Spatiotemporal Relations and Movement Trajectories in Visuomotor Synchronization

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Michael J. Hove & Peter E. Keller
Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

THIS WORK INVESTIGATES HOW SPATIAL AND TEMPORAL aspects of rhythmic movements are affected by spatial and temporal components of a visual pacing sequence. Participants synchronized finger taps with three visual pacing sequences (*Flash*, *High Finger*, and *Low Finger*) at two tempi (500 ms and 400 ms interonset interval). The Flash sequence contained only temporal information, whereas the two Finger sequences contained apparent motion of different amplitudes. Participants' finger movements were recorded with a motion capture system, and movement trajectories and timing accuracy were analyzed. Results indicated that apparent motion facilitates visuomotor synchronization accuracy, which likely stems from tight perception-action links. Stimulus amplitude modulated tap amplitudes in the same direction, but this spatial assimilation did not adversely affect timing accuracy. Flexion times toward the target were significantly shorter than extension or dwell times, and could indicate a relatively ballistic movement trajectory. Local deviations of tap timing correlated with the movement trajectories from the preceding and following movement cycle. For example, after a late tap, the following movement cycle had lower amplitude and shorter extension and dwell times. This could signify the workings of error correction mechanisms that ensure stable synchronization.

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Synchronizing movements with external rhythms is an important and ubiquitous behavior. We effortlessly step onto escalators, unconsciously synchronize movements with an interlocutor, sociably dance with a partner, and precisely play music with ensemble members. Such coordinative acts involve precise timing between our movements and rhythmic pacing sequences in various modalities. Even in music, a predominately auditory domain, co-performers use visual signals such as head movements to provide timing cues (Davidson, 2009; Goebl & Palmer, 2009), and conductors use spatiotemporal visual signals to control the timing of musicians' movements. Musicians and non-musicians can coordinate the timing of their movements with various spatiotemporal signals of a conductor (Luck & Sloboda, 2009). Questions then arise about how the spatial characteristics of the response movements are affected by the spatiotemporal characteristics of a pacing sequence. And how do the spatial and temporal aspects of movement affect each other?

Previous work on movement timing in visuomotor synchronization typically analyzed and recorded a single data point per movement cycle (e.g., when a finger strikes a response device), as opposed to examining the spatial trajectories of the movement. Such timing research using the finger-tapping paradigm has established that the timing of rhythmic movements is highly variable when participants try to synchronize with flashing visual sequences that contain only temporal information (e.g., Kolers & Brewster, 1985; Repp, 2003). Adding a spatial component to the visual pacing sequence greatly improves the temporal stability of synchronized movements, especially when the pacing sequence and movements are directionally compatible (Hove, Spivey, & Krumhansl, in press). The facilitation of synchronization with moving stimuli could partially reflect the visual system's propensity for processing spatial variation (Posner, Nissen, & Klein, 1976). But since the facilitation is strongest for directionally compatible stimulus-response (S-R) combinations, the facilitation likely stems from the degree of dimensional overlap between the observed and produced movements (i.e., S-R compatibility; e.g., Greenwald, 1970; Kornblum, Hasbroucq, & Osman, 1990) and tight perception-action links (e.g., Hommel, Müsseler, Aschersleben, & Prinz, 2001).

Observing both static and moving spatial information can modulate movement trajectories. With static stimuli,

movement trajectories can veer toward *or* away from non-target stimuli depending on multiple factors including the level of competition and distance between target and non-target stimuli (Tipper, Howard, & Jackson, 1997; Welsh & Elliott, 2004). Similarly, observing moving stimuli can modulate movement by *assimilation*, wherein produced movements are biased toward observed directions (e.g., Whitney, Westwood, & Goodale, 2003), or by *repulsion or contrast*, wherein movements are biased away from observed directions (Schubö, Aschersleben, & Prinz, 2001). Time course analyses of movement modulation suggest that *assimilation* or *attraction* occurs immediately and automatically, probably due to feature overlap of stimulus-response and automatic perception-action links, whereas *repulsion* of movement direction potentially reflects a voluntary compensation or inhibition against the automatic S-R effects (Grosjean, Zwickel, & Prinz, 2009).

Analyses of continuous movement trajectories reveal dependencies between spatial and temporal components of movement. Movement amplitude has been shown to decrease monotonically with faster frequencies during rhythmic movement paced by an auditory metronome (e.g., Kay, Kelso, Saltzman, & Schöner, 1987; Kay, Saltzman, & Kelso, 1991). This tempo-amplitude relation is consistent with the nonlinear oscillator model of Haken, Kelso, and Bunz (1985). Conversely, movement amplitudes have been found to increase at fast tempi in piano playing, which involves sequential movements of different fingers (Loehr & Palmer 2007; Palmer & Dalla Bella, 2004). Such an increase in amplitude at fast tempi potentially reflects a strategy to increase tactile sensation to improve movement timing (cf. Aschersleben, 2002; Goebl & Palmer, 2008; Palmer, Koopmans, Loehr, & Carter, 2009). Motion capture investigation of a single finger tapping repetitively with auditory stimuli revealed that movement trajectories affect movement timing (Balasubramaniam, Wing, & Daffertshofer, 2004). Participants were instructed to extend or flex on or off the metronome beat. Movement times were shorter for the movement phase *toward* the target, regardless of the implementation (flexion vs. extension). This asymmetry between flexion and extension could serve to improve timing precision, and indeed the degree of asymmetry positively correlated with timing accuracy.

