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The role of multiple internal timekeepers and sources of feedback on interval timing

Breanna E Studenka, Daisha L Cummins and Megan A Pope

Abstract

The aim of this experiment was to document the role of multiple internal clock mechanisms and external sources of temporal feedback on reducing timing variability when two fingers tap instead of one (a phenomenon known as the bimanual advantage). Previous research documents a reduction in timed interval variability when two effectors time instead of one. In addition, interval variability decreases with multiple sources of feedback. To date, however, no research has explored the separate roles of feedback and internal timing on the bimanual advantage. We evaluated the bimanual advantage in a task that does not utilise an internal clock (circle drawing). Participants performed both unimanual and bimanual timing while tapping or drawing circles. Both tasks were performed with and without tactile feedback at the timing goal. We document reduced bimanual timing variability only for tasks that utilise internal clock-like timing (tapping). We also document reduced timing variability for timing with greater sensory feedback (tactile vs no-tactile feedback tapping). We conclude that internal clock mechanisms are necessary for bimanual advantage to occur, but that multiple sources of feedback can also serve to improve internal timing, which ties together current theories of bimanual advantage.

Keywords

Bimanual advantage; event timing; emergent timing; multiple timer model; sensory feedback; tactile reafference

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Introduction

It is well documented that timing with multiple effectors (e.g., two hands) leads to timed intervals that have lower variability than timing with only one effector (e.g., the index finger; Drewing, Hennings, & Aschersleben, 2002; Helmuth & Ivry, 1996). However, research aimed at uncovering the mechanisms of such a bimanual advantage has been, to date, equivocal. One body of research points to the importance of multiple timekeepers in reducing timing variability; the other points to the importance of multiple sources of feedback in informing the internal timing model. These two leading hypotheses for the bimanual advantage have not been tested individually. In other words, tasks that employ manipulations of feedback also use tasks that require internal clocks. In this article, we aim to test the individual hypotheses that bimanual advantage depends on internal clocks and that bimanual advantage depends on multiple sources of feedback.

Humans' ability to keep track of time durations is often examined via a repetitive timing task whereby a metronome prescribes a pace (e.g., 2 Hz) and a participant attempts to maintain this pace after the tones stop. The time between taps is calculated (intervals), and timing ability is measured as the variance of a series of these interval durations. According to the classic timing model proposed by Wing and Kristofferson (1973a), two independent processes contribute to timing variability: an internal clock process measures regular intervals, and a motor implementation process translates these signals to begin each tapping movement. Variability in a time series of inter-tap intervals (V) is thought to reflect both clock (C) and motor implementation (M) variability ($V = C + 2M$). Because clock and motor variance are assumed to be independent, the lag-one covariance

Department of Kinesiology and Health Science, Utah State University, Logan, UT, USA

Corresponding author:
Breanna E Studenka, Department of Kinesiology and Health Science, Utah State University, Logan, UT 84322, USA.
Email: breanna.studenka@usu.edu

of each time series approximates the motor or implementation variance (see Wing & Kristofferson, 1973a). The clock, or central, component of variability is calculated as twice the motor variance subtracted from the total variance. Many behavioural (Keele & Ivry, 1988; Keele, Pokorny, Corcos, & Ivry, 1985; Wing & Kristofferson, 1973a, 1973b) and neurological studies (Ivry & Keele, 1989; Ivry, Keele, & Diener, 1988) support the idea that the clock and motor components of timed movement are independent and distinct (Drewing & Aschersleben, 2003; Sergent, Hellige, & Cherry, 1993; Turvey, Schmidt, & Rosenblum, 1989; Wing, 2002).

