

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/45582169>

Perceptual and Attentional Influences on Continuous 2:1 and 3:2 Multi-Frequency Bimanual Coordination

Article in *Journal of Experimental Psychology Human Perception & Performance* · August 2010

DOI: 10.1037/a0019259 · Source: PubMed

CITATIONS

42

READS

153

3 authors:



[Attila J. Kovacs](#)

University of Wisconsin - La Crosse

38 PUBLICATIONS 566 CITATIONS

[SEE PROFILE](#)



[John J. Buchanan](#)

Texas A&M University

96 PUBLICATIONS 1,787 CITATIONS

[SEE PROFILE](#)



[Charles H. Shea](#)

Texas A&M University

210 PUBLICATIONS 5,591 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Action, perceptual, and cognitive stability [View project](#)

Perceptual and Attentional Influences on Continuous 2:1 and 3:2 Multi-Frequency Bimanual Coordination

Attila J. Kovacs, John J. Buchanan, and Charles H. Shea
Texas A&M University

Two experiments were conducted to determine if multi-frequency (2:1 and 3:2) coordination between the limbs is enhanced when integrated feedback is provided in the form of Lissajous plots, attention demands are reduced, and attempts to consciously coordinate the limbs are not encouraged. To determine the influence of vision of the limbs, covered and uncovered limb groups were provided online Lissajous feedback. To determine the impact of the Lissajous feedback, a control group that was not provided Lissajous feedback was also tested. The data indicated remarkably effective performances after 5 min of practice when limbs were covered and Lissajous feedback was provided. When Lissajous feedback was provided and vision of the limbs was permitted, performance deteriorated. Performance by the group not provided Lissajous feedback was quite poor. The findings suggest that some of the difficulty associated with producing difficult bimanual coordination patterns are due to the less than optimal perceptual information available in various testing situations and the attentional focus imposed by the participant.

Keywords: bimanual coordination, perception-action dynamics, polyrhythm, focus of attention

Bimanual movements have been used extensively in the study of interlimb coordination, especially with respect to developing theories of temporal order. A large number of experiments "... have revealed quite remarkable temporal constraints between the two hands when they are functioning together" (Kelso & deGuzman, 1988), such that only a few movement patterns can be effectively performed without extensive practice. This is often illustrated in experiments wherein 1:1 rhythmic movements of the limbs (fingers, wrists, arms) at a required relative phase of 30° to 150° (Tuller & Kelso, 1989; Yamanishi, Kawato, & Suzuki, 1980), for example, are strongly attracted to in-phase ($\phi = 0^\circ$) and anti-phase ($\phi = 180^\circ$) coordination with the anti-phase pattern less stable than the in-phase pattern (e.g., Kelso, 1981, 1984; Kelso, Scholz, & Schöner, 1986). In other words, other relative phase patterns are not inherently stable and the motor system shows a bias towards what has been labeled the intrinsic dynamics of in-phase and anti-phase coordination (Schöner & Kelso, 1988). Moreover, an increase in movement frequency leads to a loss of stability in the anti-phase pattern and participants spontaneously transition to the more stable in-phase coordination pattern in many experimental tasks (e.g., Kelso, 1981, 1984, 1995). This pattern of results has been explained using concepts taken from nonlinear dynamics and modeled using nonlinearly coupled limit cycle oscillators (Haken, Kelso, & Bunz, 1985) perturbed by stochastic forces (Schöner, Haken, & Kelso, 1986). It is important to note that the tendency for in-phase and anti-phase movements of the two fingers or limbs has been thought to be due in part to a bias originating in the action

component of the perception-action system (e.g., Kagerer, Summers, & Semjen, 2003; Kennerly, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002; Peper, de Boer, de Poel, & Beek, 2008).

This tendency towards preferred coordination patterns has also been observed in bimanual multi-frequency rhythmic tasks. For example, 2:1 and 3:1 tapping ratios can be produced effectively by novice participants after 1 or 2 sessions of practice and with little or no additional practice by trained musicians (e.g., Peper, Beek, & van Wieringen 1995a, 1995b; Summers, Todd, & Kim, 1993; Walter, Corcos, & Swinnen, 1998). However, continuous limb motion performance of multi-frequency ratios appear to pose quite difficult challenges for the nervous system (e.g., Byblow & Goodman, 1994; Sternad, Turvey, & Saltzman, 1999a, 1999b; Treffner & Turvey, 1993; Swinnen, Dounskaia, Walter, & Serrien, 1997), as illustrated in the following quote:

While a 2:1 ratio in a bimanual tapping task is relatively easy to perform, producing the same ratio in tasks involving the wrist or elbow oscillations where the limbs are moving continuously is extremely difficult (Summers, Davis, & Byblow, 2002, p. 702).

More than 50 years ago, Fraisse (1946) described limitations in participants' ability to produce simple and complex ratios (e.g., 1:1, 1:2, 2:3, etc.) with difficulty functionally increasing as one moves down the branches of the Farey tree. This difficulty arises, at least theoretically, from decreasing widths of the resonance regions (see Arnold tongues), wherein higher order ratios are associated with narrower resonance channels. Thus, as one moves down the branches of the Farey tree, multi-frequency bimanual coordination can be more easily disrupted by smaller and smaller perturbations (see Kelso, 1995; Treffner & Turvey, 1993, for discussions). Thus, pattern stability and task complexity are related to the level in the Farey tree and inversely proportional to Arnold tongue width (Arnold, 1983). Indeed, some complex ratios (e.g., 2:3, 4:3, 5:3) were not only thought to be difficult but were thought

Attila J. Kovacs, John J. Buchanan, and Charles H. Shea, Department of Health and Kinesiology, Texas A&M University.