So, in summary: (1) spatial variation in stimuli can improve movement timing; (2) spatial variation in stimuli can modulate movement trajectories; and (3) movement trajectories interact with movement timing. In the current study we investigate a series of questions about how spatiotemporal information affects corresponding aspects of movement in finger tapping. Previous work examined the kinematics of rhythmic finger movements with auditory pacing sequences that did not contain spatial information (e.g., Balasubramaniam et al., 2004; Doumas & Wing, 2007; Loehr & Palmer, 2009; Palmer & Dalla Bella, 2004). No previous work to our knowledge has explored the movement kinematics in finger tapping with visual pacing sequences. Visual sequences can contain both spatial and temporal information and thus offer the possibility to manipulate spatial and temporal components separately to test effects on the spatial, temporal, and spatio-temporal aspects of movement.

The Present Study

In the current study, participants synchronized finger taps with visual metronomes at different tempi. The metronomes either contained spatial information by alternating images of fingers at different amplitudes (creating apparent motion), or contained only temporal information (a flash). Movement trajectories were recorded using a motion capture system, and were analyzed for spatial, temporal, and spatio-temporal effects both globally and locally.

Temporal Accuracy

The previously observed timing facilitation in visuomotor synchronization with compatibly moving stimuli (Hove et al., in press) could stem from simply tracking the stimuli (i.e., compatible motion stimuli provide *multiple* targets during each movement cycle that the response movements could match). In order to test this, we compared visuomotor synchronization timing accuracy with flashing stimuli versus apparent motion stimuli, which have the same temporal characteristics and no additional information to track.

Apparent motion stimuli appear to move, but this perceptual phenomenon of motion occurs when static objects are presented sequentially at different locations (Shepard & Zare, 1983; Shiffrar & Freyd, 1990). Apparent motion occurs across a wide range of stimulus distances and stimulus onset asynchronies (Burt & Sperling, 1981; Gepshtein & Kubovy, 2007). Previous behavioral work with apparent motion stimuli shows S-R compatibility effects (e.g., faster left response with apparent motion toward the left hand; Michaels, 1988; Proctor, Van Zandt, Lu, & Weeks, 1993). However, the timing and trajectory of rhythmic movements synchronized with apparent motion stimuli have not been systematically investigated. If apparent motion facilitates synchronization timing accuracy, this suggests that the compatibility effect reflects an abstract spatial coding at the stimulus-response interface that biases the response in the same direction as the perceived movement.

Spatial Effects

In order to test spatial effects of stimulus amplitude and tempo, we compared tap amplitudes at two tempi and three types of metronomes: low amplitude apparent motion, high amplitude apparent motion, and a flash that provided only temporal information. Stimulus amplitude might modulate tapping amplitude by spatial assimilation/attraction or by repulsion/contrast. Compared to the non-spatial Flash metronome (a baseline or preferred amplitude condition), are tap amplitudes higher for metronomes containing high amplitude apparent motion (assimilation), or for metronomes containing low amplitude apparent motion (repulsion)? Additionally, tempo could affect the tapping amplitude. Tapping amplitudes could be lower at faster tempi (conforming to Haken, Kelso, & Bunz, 1985), or could be higher at faster tempi (potentially reflecting a strategy to increase tactile information; Aschersleben, 2002; Palmer & Dalla Bella, 2004).

Spatiotemporal Effects

We are not only interested in the main effects of stimulus amplitude and tempo, but also potential interactions (or lack thereof). Do stimulus amplitude and tempo have independent or interactive effects on tap trajectories and timing? Three possibilities will be considered. First, tapping amplitude and timing might be independent. Since timing precision is the goal in this synchronization task, optimal amplitudes for the given tempo could be produced regardless of the task-irrelevant stimulus amplitude. Conversely, tapping amplitude and timing might be interactive. If stimulus amplitude biases tap amplitude away from optimality, tap timing accuracy could be disrupted. Or finally, stimulus amplitude could bias tap amplitude away from optimality *without* disrupting tap timing accuracy, because timing is adjusted in a compensatory manner (e.g., by increasing velocities or lengthening extension, flexion, or dwell times).

Global Analyses of Movement Trajectories

Each movement cycle in finger tapping on a hard surface consists of three distinct phases: extension, flexion, and dwell.[1] Previous research with contact-free finger tapping showed shorter durations for the movement *toward* the target, and this duration asymmetry correlated with synchronization timing accuracy (Balasubramaniam

et al., 2004). Here we examine the relative durations of the three phases for similar asymmetries and to ascertain whether phase duration asymmetries predict overall timing accuracy in a trial.

Local Timing Deviation and
Corresponding Movement Trajectory

In addition to examining movement trajectories globally in a trial, we also examined the relationship between each tap's local timing accuracy and the movement trajectory preceding and following that tap. We compared correlations between local timing deviations and the preceding and following trajectory features including amplitude, extension time, flexion time, dwell time, extension, and flexion velocities (mean and max for that tap cycle). What movement trajectory characteristically leads to a late tap? How does a movement trajectory look after a late tap? Significant correlations between timing deviation and the following cycle's movement trajectory potentially offer a look into the workings of the error correction mechanisms that allow consistent tap-to-target synchronization (cf. Torre & Balasbramaniam, 2009; see Repp, 2005, for discussion of models of error correction). Additionally we examined the serial dependencies between adjacent tapping periods (lag 1 autocorrelations), which are indicative of error correction mechanisms.