An interesting phenomenon occurs when a person times with two hands instead of just one. The overall variance, and, in particular the clock variance, of intervals produced by one finger is greater than the variance of intervals produced by that same finger when it taps along with the same finger on the opposite hand (Drewing & Aschersleben, 2003; Drewing et al., 2002; Drewing, Stenneken, Cole, Prinz, & Aschersleben, 2004; Helmuth & Ivry, 1996). Several researchers have postulated theories to explain this phenomenon (termed the bimanual advantage). One theory—the multiple-timekeeper model—proposes a coupling of internal timekeeping mechanisms leading to reduced clock variance (Helmuth & Ivry, 1996; Ivry & Richardson, 2002). The main assumptions of this model follow from the classic timing model proposed by Wing and Kristofferson (1973b) for a single effector. Reduction in timing is hypothesised to occur via the averaging of two clock signals (Ivry & Richardson, 2002). The assumption is that each effector has generated a separate temporal representation of the target interval or the desired time of the next tap. These two signals are not sent directly to each effector; rather, they are sent through a central gating mechanism which then averages the two representations and sends an output signal to each effector simultaneously. The result of this averaging is a less variable representation of interval duration or onset time, leading to the bimanual advantage over a series of timed intervals. In sum, multiple inputs to the gating mechanism lead to better estimates of the timed aspects of movement. One of the most compelling indicators that the internal timing mechanisms is involved in the bimanual advantage is the attribution of the reduction in variability to the clock rather than the motor implementation variance (Helmuth & Ivry, 1996). In addition, the reduction in timing variability approximates the resultant variability of two independent timing signals averaged together (Helmuth & Ivry, 1996), supporting the notion of a gating mechanism.

An alternate theory for the bimanual advantage—the sensory feedback hypothesis—postulates that reduced variance is accounted for by an increase in the sensory feedback when two effectors make contact with the tapping surface as opposed to only one (Drewing & Aschersleben, 2003). This sensory feedback hypothesis posits that timing improves as a result of the additional sensory feedback received from two effectors as opposed to only one. Support for this hypothesis comes from studies demonstrating bimanual advantage when two fingers on the same hand time together, instead of only one finger (Drewing et al., 2002), under the assumption that clocks may be hemisphere-specific rather than effector-specific. In addition, when both hands time together, manipulating feedback to one hand influences timing of the opposite hand, suggesting an influence of collective feedback on overall timing mechanisms. When tactile feedback received by a participant's left finger was removed, increased clock variance was exhibited by the right finger during tapping compared with when both hands received tactile feedback from table touches (Drewing et al., 2002). In addition, when auditory feedback was removed from left-hand taps, the bimanual advantage was reduced compared with when auditory feedback was present for both right- and left-hand taps (Drewing & Aschersleben, 2003). These studies indicate that feedback plays a strong role in the bimanual advantage. The precise mechanism of timing improvement due to increased sensory feedback has yet to be uncovered.

It is important to note that each of these theories is not mutually exclusive. It is plausible that internal clocks are needed for bimanual advantage to occur and also that additional feedback improves the timing mechanism's ability to match intended intervals with produced intervals, thereby reducing timing variability. To date, the unique contributions of clock and feedback mechanisms to the bimanual advantage have not been tested.

As a test of the clock hypothesis for the bimanual advantage, we had participants perform two repetitive movement tasks, one that uses an internal clock (finger taping) and one thought to rely on non-clock-like timing (repetitive circle drawing; Robertson et al., 1999; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). Repetitive circle drawing does not exhibit negative lag-one covariance, which is required by clock models of timing (Repp & Steinman, 2010; Studenka & Zelaznik, 2008); exhibits no correlation in timed interval variability with finger tapping (Robertson et al., 1999; Zelaznik, Spencer, & Doffin, 2000; Zelaznik, Spencer, & Ivry, 2002; Zelaznik et al., 2005); and is not impaired in individuals with damage to the cerebellum (known to influence clock-like timing; Spencer et al., 2003). For circle drawing, rhythmic "timed" movement purportedly emerges from the control of movement parameters such as tangential velocity, or muscular force, rather than from an internal clock mechanism. Therefore, timing for tapping is often referred to as clock or event timing, whereas timing for circle drawing is referred to as emergent or non-clock timing.

