fig. 4. We did not find an increase in positive mean asynchronies as the interval duration of visual stimuli decreased, as shown by Hove et al. (2013). Our results instead support the opposite with an interaction between stimulus modality and interval duration: an increase in asynchrony as interval duration increased during visual timing compared to tapping to an auditory stimulus at a shorter interval duration. This could occur because of internally generated uncertainty surrounding the onset of visual stimuli at slower intervals, and participants have a more variable distribution of asynchronies during slower interval durations when tapping to visual stimuli (Kurgansky 2008). Increasing task constraints on a simple tapping paradigm would likely increase variability in performance, and our finding of increased asynchrony variance during visuomotor timing compared to audiomotor timing, during syncopation compared to synchronization, and during increased duration of the interval supports this. Furthermore, our predicted increase in Weber-like variance as interval duration increased was observed for the variance of both the holding time and flexion time of movement, demonstrating that the holding and flexion phases contributed the largest source of variance to the timing interval. These results are consistent with several other studies demonstrating this same increase in variability across inter-tap intervals (ITIs) as the frequency of the metronome decreases (Gibbon 1977; Hove et al. 2014), whereas our study found that this increase of variance in ITIs is attributable to the holding phase of movement during tapping.

Nagasaki (1991) demonstrated that asymmetry of cyclic extension and flexion velocities decrease as interval duration

decreases during synchronized movements, and Nagasaki (1989) reported asymmetry of extension and flexion velocity was present in a wide range of interval durations with an exception of an intermediate interval duration of 433 ms where the observed velocity and acceleration of flexion and extension was symmetrical. The present study successfully replicated similar findings in Balasubramaniam et al. (2004). Extension velocity significantly decreased as interval duration increased (see Fig. 4) and flexion velocity remained stable across interval durations. As for novel effects, we observed significant differences in both extension and flexion velocity variance between visual and auditory tapping, with velocity during visuomotor timing increase in variability compared to audiomotor timing. We also observed significant differences in flexion velocity and its variance across synchronization and syncopation, with the velocity of the downward movement decreasing when tapping between events rather than tapping at the onset of the event, and an increase in variability. Main effects of stimulus modality and tapping style on asynchrony were not observed, meaning participants were accurate relative to their own performance for both visual and auditory timing during both synchronization and syncopation, so the modulation of velocity must be a successful error correction strategy. The time spent in extension phase and holding phase were the movement phases shown to differ the most as a function of interval duration while the time spent in flexion phase was modulated by stimulus modality and tapping style. Unlike Torre and Balasubramaniam (2009), the present study did not find that the immediate subsequent movement cycles following asynchrony were negatively correlated with relative asynchrony. This suggests that the mechanisms of trajectory formation and error correction might be quite different in finger tapping with haptic contact compared to rhythmic finger oscillations at equivalent movement speeds (Dumas and Wing 2007). However, because the time spent in both extension and holding phases of movement varied as a function of metronome frequency but did not significantly differ across stimulus modality or tapping style but flexion time was modulated by stimulus modality and tapping style, we can determine that there are multiple error correction strategies utilized, like timing strategies of legato and staccato tapping described in Hove et al. (2014), that may wash out correlations if they exist between relative asynchrony and the subsequent movement phases. The timing strategy that contributes to the differences found between visual and auditory timing appears to be a function of extension and flexion velocity variance and a modulation of flexion time, and the timing strategy that contributes to the differences found between synchronization and syncopation appears to be a function of the velocity of the downward movement and the time spent in flexion. Flexion time increases during syncopation and becomes increasingly variable, and this is

accompanied by a significant decrease in flexion velocity and an increase in variance of extension and flexion velocity. Syncopation seems to be characterized by slower movement and increased variability while approaching the onset of a stimulus, which in turn could increase variability of asynchrony during syncopation.