Method

Participants

Eight right-handed students (4 women) aged 19 to 30 years ($M = 23.8$) participated in the study. They were previously unfamiliar with the tapping task. Music training ranged from 0–15 years ($M = 6.0$); half the participants had no music training. Participants were paid six Euro/hour.

Materials and Procedure

Participants tapped their right index finger in time with three visual pacing sequences (*Flash, High Finger,* and *Low Finger*) at two tempi (500 ms and 400 ms IOI). Each of the pacing sequences consisted of two alternating images of equal duration: (1) Flash alternated between a white square (the target) and a black square (invisible against the black background); (2) High Finger alternated between an image of a hand with its index finger outstretched at the bottom of the screen (target), and with the finger extended 5 cm above the bottom; (3)

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[1]A fourth movement phase, holding at the top of the trajectory, can occur when tapping in a staccato manner or during very slow tempi.
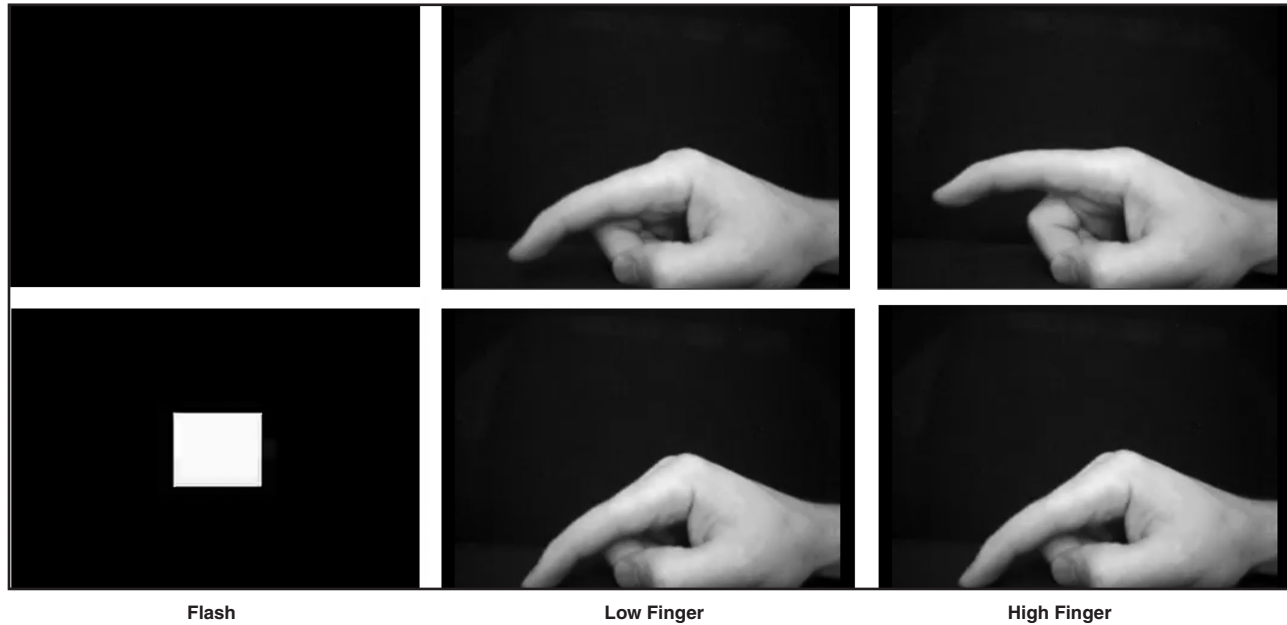
FIGURE 1. Stimuli: Stills of the alternating images for the 3 metronome types: Flash, Low Finger (apparent motion), High Finger (apparent motion). Participants were instructed to tap with the onset of the target, depicted in the bottom row.

Low Finger alternated between the same image of the finger at the bottom of the screen (target), and the finger 2 cm above the bottom (Figure 1). The Finger sequences did not contain actual motion, though the alternating images produced apparent motion. Participants were instructed to tap as accurately as possible with the onset of each target; the height of images was not mentioned, and was in this sense task irrelevant.

Each trial consisted of 30 cycles of alternating images and participants were instructed to start tapping with the fourth target in each trial. Participants tapped their right index finger on a Roland SPD-6 MIDI percussion pad. Taps on the percussion pad were recorded and visual pacing sequences were presented via a MAX/MSP/Jitter program running on a PC.[2] Additionally, the kinematics of participants' finger movement trajectories were tracked by an Optotrak Certus motion capture system (Northern Digital Inc.) with 250 Hz sampling frequency. Markers were attached to the tip of the index finger for kinematics and on the stationary hand (base knuckle) and percussion pad for reference positions. Three-dimensional information about marker position was relayed by the Optotrak System Control Unit to a second PC for storage.

This PC also received information from the parallel port of the MAX PC about trial onset times and condition. The experiment consisted of 20 blocks that contained the 6 trial types (3 metronome types × 2 tempi) in random order and lasted approximately one hour.

Analyses

Tap Timing Data

The tap timing data from the percussion pad were analyzed using circular statistical methods (e.g., Fisher, 1993). Each tap in a trial was mapped onto a unit circle in terms of its relative phase (0–360°) from the periodic metronome target (always at 0°), where for example, taps slightly after the target had a phase of 0–90° and slightly before the target, 270–360°. Synchronization typically requires a few taps to stabilize, so the first four taps were not analyzed.