As a test of the feedback hypothesis for the bimanual advantage, we had participants perform each task in two different feedback conditions (one with and one without tactile feedback pertaining to the timing goal). The aim of this experiment was to test both the role of internal clocks and the role of feedback in the bimanual advantage by manipulating

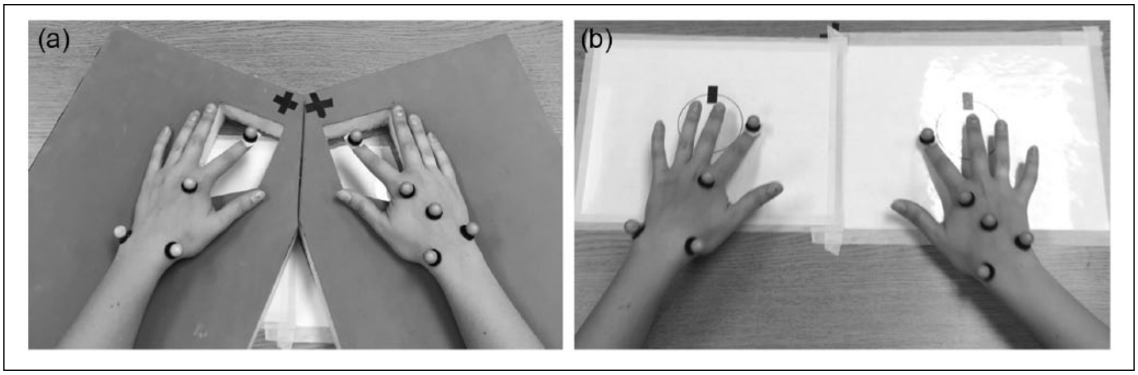

Figure 1. Picture of the Vicon motion capture set up: (a) bimanual tapping without tactile feedback task and (b) bimanual circle drawing task. For circle drawing with tactile feedback, a strip of Velcro replaced the black rectangle.

both. We hypothesised that if multiple clock mechanisms are crucial for the bimanual advantage, we should see bimanual advantage only for tapping even when feedback was present for circle drawing. Furthermore, we hypothesised that if the bimanual advantage is dependent only on enhanced sensory feedback, we should see bimanual advantage when tactile feedback was present for both the clock and the non-clock timed task and that bimanual advantage would be reduced or eliminated when tactile feedback was not present.

Method

Participants

In total, 33 right-handed participants and two left-handed participants were recruited to participate. Two participants could not perform the task (mean interval duration was greater than 1000 ms) and three participants did not comply with experimental protocol (e.g., closed their eyes, were chewing gum). Data from the 28 remaining right-hand-dominant participants—18 females and 10 males—were analysed. Participants had a mean age of 21 ± 4 years. Participants had an average of 5.3 ± 4.8 years of musical experience. Informed consent procedures were approved by the Utah State University Institutional Review Board (IRB).

Apparatus and tasks

Once consent was obtained, a participant was seated at a 71-cm-high table. A participant rested both hands on top of the tabletop over two pieces of paper, 21.59 cm × 27.94 cm, with a circle template printed on them (3 cm radius). The tip of the participant's index finger of each hand was covered with masking tape and a Vicon reflective marker was placed on top of the fingertip. A participant performed eight tasks: unimanual (right hand) and bimanual tapping, unimanual and bimanual circle drawing, unimanual and bimanual tapping in the air, and unimanual and bimanual circle drawing over a Velcro target (see Figure 1). For each circle drawing task, a participant was instructed to complete one cycle of drawing by passing over the mark (1 cm × 2 cm printed rectangle or Velcro square) at the top of the circle template. For bimanual circle drawing, circles were drawn in an in-phase pattern moving upwards and then inwards for each hand. For each tapping task, a participant was instructed to complete each cycle by touching the tabletop or by reaching the level of the tabletop. For all tasks, a synchronisation-continuation paradigm was used. A metronome created via custom-written MATLAB code sounded for 10 tones spaced 800 ms apart. A participant attempted to complete each tap or circle coincident with a metronome tone (10 ms, 717 Hz). When the metronome stopped, the participant was instructed to continue to move at the prescribed pace until another, higher pitched tone (550 ms, 860 Hz) sounded (22 additional seconds). Sennheiser HD 239 noise cancelling headphones were worn for all trials.

Procedure

The experimenter greeted a participant, the experiment was explained, and consent was obtained. After being seated, reflective markers were attached to a participant's right and left hands. Each of eight blocks consisted of eight trials each. Each trial consisted of 10 intervals (800 ms) of synchronisation followed by approximately 30 additional circles or tapping intervals. Following the completion of a trial, the experimenter reminded the participant of the timing goal and verbally provided the mean of his or her own performance. If the participant's mean interval duration was above 850 ms or below 750 ms, the experimenter reminded the participant to stay on pace. The experimental session lasted approximately 60 min.