Correspondence concerning this article should be addressed to Charles H. Shea, Department of Health and Kinesiology, Texas A&M University, College Station, TX 77843-4243. E-mail: cshea@tamu.edu

to be virtually impossible to perform effectively in continuous movement tasks. Although difficult to perform, higher order frequency ratios have been investigated in tapping tasks (Boonstra, Daffertshofer, Breakspear, & Beek, 2007; Klapp, Nelson, & Jagacinski, 1998; Kurtz & Lee, 2003) and most often with skilled musicians (e.g., Bogacz, 2005; Collier & Wright, 1995; Peper et al., 1995a, 1995b; Summers et al., 1993). They have also been investigated in continuous motion tasks using hand held pendulums in one or both hands (e.g., Treffner & Turvey, 1993) and have been found to spontaneously emerge in a bimanual circle tracing task but not maintained for a prolonged period of time (Buchanan & Ryu, 2006).

The reason for this difficulty in producing simple and complex ratios was thought to arise from the strong phase attraction toward 1:1 coordination, specifically in-phase and anti-phase, that is intrinsic in the human and animal nervous system. Indeed, not only motor but perceptual/cognitive explanations have been explored. Mechsner, Kerzel, Knoblich, and Prinz (2001), for example, altered the perceptual information by changing the position of one hand relative to the other (e.g., from pronation-pronation to pronation-supination) in a 1:1 finger task. With this information, Mechsner et al. (2001) demonstrated that the symmetry bias toward in-phase was actually based on spatial and perceptual constraints without regard to the muscles involved (see also Riek, Carson, & Byblow, 1992, and Riek & Woolley, 2005, for similar experiments with different outcomes at faster frequencies). Thus, the authors argued for the notion that movements are organized in terms of their perceptual goals and that resulting motor activity "is spontaneously and flexibly tuned in." Work examining intra-limb wrist-elbow (Buchanan & Kelso, 1993; Kelso, Buchanan, & Wallace, 1991), shoulder-leg (Meesen, Wenderoth, Temprado, Summers, & Swinnen, 2006), and wrist-ankle (Baldiessa, Cavallari, & Civaschi, 1982; Baldiessa, Cavallari, Marini, & Tassone, 1991) coordination has also shown that joint rotation and/or direction can override the biases associated with flexion-extension muscle activity based on the orientation (e.g., pronation-supination) of the limbs. Mechsner et al. (2001) also demonstrated that a complex 4:3 polyrhythm could be performed relatively well when perceptual symmetry was established. Participants attempted to move two visible flags by way of cranks hidden under the table. The gears for one flag were set at 1:1 so that each full turn of the crank resulted in one full circle of that flag while the gears for the other flag were set at 4:3 requiring a $[3/4]$ turn to produce one full revolution of that flag. The participant was instructed to turn the cranks so the movements of the flags were coordinated in an in-phase (0°) or anti-phase (180°) pattern. Provided this perceptual information, participants were able to perform the 1:1 in-phase and anti-phase flag patterns (i.e., an actual 4:3 bimanual polyrhythm) relatively well after only 20 minutes of practice.

Another perceptual manipulation involves the use of Lissajous plots, which integrate the position of the two limbs into a single point in one plane, to provide concurrent and/or terminal feedback information to the performer (see Amazeen, DaSilva, & Amazeen, 2008 for an alternative method of providing salient feedback). Lissajous feedback has been used with some success in bimanual experiments requiring individuals to learn novel 1:1 coordination patterns with various phase lags (e.g., Hurley & Lee, 2006; Lee, Swinnen, & Verschueren, 1995; Swinnen, Dounskaia, Verschueren, Serrien, & Daelman, 1995; Swinnen, Lee, Verschueren,

Serrien, & Bogaerts, 1997; Swinnen, Verschueren, et al., 1998) and to learn 2:1 coordination patterns (e.g., Summers et al., 2002; Swinnen, Dounskaia, et al., 1997). For example, Swinnen, Lee, et al. (1997) had participants practice a 1:1 bimanual coordination pattern with a 90° phase offset for three days (50 trials per day) under various feedback conditions. Most relevant to the present discussion were conditions with and without online Lissajous feedback. The Lissajous plot integrates the movement of the two limbs into a single point by having the movement of one limb move the cursor horizontally while the motion of the other limb moves the cursor vertically. Thus, a 1:1 movement pattern with 90° phase offset would result in circular movement of the cursor. Swinnen, Lee, et al. (1997) found enhanced performance during acquisition for the group provided the Lissajous feedback relative to the group without the Lissajous information. Performances on retention and transfer tests were also enhanced following acquisition with Lissajous feedback.

It should be noted that a Lissajous plot as a source of perceptual information may serve to reduce attentional demands because the participant's attention does not have to be split between the two limbs in order to determine the coordination pattern between the limbs. Instead, attentional resources may be directed towards the integrated representation of the two limbs in the Lissajous plot. That is, coordination errors may be more easily detected and thereby corrected, especially when a goal movement pattern template is provided in the Lissajous plot. However, if participants do split attention between the limb movements and the Lissajous feedback, the information could be somewhat conflicting because the limb movements and the Lissajous display coordinate systems are different. That is, in a Lissajous plot, the movement of each limb is mapped to a specific axis. For example, the Lissajous plot could be defined such that movement of the right limb results in horizontal (flexion-left and extension-right) and movement of the cursor with left limb movement resulting in vertical (flexion-down and extension-up) movement of the cursor. This is quite different from the actual movements of the limbs in Cartesian coordinates. In the 4:3 polyrhythm experiment by Meschsner et al. (2001, Exp. 3), the participants' attention was directed towards the flags rotating in the horizontal plane and not toward the actual motion of their limbs that was blocked from view. Covering of the limbs may have been a critical design feature for two reasons: first, because vision of the limbs moving could conflict with the movement displayed by the flags, and second, because participants appear to have a strong tendency to attempt to consciously control limb motion when the limbs are visible. Research on attentional focus has shown that participants tend to relinquish conscious control when limb motion is hidden from view and/or when the participant's attention is directed to other salient information (see Wulf, 2007, for review). For example, McNevin, Shea, and Wulf (2003) found an improvement in stabilometer performance when participants' attentional focus was directed away from their feet and legs. Frequency analysis (FFT) of the platform's motion indicated an overall increase in mean power frequency of the platform's motion with an overall decrease in amplitude when attention was directed away from the feet and legs relative to when participants were instructed to monitor their lower limb movements. The authors argued that focusing attention on the lower limbs compromised (or constrained) the normal regulatory processes involved in balance. That is, when focusing on their lower limbs, participants actively