Synchronization performance can be assessed in terms of circular variance, a measure of the variability of the taps' relative phases (the stability of tap-to-target synchrony). Another indicative measure of synchronization performance, if synchronization is difficult, is the percentage of trials in which tap-to-target phases never stabilize (Repp, 2003). Each trial's tap-to-target synchronization performance was assessed using a Rayleigh (R)

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[2]The monitor refresh rate of 85 Hz (11.7 ms) led to slight deviations of frame timing, as the presentation was not synchronized to the refresh rate.
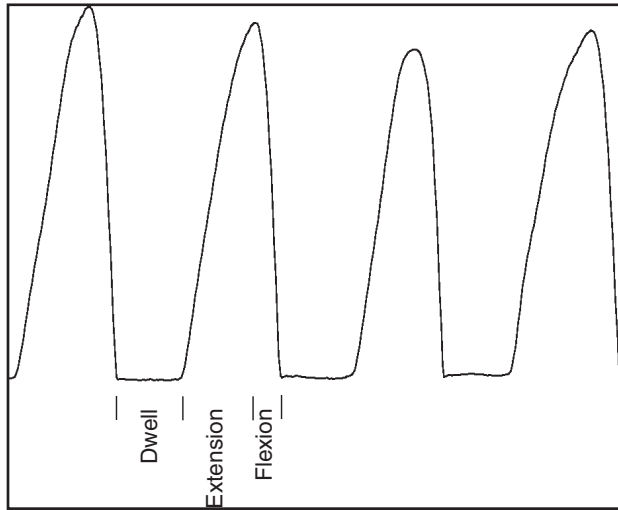
FIGURE 2. Motion capture data: An example of the finger's amplitude profile when tapping on a hard surface. Three distinct phases occur in each movement cycle: extension, flexion, and dwell.

test of uniformity, which tests the null hypothesis of a uniform distribution of relative phases around the unit circle against the alternative hypothesis of a unimodal distribution of relative phases (Berens, 2009). For each trial, the null hypothesis was rejected if the Rayleigh test p value was less than .05; these trials had a unimodal distribution of tap-to-target relative phases and were defined as successful, as opposed to trials with a more nearly uniform distribution of taps that would occur with irregular tapping or substantial phase drift. Success rates and circular variance were analyzed for the different metronomes and tempi.

Motion Capture Data

Additional measures of movement timing and kinematics were computed from the finger motion data. Movement amplitude for each tap was measured by calculating the difference between the local maximum and minimum vertical position of the finger. *Mean amplitude* and *variability of amplitudes* (average within-trial standard deviation of amplitudes) were subsequently computed for each participant in each condition.

In finger tapping on a surface, three distinct phases arise in each movement cycle: *extension* away from the surface, *flexion* to the surface, and *dwell time* at the surface (see Figure 2). Information about each movement phase was extracted from the finger trajectories by finding the three appropriate time points: the local maximum in vertical position, the point of surface contact,

and the point of breaking contact.[3] The relative timing of each movement phase can be analyzed, in addition to velocity profiles during flexion and extension.

Results

Tap Timing and Synchronization Success

First, synchronization performance was examined for the different metronomes (Flash, High Finger, Low Finger) and tempi (500 or 400 ms IOI) in terms of circular variance (the tap-to-target variability) and the percentage of trials with a unimodal distribution of relative phase (indicating stable, non-drifting tap-to-target relative phase as determined by Rayleigh test of uniformity). A 3 (metronome type) × 2 (tempo) repeated measures analysis of variance (ANOVA) on circular variance indicated that tapping variance was higher for the Flash metronome than for the two Finger metronomes, $F(2,14) = 12.02$, $p = .001$, $\eta_p^2 = .63$, (Figure 3a). No significant difference occurred between the High Finger and Low Finger metronomes, $p > .15$ (using the least significant difference test, as do subsequent pairwise comparisons). Tapping variance was higher at the fast tempo (400 ms IOI) than the slow tempo (500 ms IOI), $F(1,7) = 10.23$, $p = .015$, $\eta_p^2 = .59$. The tempo × metronome interaction was not significant, $p > .70$. A similar ANOVA on the percentage of trials exhibiting successful synchronization yielded qualitatively identical results (Figure 3b).

Together these results demonstrate that visuomotor synchronization performance is facilitated by apparent motion, as indicated by more stable synchronization with the two metronomes containing apparent motion compared to the Flash metronome. However, stimulus amplitude did not affect synchronization success. Tapping performance was more variable and less successful at the faster tempo, reflecting the performance difficulties as tempi move from preferred rates of tapping toward the upper rate limits for visuomotor synchronization.