Design

The main design was a three-way comparison between task (tapping and circle drawing), feedback (tactile vs no-tactile feedback), and condition (unimanual vs bimanual). The order of all tasks was counterbalanced across participants.

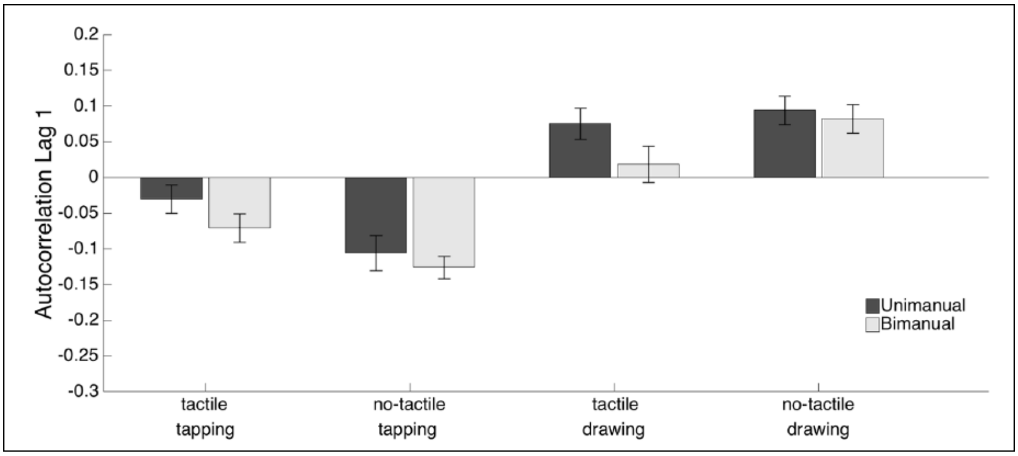

Figure 2. Lag-one autocorrelation for unimanual and bimanual, and tactile feedback and no-tactile feedback conditions of tapping and circle drawing.

Data collection and reduction

Kinematic data were collected using the Vicon Nexus Bonita motion capture system (VICON Motion Systems, Oxford, UK). Reflective markers (14 mm in diameter) were placed on the participant's right and left index finger, knuckle, and on the medial and lateral condyle of the wrist. For the right hand, one marker was placed on the hand for the Nexus software modelling to distinguish the right from the left hand in real time. The real-time three-dimensional (3D) position—sampled at 250 Hz—was fed into a custom-written MATLAB program. Intertap duration was calculated based on a custom-written algorithm that detected cycle end-points based on when each cycle trajectory reached 3% of maximal velocity towards the timing target. Each time series was checked via another custom-written MATLAB program to verify that each calculated end-point was accurately detected. This series of cycle durations was detrended removing any within-trial drift. Averages and variances for cycle duration were calculated for every trial and then averaged over the eight trials for each task.

Dependent variables were calculated for the continuation portion of movement. Values for lag-one autocorrelation and clock variance were calculated based on the Wing and Kristofferson (1973b) derivations and later modifications made by Vorberg and Wing (1996). Coefficient of variation (CV) was calculated as the standard deviation of the interval time series divided by the mean of the tapping intervals and multiplied by 100. It is well known that variability scales with the temporal interval produced (Ivry & Hazeltine, 1995; Spencer et al., 2003). The CV is calculated as our main measure of variance to allow for comparison of the variability between trials and participants where the mean of tapping intervals is slightly different.