intervened in the normal balance processes resulting in less stable performance. McNevin et al. (2003) referred to this as the “constrained action hypothesis” because it appeared that attention directed to the limbs increased the likelihood that participants exerted conscious control of the limbs, thereby inhibiting more efficient reflexive control processes. Similar findings have been observed in shooting and pointing experiments (e.g., Keogh, Morrison, & Barrett, 2004) wherein participants had to hold the extended arm as still as possible and maintain a stable hand position while holding a pistol or laser pointer—given a brief rest period—then asked to again maintain a stable limb position. The counter intuitive findings were that participants were more stable during the rest period than during the test period when they were specifically asked to be as stable as possible. These data are consistent with the notion that conscious attempts to intervene in the control processes can be detrimental to performance.

As suggested by the stabilometer study, providing vision of the limbs during a bimanual coordination task may well increase the likelihood that participants attempt to consciously intervene in the control of one or both limbs to the detriment of bimanual performance. It is interesting to see that Mechsner et al. (2001) noted that “Anecdotal evidence seems to suggest that attention to the hands disrupts control of the iso-frequency relationship between the flags” (p. 72). Indeed, the role of attention in general in bimanual movements has received a good deal of experimental investigation (e.g., Byblow, Bysouth-Young, Summers, & Carson, 1998; Hiraga, Summers, & Temprado, 2004; Summers, Maeder, Hiraga, & Alexander, 2008). Empirical findings by Temprado, Zanone, Monno, and Laurent (1999) showed that the stability of the intrinsic dynamics (i.e., in-phase and anti-phase) as well as the difference between them depends on the attentional priority given to the coordination task. When attention to the bimanual task was somehow released (i.e., shared attention in a dual-task condition or focus on the secondary task) both intrinsic patterns showed a consistent increase in variability with a higher increase for the anti-phase compared with the in-phase pattern. Conversely, when attention was directed to the bimanual task, variability of both patterns decreased with a stronger effect for the anti-phase pattern. Furthermore, these effects observed at the level of the coordination pattern were also reflected at the component level (individual limbs). The findings of Temprado et al. (1999) might at first glance seem contradictory to the notion that attentional focus directed away from the limbs might increase movement pattern stability as suggested by the stabilometer studies. However, it should be noted that in the Temprado et al. (1999) study attentional focus was not manipulated *per se* but it was confounded with increased and/or decreased attentional load by introducing a secondary task. What the Temprado et al. (1999) study clearly demonstrated is that attentional load or demands directly interact with the intrinsic dynamics, destabilizing to a greater extent coordination patterns that are inherently less stable (anti-phase).

In the Temprado et al. study (1999), the influence of the attentional load and focus was pertinent to the stability of the collective behavior (relative phase) while preserving the asynchrony between the limbs. However, there is quite a bit of experimental evidence indicating that handedness and attentional focus directed to one or the other limb influences the symmetry of the coupling between the components (e.g., Amazeen, Amazeen, Treffner, & Turvey, 1997; Peters, 1989; Treffner & Turvey, 1995, 1996). For example,

Amazeen et al. (1997) have provided evidence for handedness-related coupling asymmetry in a 1:1 frequency locked bimanual coordination task with left-handed participants tending to lead with their left hand while right-handed participants tended to lead with their right hand, in agreement with previous findings (Treffner & Turvey, 1995, 1996). Additionally, the results of Amazeen et al. (1997) extend previous findings, indicating that attentional focus to one or the other limb is also a mediating variable that influences asymmetric coupling between limbs. Indeed, Peters (1989) suggested that the expression of handedness in bimanual coordination may be the reflection of an inherent attentional bias, with right-handed participants preferentially attending to their right limb and left-handed participants preferentially attending to their left limb. However, the results of Amazeen et al. (1997) indicate that the effects of an imposed attentional asymmetry are similar to those resulting from the intrinsic bilateral asymmetry (handedness), but this symmetry does not necessarily imply causality, suggesting that attention and handedness are related through their mutual effects on the bimanual coordination dynamics (for similar results see de Poel, Peper, & Beek, 2008). In terms of attentional factors influencing multi-frequency tapping patterns (i.e., 2:3), Peters & Schwartz (1989) failed to find asymmetries due to which hand had to produce the faster frequency, but they did find that attention directed to the slower moving limb resulted in larger performance decrements than attention directed to the faster moving limb. This decrement was found in right-handed participants untrained and trained in music.