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[3]The start and end points of the dwell phase were extracted from each tapping cycle with an algorithm that identified the minimum vertical finger position during that cycle; then it scanned backwards and forwards for the first points that were 10% higher than this minimum (approximately 3 mm, which was much greater than the elasticity or rebound of the finger tissue or the noise in the motion capture system); finally the algorithm moved back toward the minimum by 2 samples (8 ms) to give the "start" and "end" points of dwell. Extensive visual inspection indicated that this was an accurate and appropriate technique.
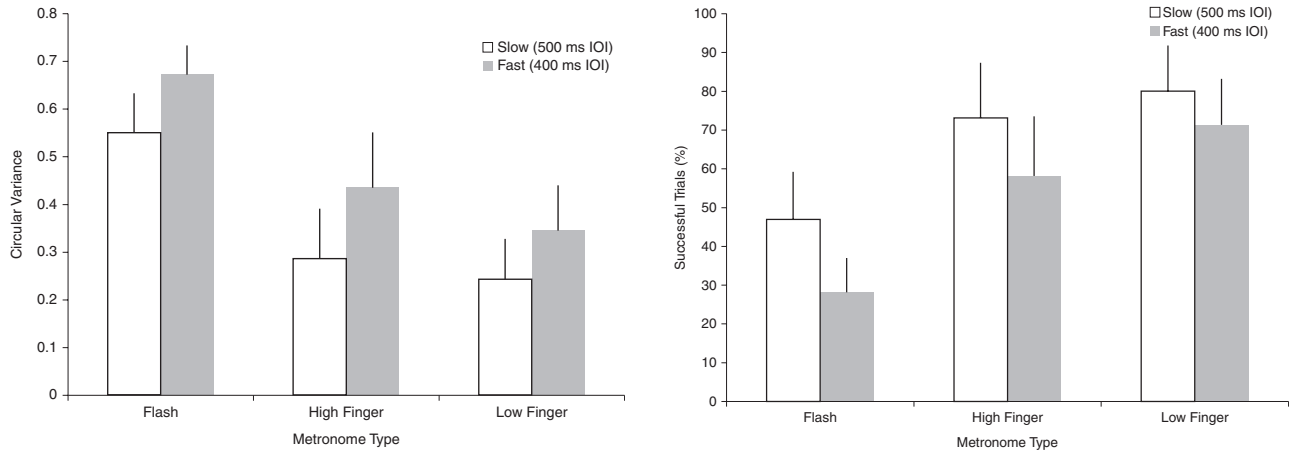
FIGURE 3. Synchronization success by condition as quantified by (a) circular variance, and (b) proportion of trials showing successful, stable synchronization as determined by a Rayleigh test of uniformity. Error bars represent *SE.* Synchronization performance was more stable with the apparent motion "Finger" metronomes than the Flash metronome and more stable at the slow tempo.

Tap Amplitude by Condition

Next we examined tapping amplitudes by condition in a 3 (metronome) × 2 (tempo) repeated measures ANOVA (Figure 4). Metronome type affected average tap amplitudes, $F(2, 14) = 12.95$, $p = .001$, $\eta_p^2 = .65$. Tap amplitudes were higher for the high finger metronome than low finger metronome ($p = .001$), with amplitudes for the baseline flash condition intermediate ($ps < .08$). Tapping amplitudes were lower at the fast tempo than at the slow tempo, $F(1, 7) = 33.67$, $p = .001$, $\eta_p^2 = .82$. There was no significant tempo x metronome interaction, $p > .70$.
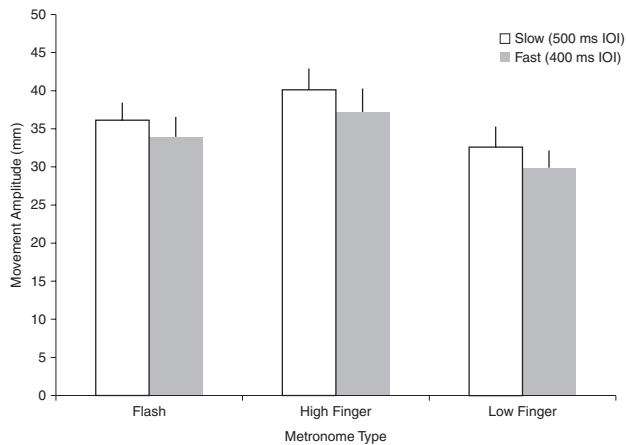

FIGURE 4. Mean movement amplitudes (in mm + *SE*) show higher tap amplitudes at the slow tempo. Tap amplitudes were higher for the High Finger metronome than the Low Finger metronome, with amplitudes intermediate for the "baseline" Flash condition.

Stimulus amplitude drove finger movement amplitude by spatial assimilation/attraction, despite being task irrelevant, and thus suggests automatic tight perception-action links. However, as noted above, differences in stimuli amplitude did not affect synchronization timing accuracy; success rates (Rayleigh test) and tap-to-target variability (circular variance) were the same for High Finger and Low Finger. This raises the following question: How did participants compensate for changes in tapping amplitude without compromising timing accuracy?

Movement Velocities by Condition

One clear way to compensate for amplitude changes is by modulating velocity. Mean extension and flexion velocities were analyzed separately in 3 (metronome) × 2 (tempo) ANOVAs. Mean *extension* velocities were faster with the high amplitude metronomes than the low amplitude metronomes, with Flash metronomes intermediate, $F(2, 14) = 11.67$, $p = .001$. Additionally, extension velocities were faster at the fast tempo, $F(1, 7) = 7.37$, $p = .03$. Similarly, mean *flexion* velocities were faster with the high amplitude metronomes than the low amplitude metronomes, with Flash metronomes intermediate, $F(2, 14) = 11.54$, $p = .001$. However, the difference between flexion velocities between fast and slow tempi did not attain statistical significance, $F(1, 7) = 4.96$, $p = .061$.