Results

First, lag-one autocorrelation was calculated as a test for the use of internal timing mechanisms in both feedback conditions of tapping and circle drawing (see Figure 2). The Wing and Kristofferson timing model states that lag-one autocorrelation should be between −0.5 and 0 if the model is to be used to decompose timing into clock and motor components. Therefore, the exhibition of lag-one autocorrelation between −0.5 and 0 is often considered a hallmark indication of the use of event timing. For the lag-one autocorrelation, 95% confidence intervals (CIs) were run, with intervals falling between 0 and −0.5 theoretically indicating the use of event timing. The CIs of both unimanual (95% CI = [–0.06, –0.0002]) and bimanual (95% CI = [–0.10, –0.04]) table tapping were negative. CIs for both unimanual (95% CI = [–0.14, –0.08]) and bimanual (95% CI = [–0.16, –0.10]) tapping without tactile feedback were also negative. The values for unimanual and bimanual circle drawing with tactile feedback (95% CI = [0.05, 0.11], 95% CI = [–0.01, 0.05]) and circle drawing (95% CI = [0.06, 0.12], 95% CI = [0.05, 0.11]) were all significantly positive or zero indicating non-clock timing for all circle drawing tasks.

CV is plotted for both unimanual and bimanual tapping and circle drawing for both feedback conditions (tactile feedback and no-tactile feedback; Figure 3). A two-task (circle drawing vs tapping) by two-condition (unimanual vs bimanual) by two-feedback (tactile vs no-tactile) analysis of variance (ANOVA) revealed a significant task effect, $F(1, 27) = 96.26$, $p < .0001$, a significant feedback effect, $F(1, 27) = 90.96$, $p < .0001$, and a significant condition effect, $F(1, 27) = 12.48$, $p = .002$. There was a significant task by feedback interaction, $F(1, 27) = 62.72$, $p < .0001$, reflecting the greater CV for no-tactile feedback tapping than for tactile feedback tapping but no difference between

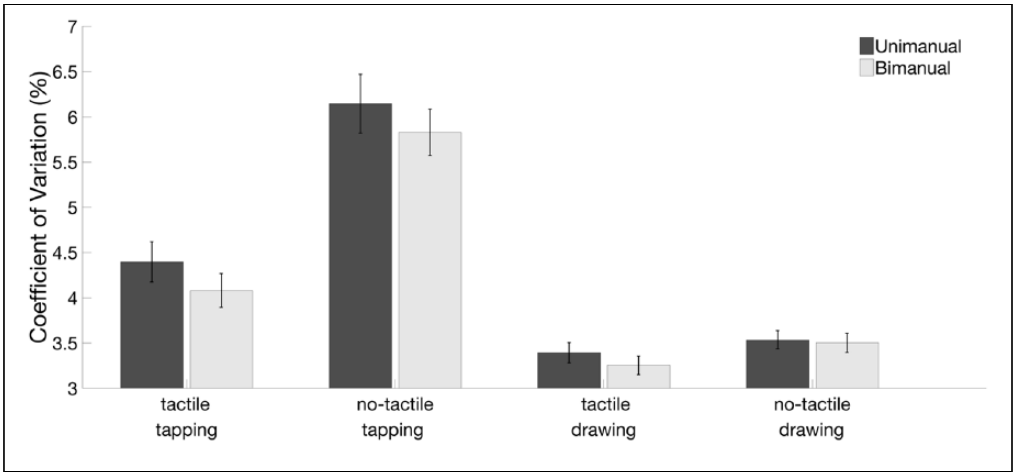

Figure 3. Coefficient of variation percentage for unimanual and bimanual, and feedback and no-feedback conditions of tapping and circle drawing.

the two feedback conditions for circle drawing. A priori contrasts revealed that, for both tactile and no-tactile feedback tapping, bimanual timing had less variance than unimanual timing, $F(1, 27)=4.78$, $p=.04$, $F(1, 27)=4.73$, $p=.04$. For tactile and no-tactile feedback circle drawing, no difference was seen between unimanual and bimanual timing, $F(1, 27)=.93$, $p=.34$; $F(1, 27)=.05$, $p=.82$. Furthermore, CV was not significantly reduced for the tactile feedback circle drawing tasks over the no-tactile feedback circle drawing tasks, $F(1, 27)=3.65$, $p=.07$.