Two bimanual coordination experiments were conducted in an attempt to demonstrate that multi-frequency coordination between the limbs is more stable than typically demonstrated when (1) salient, integrated feedback is provided, (2) attention demands are reduced, and (3) attempts to consciously coordinate the limbs are not encouraged. In Experiment 1, the goal was a 2:1 ratio, and in Experiment 2, the goal was a more complex 3:2 ratio. In both experiments, participants were asked to produce the required multi-frequency ratio by continuously flexing and extending the elbows in the horizontal motion plane. One group of participants was permitted vision of their limbs and provided Lissajous feedback (uncovered limb-Lissajous group). Two additional groups performed the task while the limbs were blocked from view; one group was provided Lissajous feedback (covered limb-Lissajous) and the other was not provided the Lissajous feedback (covered limbs-no Lissajous). Participants in the Lissajous conditions were provided not only a Lissajous plot of the goal pattern but a cursor depicting the position of the two limbs which they could move over the goal pattern. Comparison of the uncovered and covered limb Lissajous groups allows the determination of the effect of vision of the limbs while using Lissajous feedback. We hypothesize that the uncovered limbs-Lissajous condition will encourage participants to attend to the two limbs' flexion-extension motions and the relationship of these motions to the cursor on the screen, whereas the covered limb-Lissajous condition will direct the participants' attention primarily to the motion of the cursor on the screen. We predict the difference in attention allocation will result in a significantly more stable production of the multi-frequency ratios by the covered limb-Lissajous group with minimal practice (4.5 minutes) in comparison to the uncovered limb-Lissajous group. Comparison of the performance of the covered limb-Lissajous and covered limb-no Lissajous conditions allows the

determination of the influence of Lissajous feedback. The above predictions regarding the simple and complex ratio patterns are based on recent work that has demonstrated that the use of Lissajous plots when vision of the limbs is blocked allows participants to rapidly tune in (<5 minutes of practice) a variety of 1:1 bimanual coordination patterns such as 30°, 90°, and 120° relative phase (Kovacs, Buchanan, & Shea, 2009a, 2009b).

We also encouraged participants in each group to increase their movement frequency following any trials in which the frequency of the faster moving (right, dominant) limb fell below 1 Hz. We used this method because our recent research indicated that the use of metronomes introduced attentional demands and control strategies that can negatively influence bimanual coordination when Lissajous feedback was provided. Kovacs, Buchanan, and Shea (2009a) asked participants to produce a 90° relative phase bimanual coordination pattern (elbow flexions and extensions). All participants in the Kovacs et al. (2009a) experiment received concurrent Lissajous feedback with and without a metronome (1 Hz). Participants not provided a metronome were simply encouraged to increase their cycling frequency if their frequency fell below the 1 Hz goal. Retention performance after 5 min of practice indicated substantially better performance for the no-metronome condition (relative phase variability and absolute error in relative phase <10°) compared to the metronome condition (relative phase variability and absolute error in relative phase ~30°). It is important to note that this factor may help explain why participants provided with Lissajous feedback and a pacing metronome and did not see their limbs when tested in a fMRI scanner (e.g., Debaere et al., 2001; Debaere, Wenderoth, Sunaert, Van Hecke, & Swinnen, 2003; Puttemans, Wenderoth, & Swinnen, 2005) or had vision of their limbs occluded for some other reason (e.g., Summers et al., 2002) did not perform as well as participants in the Kovacs et al. (2009a, 2009b; Kovacs & Shea, 2010) experiments.

Experiment 1: Ratio of 2:1

The use of Lissajous plots as a means of providing concurrent and terminal feedback when learning rhythmic bimanual coordination tasks is a relatively common occurrence in the motor control literature (e.g., Summers et al., 2002; Summers et al., 2008; Swinnen et al., 1997, 1998). To the best of our knowledge, whether a 1:1 or a multi-frequency ratio was the goal pattern, vision of the limbs was typically available to the participants during training (see exceptions above). We propose that vision of the limbs during multi-frequency bimanual coordination tasks promotes the conscious control of the movements to the detriment of continuously moving the limbs to achieve the coordination goal. If the Lissajous plot provides salient feedback for performance, then eliminating vision of the limbs will focus attention towards the feedback display and away from the limb's actual motions and allow for a quick tuning (Mechsner et al., 2001) of a coordination pattern thought to be quite difficult to perform with continuous motion of the limbs (Summers et al., 2002). This experiment will involve three groups with the test block occurring after only 4.5 min of practice (nine trials of 30 s). Instructions were identical for the three groups. One group could not view their limbs and were provided Lissajous feedback (covered limb-Lissajous), a second group were able to view their limb movements and were provided Lissajous feedback (uncovered limb-Lissajous). The final group

could not view their limbs and were not provided Lissajous feedback (covered limb-no Lissajous). Thus, comparison of the covered and uncovered Lissajous groups provided a measure of the effect of vision of the limbs and a comparison of the cover limb-no Lissajous and Lissajous groups was used to assess the influence of the Lissajous feedback.

Methods

Participants. Self declared right-handed undergraduate students ($N = 24$; 8 per group) volunteered to participate in the experiment after reading and signing a consent form approved by the IRB for the ethical treatment of experimental participants. None of the participants was an active musician, had significant musical training, or had participated in a previous bimanual coordination experiment. Participants received class credit for their participation.

Apparatus. The apparatus consisted of two horizontal levers and a projector. The levers were affixed at the proximal ends to near frictionless vertical axles. The axles, which rotated freely in ball-bearing supports, allowed the levers to move in the horizontal plane over the table surface. Near the distal end of each lever, a vertical handle was attached. The positioning of the handle was adjustable. When the participants rested their forearm on the lever, their elbow was aligned over the axis of rotation so that they could comfortably grasp the handle (palm vertical). The horizontal movement of the levers were monitored (200 Hz) by potentiometers that were attached to the lower ends of the axles. An example of displacements that produce a “perfect” 2:1 movement pattern is provided in Figure 1A. The on-line data were used to present a cursor (as a circle) on a screen directly to the front of the partic-