Both flexion time and flexion velocity significantly differed when participants syncopated to the event compared to participants synchronizing to the event. Synchronization and syncopation are not functionally equivalent, refuting Balasubramaniam et al.'s (2004) finding that these two styles of tapping could be functionally equivalent because they found no significant differences, and our results suggest that this difference is reflected by the downward movement trajectory. One explanation for this could be the way the movement trajectories were defined: Balasubramaniam et al. (2004) only investigated extension and flexion, whereas we subdivided movement trajectories into extension, flexion, and holding phases. Dividing the holding movement between extension and flexion time could have prevented differences from existing between the movement phases in previous work. Semjen et al. (1992) found that at interval durations greater than 500 ms, the variability of ITIs during anti-phase tapping decreases as interval duration increases. Our results suggest the opposite: variance increased during flexion in anti-phase and additionally increased with interval duration, and both flexion and extension velocity variance increased during syncopation. Semjen (2000) suggests that this could be because participants were unprepared to syncopate, however participants in the present study were informed before the presentation of each trial to either synchronize or syncopate with the stimuli, and were explicitly told to tap between the stimuli for syncopation. This increase in variability for flexion velocity could be reflecting the underlying neural processes that differentiate synchronization and syncopation. Mayville et al. (2001) found results indicating that syncopation movements were updated on a cycle by cycle basis, recruiting more neural resources for prediction and attentional demands than synchronization required. Syncopation recruits an extensive neural network, including the basal ganglia, dorsolateral premotor cortex, areas of supplementary motor cortex (SMA), and prefrontal and temporal association cortices (Mayville et al. 2001). The present study supports those results through behavioral data, however further investigation is still needed to investigate the underlying neural processes for auditory and visual syncopation. One future direction is the application of transcranial magnetic stimulation (TMS) to areas involved in sensorimotor timing, and how down-regulation using continuous theta-burst stimulation (cTBS) or up-regulation using intermittent theta-burst stimulation (iTBS) of these areas influence both our perception of time and how it affects timing accuracy (Huang et al. 2005).

The results of the present study also indicate through an interaction that asynchrony significantly increased when participants tapped to a visual stimulus at larger interval durations than when they tapped to an auditory stimulus at shorter interval durations (shown in Fig. 5). This could demonstrate a weaker temporal coupling for visual system compared to the auditory system, supporting previous work (Repp 2003; Patel and Iversen 2014; Comstock and Balasubramaniam 2018). The reactive mode of timing, indicated by positive asynchronies which could reflect reacting to an event rather than predicting its location in a temporal sequence, could occur because the neural networks underlying visual timekeeping processes are better adapted to reacting to stimuli rather than predicting the upcoming beat (Repp and Penel 2002; Repp 2003; Patel 2014). Jäncke et al. (2000) and Penhune et al. (1998) both suggest that in tapping synchronization tasks, different areas of the cerebellum are active depending on the sensory modality of the stimulus, and that only audiomotor synchronization utilizes the SMA. In addition, Hove et al. (2013) demonstrated in an fMRI study that the putamen is significantly more active in audiomotor synchronization than in visuomotor synchronization to isochronous stimuli. The tight perception–action coupling between the audiomotor cortices likely aids audiomotor synchronization and syncopation (Patel and Iversen 2014), while visuomotor integration takes much more processing time. A spatial component like motion added to visual synchronization can improve accuracy (Hove and Keller 2010; Hove et al. 2010, 2013). Future work should investigate the contribution of movement phases in response to stimuli that are altered spatially and temporally. The investigation of how brain networks underlying these different kinds of error correction are modulated by the type of stimulus presented is likely to be a fruitful area for further research (see for, e.g., Comstock and Balasubramaniam 2018).

In summary, these results demonstrate that timing is modulated through extension, flexion, and holding phases continuously as interval duration increases. However, the flexion phase seems to serve as the period of adjustment for visual timing and anti-phase tapping. Additionally, velocity becomes much more variable during syncopation. This, accompanied by increased variance of asynchrony for longer interval durations, for visuomotor timing, and for syncopation, supports previous literature arguing that not only do audiomotor and visuomotor timing networks utilize different pathways, but synchronization and syncopation timing may also utilize different neural networks. A lack of correlations occurring between relative asynchrony and its subsequent movement phases across all conditions likely indicates that there are multiple kinds of timing strategies utilized that require deeper investigation.

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Compliance with ethical standards

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

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