To document any difference in bimanual advantage due to the manipulation of tactile feedback, clock variance was plotted for tactile versus no-tactile tapping (see Figure 4). One subject was removed from the clock analysis because he exhibited no trials that fit the Wing and Kristofferson model for the bimanual condition of no-tactile feedback tapping. In typical timing research, it is not uncommon for some trials to exhibit positive lag-one covariance. Due to the small number of trials (less than half) that exhibited lag-one autocorrelation between −0.5 and 0 for circle drawing tasks, statistics were only run on tapping tasks. A summary of trials that fit the Wing and Kristofferson timing model for each condition is presented in Table 1. An ANOVA was run comparing condition (unimanual vs bimanual) and feedback (tactile vs no-tactile). Bimanual conditions had significantly smaller clock variance than unimanual conditions, $F(1, 26)=14.83$, $p=.0007$. Furthermore, no-tactile feedback tapping had significantly greater clock variance than tactile feedback tapping, $F(1, 26)=46.48$, $p<.0001$. The lack of a significant condition by feedback interaction, $F(1, 26)=0.09$, $p=.76$, supported the finding that the bimanual advantage was comparable within feedback settings. Post hoc contrasts revealed that *unimanual* no-tactile feedback tapping had significantly greater variance than tactile feedback tapping, $F(1, 26)=45.86$, $p<.0001$, and that bimanual tapping with tactile feedback had significantly lower clock variance than bimanual tapping without tactile feedback, $F(1, 26)=40.17$, $p<.0001$.

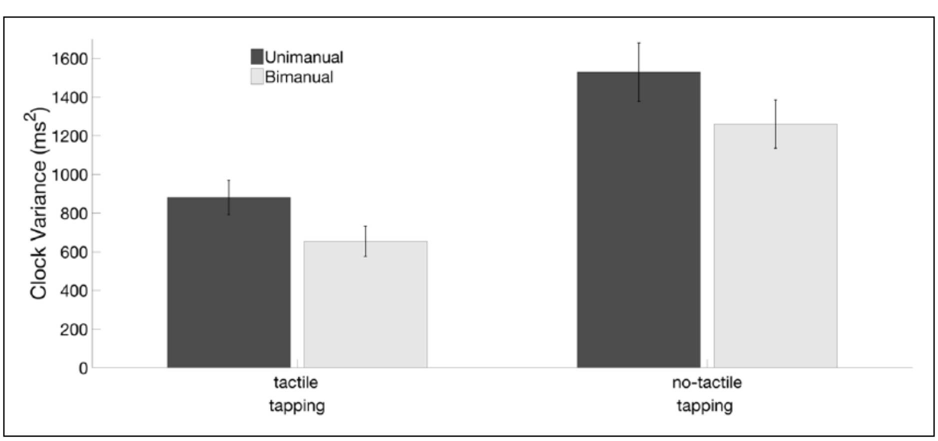

Figure 4. Clock variance for unimanual and bimanual tapping under both feedback conditions.

Table 1. Descriptives.

		MT (*SD*)	NumTrials	Clock (*SD*)	Motor (*SD*)
Tactile tapping	Unimanual	779 (28)	123	881 (462)	229 (187)
	Bimanual	771 (32)	113	654 (409)	212 (134)
No-tactile tapping	Unimanual	769 (32)	145	1,529 (792)	535 (482)
	Bimanual	767 (36)	132	1,261 (649)	471 (215)
Tactile circle drawing	Unimanual	783 (36)	72	—	—
	Bimanual	779 (24)	62	—	—
No-tactile circle drawing	Unimanual	795 (29)	76	—	—
	Bimanual	784 (31)	81	—	—

MT: average movement time; NumTrials: the number of trials that fit the Wing and Kristofferson (1973) model for clock timing; Clock: clock variance (ms^2); Motor: motor variance (ms^2); SD: standard deviation.

Discussion

The main aim of this experiment was to examine both the role of multiple internal clocks and multiple sources of feedback in the bimanual advantage. Our first hypotheses, that the bimanual advantage would exist only for clock-timed tasks, was supported. The bimanual advantage was only seen for clock-timed tasks (tapping), and not for emergently timed tasks. Circle drawing, both with and without tactile feedback at the timing goal, exhibited equal variance for both unimanual and bimanual conditions. This is the first study comparing bimanual advantage in one task that utilises an internal clock and another task that does not. We show definitively here that multiple clocks are necessary to elicit the bimanual advantage and that feedback alone (without internal clocks) does not reduce timing variability when two hands time instead of one.