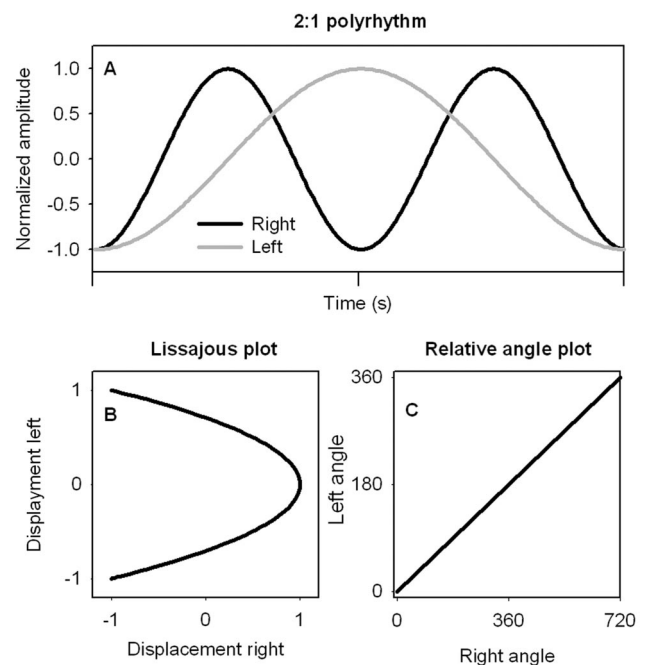


Figure 1. Displacements (A), Lissajous (B), and relative angle (C) plots for simulated left and right limb movements that result in a perfect 2:1 ratio.

ipant with the motion of the left lever moving the cursor up and down. The motion of the right lever resulted in moving the cursor left and right. Projected onto the screen was the required Lissajous plot that represented a 2:1 pattern of continuous sinusoidal motion (Figure 1B). The cursor and Lissajous plot were generated with customized software and displayed with a projector mounted above and behind the participant. Provision of this visual Lissajous feedback occurred in real time: The delay was only limited by the screen refresh rate (60 Hz).

Procedure. Participants sat at a table with their forearms resting on the levers that limited elbow motion to flexion-extension in the horizontal plane. Participants were seated on a height adjustable chair with the horizontal eye line corresponding with the midway point on the Lissajous plot projected onto the screen. Participants were randomly assigned to the uncovered limb-Lissajous or covered limb-Lissajous groups. A third control group, the covered limb-no Lissajous group was suggested by an anonymous reviewer and collected at a later date using the same subject pool. All participants were provided the instruction to make continuous movements of the left and right limbs such that the right limb made two complete cycles for every one of the left limb. They were told that a complete cycle involved extension and flexion of the limbs of about 60 degrees. After these instructions, the experimenter demonstrated 60 degrees of extension and flexion but informed them that maintaining the cycling relationship was more important than maintaining the precise amplitude of movement. In the uncovered limb-Lissajous condition, participants could see the motion of their limbs and view the Lissajous plot illustrating the goal movement pattern (2:1) with the current position of their limbs indicated by the cursor overlaid on the plot. In the covered limb-Lissajous condition, participants were provided the same Lissajous plot and cursor but their limbs were blocked from view. Participants in the covered limb-no Lissajous condition could not view their limbs and were not provided the Lissajous plot. Comparison of the covered and uncovered limb-Lissajous groups provided a measure of the effect of vision of the limbs and a comparison of the cover limb-no Lissajous and Lissajous groups was used to assess the influence of the Lissajous feedback. Comparisons between the covered limb-no Lissajous group and the uncover limb-Lissajous group are not be discussed because of the difficulty in attributing the differences to either the Lissajous feedback or the vision of the limbs.

All participants were informed that they were to attempt to move their right and left limbs back and forth (range approximately 60 degrees) and that the right limb should cycle two times for every cycle of the left limb. After any trial in which the average frequency of the faster limb was below 1.0 Hz, the experimenter encouraged the participants to increase their movement speed without disrupting the intended movement pattern. All participants completed 10 trials (30 sec each). They were informed that Trials 1–9 were practice trials and Trial 10 was a test trial. After completing the nine practice trials, participants were provided a short break followed by the test trial. The test trial was conducted under the same conditions as experienced during the nine practice trials.

Measures and data reduction. All data reduction was performed using MATLAB. The potentiometer signals representing the limbs' displacements were low-pass filtered with a second order dual pass Butterworth with a cutoff frequency of 10 Hz. Velocity and acceleration signals were computed with each signal

filtered (Butterworth, 10 Hz) before performing the next differentiation. The analyses presented will focus on both bimanual coordination performance of the required multi-frequency ratio and unimanual motion performance of the right and left limbs.

Unimanual measures. Cycle durations and cycle duration variability were computed on a cycle basis with each cycle representing every other zero crossing in the displacement trace (Cycle duration = $Z_{Ci+2} - Z_{Ci}$). Cycle duration variability was defined as the standard deviation of the cycle to cycle durations. Windows between a pair of zero crossings in the displacement trace were defined in order to compute an index of movement harmonicity (H; Guiard, 1993). Each non-overlapping time window comprised a single movement reversal. Within each time window, all deflections of the normalized acceleration trace were identified. When the acceleration trace was positive (negative displacement) within this window, H was computed as the ratio of minimum to maximum acceleration. Conversely, when the acceleration trace was negative (positive displacement) within this time window, H was computed as the absolute ratio of maximum to minimum acceleration. When a single peak (sinusoidal acceleration) occurred in the acceleration trace within this window, the value of H was set to 1, indicating harmonic motion of the limb. If the acceleration trace crossed from positive to negative (or vice versa) within this window, the value of H was set to 0, indicating inharmonic motion. Finally, the individual harmonicity values of each time window for a trial were averaged yielding a global estimate of H.