Overall, mean flexion velocities ($M = .41$ mm/ms) were faster than mean extension velocities ($M = .20$ mm/ms), $F(1, 7) = 61.77$, $p < .001$. Based on the results of Balasubramaniam et al. (2004) showing faster movement for whichever phase was to align with the metronome beat (i.e., faster extension when participants were instructed
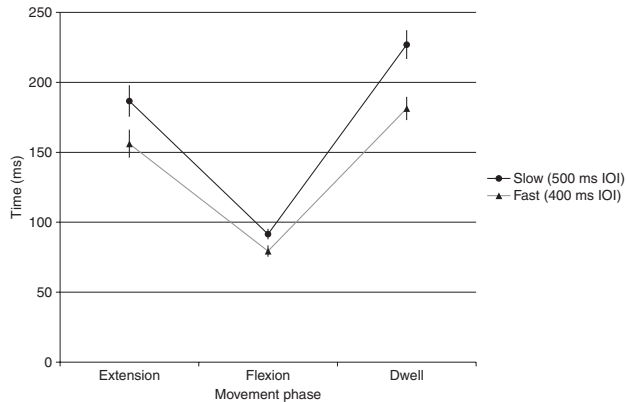
FIGURE 5. The average time of each movement phase (extension, flexion, and dwell) for fast and slow tempi. Participants spent considerably more time in the extension and dwell phases than in flexion; and flexion was relatively stable across tempi.

to extend on the beat, and faster flexion when they were instructed to flex on the beat), this result reflects faster movement *toward* the target, rather than biomechanical peculiarities of flexion vs. extension.

Movement Times for Extension, Flexion, and Dwell

We examined the mean durations of each movement phase in a 3 (movement phase: extension, flexion, dwell) × 2 (tempo: fast, slow) × 3 (metronome: Flash, High Finger, Low Finger) repeated measures ANOVA. Results showed asymmetric durations for different movement phases. Participants spent considerably less time flexing than extending or dwelling at the surface, $F(2, 14) = 51.88$, $p < .001$, $\eta_p^2 = .88$. For example, at the 500 ms target tempo, the average cycle consisted of 186 ms extension, 91 ms flexion, and 226 ms dwell (Figure 5). Incidentally, this movement asymmetry indicates that participants were not using the onset of the non-target frame as a temporal target for their off-beat extension (i.e., they were not subdividing the cycle into two temporal target events, as was observed by Kelso, DelColle, & Schöner, 1990).

Movement times for each phase were obviously shorter at the fast tempo, $F(1, 7) = 212.91$, $p < .001$, $\eta_p^2 = .97$. However, when examining tempo effects for the different movement phases, flexion times were relatively stable across tempi compared to extension times and dwell times, as indicated by the phase × tempo interaction, $F(2, 14) = 15.93$, $p < .001$, $\eta_p^2 = .70$. While the relatively small difference in flexion time between slow and fast tempi could reflect its overall shorter duration (i.e., the smaller absolute difference between tempi reflects a similar proportional difference), comparisons between

Extension-Flexion ratios (extension time divided by flexion time) mitigate this interpretation. Extension-Flexion ratios were significantly higher at the slow tempo ($M = 2.18$) than at the fast tempo ($M = 2.04$), $F(1, 7) = 8.82$, $p = .021$, $\eta_p^2 = .55$, indicating the relative stability of flexion times at different tempi. The stability of flexion across tempi could reflect a relatively ballistic movement profile for movements toward the target.

Autocorrelation of Successive Tapping Periods

Autocorrelations of the intertap intervals were computed to explore serial dependencies and processes underlying synchronization (cf. Semjen, Schulze, & Vorberg, 2000; Torre & Balasubramaniam, 2009; Vorberg & Wing, 1996). A negative lag 1 autocorrelation reflects a serial dependence characterized by alternating long and short tap intervals. Such negative lag 1 autocorrelations have been observed when the task is tapping without a metronome (wherein negative values likely arise from motor implementation variance, Wing & Kristofferson, 1973); in synchronization tasks, this autocorrelation will be driven more negative via error correction mechanisms (Semjen et al., 2000). The autocorrelations were calculated for each trial of each participant, transformed into Fisher Z scores, and averaged across trials for each participant.[4] Correlation analyses were run on transformed Fisher Z scores, and Pearson correlation values are reported.

Lag 1 autocorrelations on intertap intervals were examined in a 3 (metronome) × 2 (tempo) repeated-measures ANOVA. Lag 1 autocorrelations differed between metronomes, $F(2, 12) = 6.45$, $p = .013$, but not between tempi, $p > .90$. The lag 1 autocorrelations for the High Finger metronome ($r = -.12$) and the Low Finger metronome ($r = -.09$) were lower than for the Flash metronome ($r = .01$). Correlations were tested for significance in one-sample t-tests against 0. Autocorrelations were significantly less than 0 for the apparent motion metronomes ($ps < .05$), but not for the Flash metronome ($p > .60$). Since motor implementation variance can be assumed to be constant between conditions, the negative lag 1 autocorrelations suggest that error correction occurs when synchronizing with the apparent motion metronomes. The non-negative autocorrelation with the Flash potentially reflects a lack of error correction and slow drift.[5] These differences parallel the differences in

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[4]One participant failed >80% of trials, and was excluded from analyses on autocorrelations and local timing deviations.