Despite other studies that suggested potential utilisation of an internal clock when emergent timing was performed with feedback at the timing goal (Studenka & Zelaznik, 2011; Studenka, Zelaznik, & Balasubramaniam, 2012), no bimanual advantage was seen for circle drawing in this study. It is likely that, for emergent tasks, feedback at the timing goal serves to aid synchronisation based on mechanisms of improved phase correction. Phase correction is a separate mechanism from the keeping of an internal pace (a task attributed to the internal clock; Thaut, Miller, & Schauer, 1998). Further work will need to examine the unique role of feedback for non-clock-timed tasks.

Our second hypothesis, that feedback pertaining to the timing goal would influence the bimanual advantage, was only supported for clock-timed tasks. No bimanual advantage was seen for tactile feedback circle drawing. Paired with the lag-one autocorrelation results indicating that both tactile and no-tactile feedback circle drawing did not use an internal clock, we conclude that multiple clocks are crucial to the bimanual advantage. Of further interest to the understanding of the bimanual advantage was the interaction between feedback and clock timing. In many of the experiments showing reduced timing variance due to increased tactile feedback, the unimanual condition involved tactile feedback, and the bimanual condition (at least for one hand) did not (Drewing et al., 2002). Perhaps surprisingly, in this study, no bimanual advantage was seen when comparing tactile feedback unimanual tapping with no-tactile feedback bimanual tapping, leading to the conclusion that multiple clocks are not sufficient in and of themselves to elicit a timing advantage; rather, enhanced feedback serves to reduce timing variability overall. These findings support the literature indicating that enhanced sensory feedback pertaining to timing goals improved both unimanual and bimanual timing (Drewing & Aschersleben, 2003; Drewing et al., 2002), as well as the literature supporting the crucial role of multiple clocks in the bimanual advantage (Helmuth & Ivry, 1996). We conclude that internal clock mechanisms are necessary for the bimanual advantage to occur and that additional sources of feedback serve to augment the already utilised internal timing mechanisms.

The bimanual advantage was not elicited when additional tactile feedback was added to circle drawing, suggesting that the role of feedback is specifically related to informing and updating internal clock models for timing. So, how does feedback served to improve the internal clock? The classic Wing and Kristofferson timing model is assumed to be open-loop, with no incorporation of feedback from previous taps; however, the role of feedback in improving timing is also well documented. Wing (1977) presented a study in which delayed auditory feedback from one tap influenced the immediately subsequent tap interval, indicating some level of closed-loop control. Drewing and colleagues proposed a mechanism whereby increased sensory information pertaining to a timing goal may serve either to improve detection of timing errors or to improve the ability to predict future movement consequences (see Drewing & Aschersleben, 2003). Drewing and colleagues (2002) proposed a modification of the Wing and Kristofferson model whereby the timekeeper uses sensory reafferences not as a means for correcting errors in taps but as a means for planning more precise future movements. In other words, accurate timing depends upon being able to produce actual sensory reafferences that coincide with predicted sensory reafferences. Enhanced feedback at the timing goal, thus, serves to improve the prediction of sensory reafference, thereby reducing variability in producing timed intervals. Similarly, multiple sources of sensory reafference lead to multiple simulations of the timing goal, which serves to reduce variability of this prediction explaining the advantage seen both when tactile feedback is enhanced and when multiple sources of tactile feedback are present (e.g., via different hands tapping together).

Conclusion

In sum, our findings show, for the first time, a lack of bimanual advantage in an emergently timed task. In addition, the role of feedback in improving timing is supported by improved timing in unimanual tapping with (vs without) tactile feedback. In further support of the role of feedback, no bimanual advantage was seen in tapping without feedback compared with unimanual tapping with feedback. These findings link the two main hypotheses for the bimanual advantage by supporting that the effects of multiple clocks and multiple sources of feedback are additive in improving timing variability. Further work will need to explore specific mechanisms of improved timing related to improved predictions of the timing goal (via utilisation of sensory reafference) and improved precision of the timing of motor commands (via an averaging of multiple clock signals).

Author note

Daisha L Cummins and Megan A Pope were undergraduate researchers in the Department of Kinesiology and Health Science at the time the research was conducted.

Declaration of conflicting interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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