Bimanual measures. The individual limb mean cycle frequencies were used to compute a frequency ratio of right-arm to left-arm motion. This measure provides a temporal measure of goal attainment that is independent of limb coordination tendencies and actual limb trajectories. To examine the spatial-temporal coordination of the limbs' motion, a continuous relative phase between the two limbs was computed. Prior to computation of the left and right limb individual phase angles, displacement and velocity traces were normalized in two steps: first, the mean of each data series was subtracted from each data point in the series to center the time series around zero, and second, each data point in the centered time series was divided by the highest absolute value (minimum or maximum) of the time series. The phase angle (θ_i) for each limb ($i = \text{right, left}$) was computed for each sample of the displacement time series as follows (Kelso et al., 1986):

$$\theta_i = \tan^{-1}[(dX_i/dt)/X_i]$$

with X_i representing the normalized position of the right and left limbs and dX_i/dt the instantaneous normalized velocities for the right and left limbs.

Next, the individual phase angles θ_i were unwrapped by finding absolute jumps greater than 2π and adding appropriate multiples of 2π to each data point following the jump. After the unwrapping, the continuous relative phase between the right and left phase angles was computed for each epoch comprising two complete cycles of the right limb (faster moving). The continuous relative phase values over each epoch were subtracted from a relative phase representing a pure 2:1 ratio between harmonic oscillators to generate a relative phase error, with the faster oscillator representing motion of the right limb. The line in Figure 1C represents the continuously changing continuous relative phase target values generated between two oscillators (Figure 1A) at a 2:1 ratio. The phase errors in each epoch were used to compute a root mean square error (RMSE) and the epoch

RMSEs were averaged across the trial. The RMSE provides a measure of goal attainment, with smaller values representing more accurate performance of the required continuous 2:1 ratio. The signed phase errors in each epoch were used to compute relative phase variability (VE) as standard deviation of the signed relative phase.

Results

Practice trials. Mean relative phase variability, and RMSE of relative phase were analyzed in 3 Group (covered limb-Lissajous, uncovered limb-Lissajous, covered limb-no Lissajous) \times Trial (1–9) ANOVAs with repeated measures on trial. Duncan's new multiple range test and simple main effects post-hoc tests were performed when appropriate ($\alpha = .05$).

The analysis of relative phase variability (Figure 2A) indicated a main effect of group, $F(2, 21) = 5.46, p < .05, \eta_p^2 = .35$, and trial, $F(8, 168) = 10.60, p < .05, \eta_p^2 = .39$. In addition, the Group \times Trial interaction, $F(16, 168) = 2.94, p < .05, \eta_p^2 = .16$, was also significant. Simple main effects analysis failed to detect a decrease in relative phase variability across trials for the covered

limb-no Lissajous group but did detect decreases across practice trials for the covered limb-Lissajous and uncovered limb-Lissajous groups. Simple main effects analysis also detected reduced relative phase variability for the covered limb-no Lissajous group relative to the covered and uncovered Lissajous groups on Trials 1–3 but reduced relative phase variability was found for the covered limb-Lissajous group on Trials 8–9, relative to the uncovered limb-Lissajous and covered limb-no Lissajous groups.

The analysis of RMSE of relative phase (Figure 2B) indicated a main effect of trial, $F(8, 168) = 12.04, p < .05, \eta_p^2 = .37$. In addition, the Group \times Trial interaction, $F(16, 168) = 2.79, p < .05, \eta_p^2 = .25$, was significant. Simple main effects analysis failed to detect a decrease in RMSE of relative phase across trials for the covered limb-no Lissajous group but did detect decreases in the covered limb-Lissajous and uncovered limb-Lissajous groups across practice trials. Simple main effects analysis also detected reduced relative phase RMSE for the covered limb-Lissajous group relative to the uncovered limb-Lissajous and covered limb-no Lissajous groups on Trials 7–9.

Test trial. Examples of displacement, Lissajous, and continuous relative phase plots on the test trial for two participants from each group are provided in Figure 3. As the time series illustrate, participants in the covered limb-Lissajous group were good at producing two cycles of right-arm motion for every one cycle of left-arm motion with the cycles converging at elbow flexion. In general, the limb trajectories from the covered limb-Lissajous group were more sinusoidal and the Lissajous plots and phase angle plots reflect less variation in performance compared to the uncovered limb-Lissajous and covered limb-no Lissajous groups.

Mean frequency ratio, relative phase variability, and relative phase RMSE were analyzed in 3 group (covered limb-Lissajous, uncovered limb-Lissajous, covered limb-no Lissajous) ANOVAs and these results are presented in the bimanual performance section. Mean harmonicity, cycle duration, and standard deviation of cycle duration data were analyzed in 3 group (covered limb-Lissajous, uncovered limb-Lissajous, covered limb-no Lissajous) \times 2 limb (left, right) ANOVAs with repeated measures on limb and these results are presented in the unimanual performance section. Duncan's new multiple range test and simple main effects post-hoc tests were performed when appropriate ($\alpha = .05$).

Bimanual performance. The analysis of the cycle frequency ratio (Figure 4A) revealed a main effect of group, $F(2, 21) = 4.01, p < .05, \eta_p^2 = .32$. The Duncan's new multiple range test indicated that the covered limb-Lissajous and uncovered limb-Lissajous groups, which were not different from each other, were different from the covered limb-no Lissajous groups.