[5]Non-negative lag 1 autocorrelations on inter-tap intervals are also observed in continuous, or "emergent" tasks such as circle drawing (e.g., Delignières, Lemoine, & Torre, 2004; Torre & Balasubramaniam, 2009).

synchronization success rates between metronomes. When examining only *successful* trials (as determined by a Rayleigh test $p < .01$), the lag 1 autocorrelations decreased slightly for the High Finger ($r = -.16$) and Low Finger metronomes ($r = -15$), whereas the Flash remained similarly non-negative ($r = .00$). This non-negative lag 1 autocorrelation for *successful* Flash trials indicates that participants might simply pick up and maintain the correct tempo (on some trials), rather than using tap-to-tap error correction. Lag 2 autocorrelations for successful trials across conditions did not significantly differ from 0 (mean $r = -.03$, $p > .10$).

Local Timing Deviation and Movement Trajectories

In addition to examining global movement signatures, we also examined the relationships between each tap's local timing accuracy and the movement trajectory preceding and following that tap. Each tap's local timing accuracy was calculated based on the motion capture data and quantified as the deviation from that trial's mean relative phase (which we assume to indicate the point of subjective synchrony; see Aschersleben, 2002). Late taps had positive deviations and early taps had negative deviations. After extracting each tap's relative timing deviation and trajectory profile from the raw motion capture data, the series of timing deviations was correlated with the series of preceding and following trajectory variables including amplitude, extension time, flexion time, dwell time, extension velocity (mean and max within that cycle), and flexion velocity (mean and max within that cycle). What trajectory profiles characteristically precede a late tap? How does a movement profile look after a late tap? For these analyses, only trials showing successful synchronization were included, where a trial was deemed successful if it had a unimodal distribution of relative phases, indicated by a Rayleigh test of uniformity $p < .01$. Fifty-seven percent of all trials met this criterion.

Overall, movement trajectories predicted tap timing in relatively small but consistent correlations. First, the effects of the movement cycle *preceding* a tap will be considered. Tap timing deviations positively correlated with the preceding movement amplitude, $r = .12$, $t(6) = 3.22$, $p = .017$; in other words, high amplitudes preceded late taps. Timing deviation also positively correlated with the preceding dwell time, $r = .18$, $t(6) = 4.36$, $p = .005$, and the preceding extension time, $r = .10$, $t(6) = 2.57$, $p = .04$; when dwell and extension times lasted relatively long, taps occurred late. Conversely, the preceding flexion time did not correlate with timing deviation, $r = .03$, $p > .50$; variability in flexion time does not strongly contribute

to movement timing, which substantiates flexion's relatively ballistic movement profile. Tap timing deviations correlated with the preceding cycle's mean extension and flexion velocity, but not maximum velocity. *Slower* mean extension velocities correlated with late taps, $r = -.16$, $t(6) = 3.54$, $p = .011$, whereas *faster* mean flexion velocities correlated with late taps $r = .10$, $t(6) = 4.86$, $p = .003$; this could be a consequence of the higher amplitudes that also precede late taps.

Next, the effects on the movement cycle *following* a tap will be considered. Timing deviation correlated negatively with the following movement amplitude, $r = -.15$, $t(6) = 3.95$, $p = .008$; in other words, a late tap leads to a lower subsequent amplitude. Tap timing deviations also correlated negatively with the following dwell time, $r = -.16$, $t(6) = 5.04$, $p = .002$, and the extension time, $r = -.08$, $t(6) = 3.87$, $p = .009$; when a tap occurs late, the following dwell time and extension time are shortened. However, again no significant relation was observed between local timing deviation and flexion time, $r = -.03$ $p > .20$. Timing deviation did not correlate with flexion or extension velocities on the following movement cycle. The correlations between tap timing deviations and subsequent movement profiles potentially reflect the error correction necessary to ensure successful tap timing. Interestingly, subsequent changes in amplitude, extension time, and dwell time compensated for timing deviations, whereas flexion time and velocities were inconsequential. This suggests that the spatial component, amplitude, is used to compensate for temporal deviations.

Discussion

In this experiment, participants synchronized finger taps with visual metronomes that either contained apparent motion at different amplitudes or contained only temporal information. Sequences were presented at two tempi. Results show that spatial and temporal stimulus information affects spatial, temporal, and spatiotemporal aspects of tapping. The results bear on a number of issues in motor control and timing.

Timing Facilitation with Apparent Motion Stimuli

Tap timing was more stable with pacing sequences that contained apparent motion than with flashes. Temporal information in the stimuli was consistent across all metronomes, indicating that the compatible apparent motion facilitates synchronization timing accuracy. Even though the visual system is better at processing spatial variation than temporal variation (e.g., Posner et al., 1976), the

tapping facilitation with apparent motion does not simply result from differences in perceptual acuity. We previously reported facilitative effects in tap timing accuracy with compatible *but not* incompatible linear motion stimuli (Hove et al., in press). The facilitation with apparent motion extends those results and further supports S-R compatibility and tight perception-action linkages. Perceiving movement in a certain direction biases the system in that same direction and engenders more stable performance.

Apparent motion and linear motion stimuli produce similar facilitative effects in tapping and are processed by similar brain circuits. Area MT, an area in the dorsal visual stream that responds to moving stimuli, responds similarly to apparent motion stimuli (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998). The facilitation of synchronization by apparent motion demonstrates the constructive nature of vision and that the perceptual system "extrapolates movement beyond what is actually perceived" (Wilson & Knoblich, 2005, p. 465). This extrapolated movement affects corresponding action, via the perception-action interface. Here apparent motion stimuli were used in order not to "drive" the response movement trajectory, but future work could compare movement trajectories for apparent, linear, and biological motion to determine whether the stimulus trajectory influences the produced response trajectory.