The analysis of relative phase variability (Figure 4B) indicated a main effect of groups, $F(2, 21) = 11.72, p < .01, \eta_p^2 = .48$. Duncan's new multiple range test indicated relative phase variability was smaller in the covered limb-Lissajous group than in the uncovered limb-Lissajous and the covered limb-no Lissajous group. In terms of relative phase RMSE (Figure 4C), a measure of accuracy in achieving the desired relative phase that considers both bias and variability, the analysis indicated a main effect of group, $F(2, 21) = 7.42, p < .05, \eta_p^2 = .41$. The multiple range test indicated smaller relative phase RMSE for the covered limb-Lissajous group with RMSE values more than 2.5 times higher in the uncovered limb-Lissajous group. The covered limb-no Lissa-

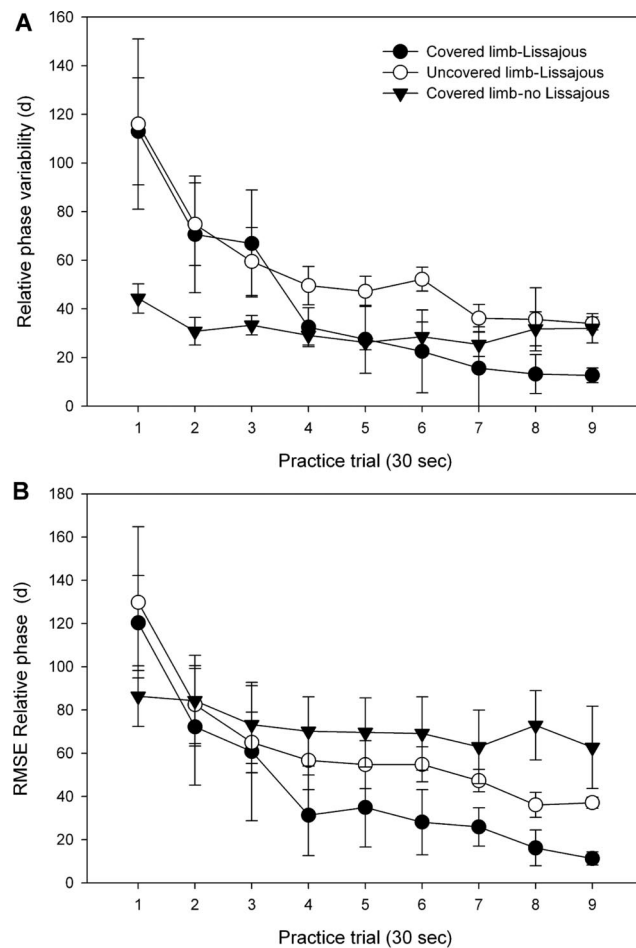
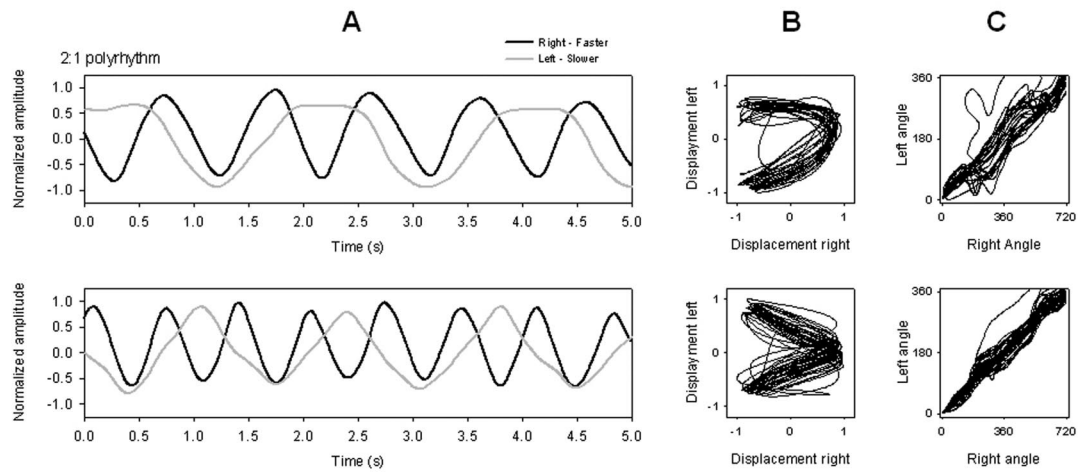
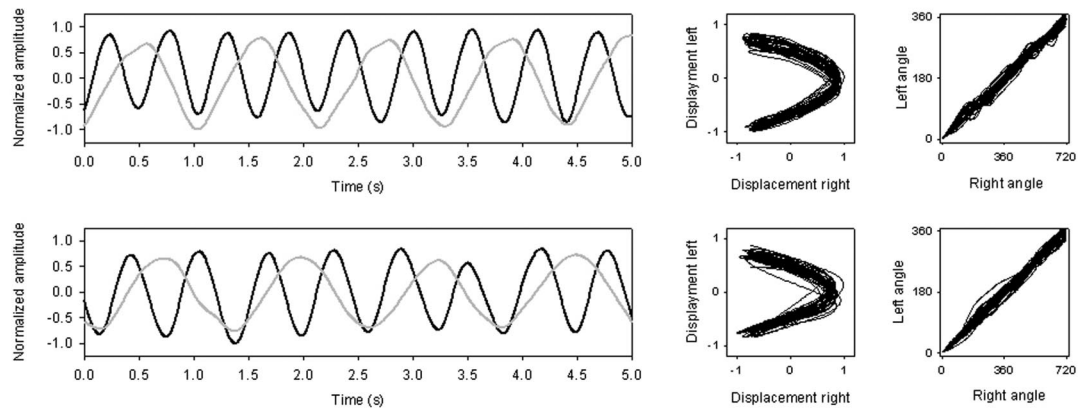


Figure 2. Mean relative phase variability (A) and RMSE (B) relative phase for practice trials 1–9 in Experiment 1. Error bars represent +/- standard errors.