Effects of Stimulus Amplitude and Tempo on Tapping Amplitude

Tapping amplitude was affected by both spatial and temporal stimulus information. Tapping amplitudes were lower at faster frequencies; this amplitude-frequency relationship has been reported previously (e.g., Kay et al., 1987) and conforms to predictions of nonlinear oscillator models (Haken, Kelso, & Bunz, 1985). Tapping amplitude also was modulated in the same direction as stimulus amplitude: compared to the baseline Flash condition, taps were higher with high amplitude stimuli and lower with low amplitude stimuli. Thus, the spatial modulation occurs by *assimilation,* which likely reflects feature overlap at the S-R interface and automatic perception-action links (Grosjean et al., 2009). Interestingly, the spatial modulation of tap amplitude away from optimal amplitude did not adversely affect tap timing due to compensatory timing adjustments, largely in velocity profiles. The trajectory modulation by assimilation with a task irrelevant stimulus feature occurred automatically, whereas the temporal coordination was at least partially under top-down control (as participants did not synchronize with the non-target off-beat images).

Movement Asymmetries

Analyses revealed that flexion times were much shorter than extension times and dwell times. This asymmetry does not reflect biomechanics, as previous work shows faster times *toward* the target than *away* from the target, i.e., extension times are shorter when participants are instructed to extend on the beat (Balasubramaniam et al., 2004). Thus, asymmetry of phases within a movement cycle is thought to assist timing (cf. Torre & Balasubramaniam, 2009). Additionally, flexion is relatively stable across tempi: at the fast tempo, extension and dwell times diminished considerably more than flexion times. Finally, a deviation in tap timing does not affect the following flexion phase, nor does variability in flexion lead to a deviation of the next tap.

Together, these results suggest that the movement phase toward the target (here, flexion) is relatively ballistic, whereas the other movement phases (dwell and extension) are corrective. These two stages coincide with findings in the motor control literature on aiming movement: nearly all aiming movements have ballistic and corrective stages (Rosenbaum, 2009). Aiming is composed of an initial ballistic impulse that brings the effector close to its target, followed by a stage of adjustment and homing-in on the target (Elliott, Helsen, & Chua, 2001; Woodworth, 1899). In the present synchronized tapping paradigm, the tradeoff between speed and spatial accuracy does not apply, as spatial accuracy is not a concern. However, some of the underlying logic holds: due to inherent noise in the motor system, variability of movement timing is proportional to the overall movement time; thus, in order to minimize variability of timing it pays to minimize movement time. In addition to decreased timing variability in rapid ballistic movements, higher velocities also provide increased tactile information, which could assist timing (Balasubramaniam, 2006; Goebl & Palmer, 2008).[6]

Local Timing and Error Correction

We observed negative lag 1 autocorrelations in tapping periods with apparent motion stimuli, but not with flashing stimuli. Previous visuomotor work using flashing sequences reported non-negative autocorrelations and high tapping variability (Chen, Repp, & Patel, 2002). In the current context, the negative autocorrelations suggest error correction and parallel the more

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[6]However, in the current study, neither maximum velocity nor the degree of movement asymmetry correlated with timing accuracy on a local or global scale.

stable synchronization with apparent motion stimuli. The negative autocorrelations are noteworthy, in that they were not previously reported in visuomotor synchronization to our knowledge.

Examinations of the relationships between tap timing deviations and the following movement cycle's trajectory intimate the workings of error correction more directly. After a late tap, the following amplitude is lower, and extension and dwell times are shorter. These compensatory mechanisms keep tapping on course and suggest that spatial adjustments of amplitude are used to modulate timing. As synchronization performance is still more stable with auditory stimuli than with moving visual stimuli (Hove et al., in press), future examination of movement trajectories with auditory sequences containing phase perturbations (Repp, 2001) could further elucidate error correction processes. Additionally, in light of the auditory advantage for *timing* of synchronized actions, future work could examine movement timing and trajectories when synchronizing with auditory stimuli in competition with phase perturbed moving visual stimuli (cf. Repp & Penel, 2004); this would parallel synchronization in musical ensembles while hearing and seeing complementary (or discrepant) co-performers' actions.

Conclusion

Together these results underscore the tight connections between perception and action and between movement trajectories and timing. Spatial and temporal aspects of the visual pacing sequence had strong effects on corresponding aspects of movement. Adaptations in movement trajectory assisted accurate movement timing.

In addition to contributing to understanding motor control and timing, these results can be applied to improve synchronization performance, which can lead to increased social cohesion in interpersonal contexts (Hove & Risen, 2009), and can improve musical performance. These results support the use of imitation in musical instrument pedagogy (e.g., Haston, 2007). In musical ensemble performance, conductors indicate their expressive intentions by embellishing their beat gestures (Luck & Sloboda, 2007; Luck & Toiviainen, 2010). The embellishment of spatial aspects of conducting gestures may affect the ensemble's expressive performance via a process of assimilation that is grounded in perception-action coupling. When directing a decrescendo for example, a decrease in the conductor's movement amplitude will similarly decrease a performer's movement amplitude, which correspondingly decreases loudness in many instruments. Instrument and expression specific spatiotemporal signals can effectively modulate performance.

Author Note

Correspondence concerning this article should be addressed to Michael Hove, Max Planck Institute for Human Cognitive and Brain Sciences, Music Cognition and Action Group, Stephanstrasse 1a, 04103 Leipzig, Germany. E-MAIL: hove@cbs.mpg.de

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