Limbs uncovered/Lissajous



Limbs covered/Lissajous



Limbs covered/No Lissajous

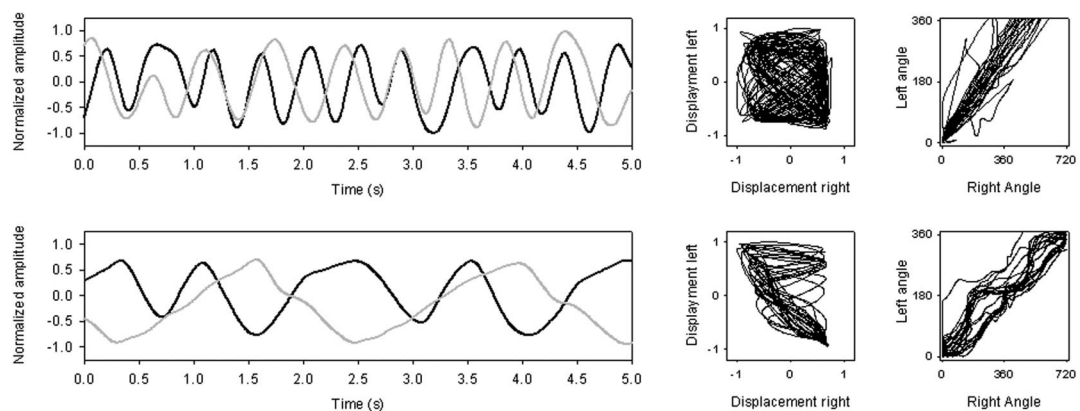


Figure 3. Examples of the time series for two participants in the uncovered limb-Lissajous (top), covered limb-Lissajous (middle), and covered limb-no Lissajous (bottom) conditions in Experiment 1. Normalized left and right limb displacements (A), Lissajous plot (B), and relative angle plots (C) from the test trial are provided.

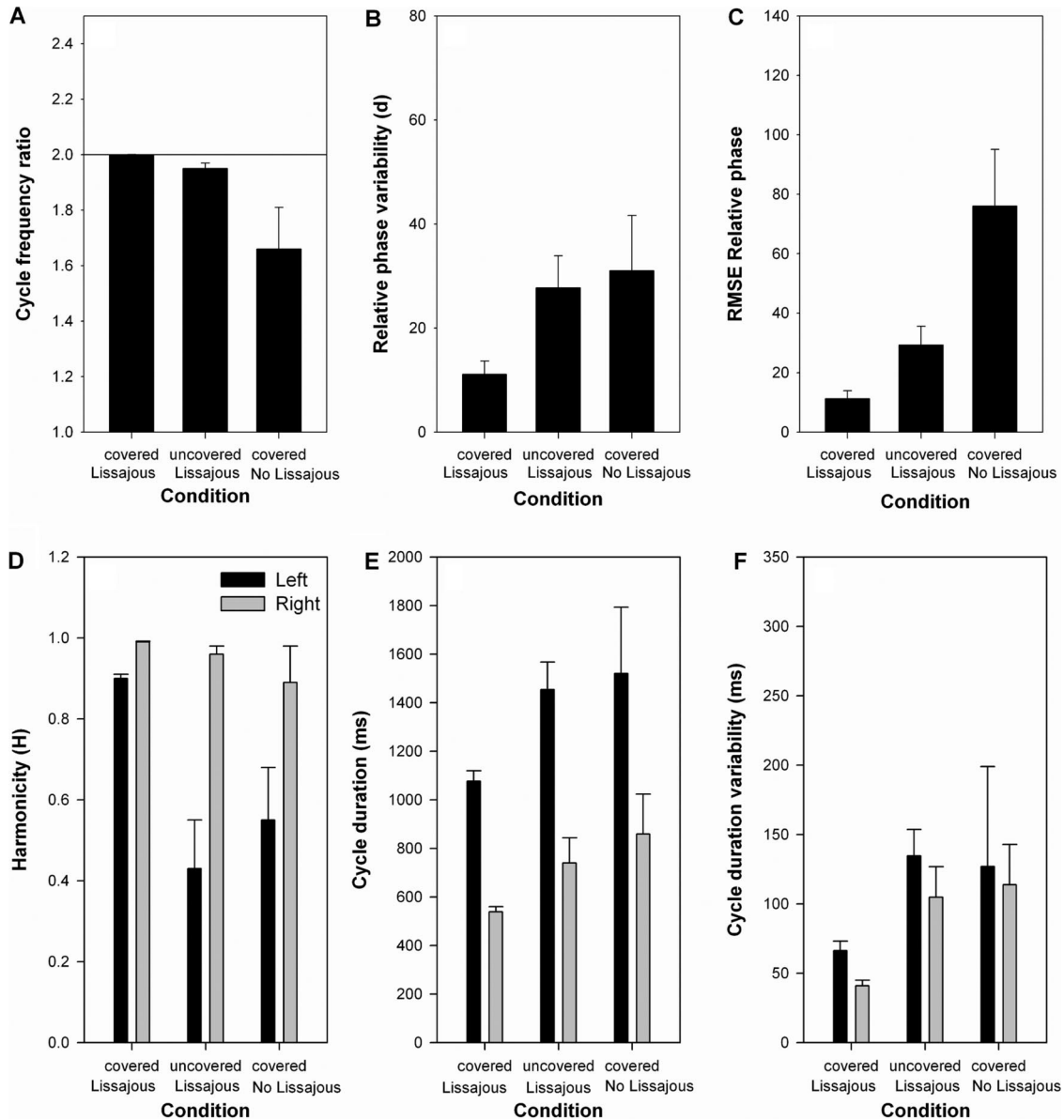


Figure 4. Mean cycle frequency ratio (A), relative phase variability (B), relative phase RMSE (C), harmonicity (D), cycle duration (E), and cycle duration variability (F) in Experiment 1. Error bars represent \pm standard errors.

jous group produced substantially higher RMSE values than the two groups provided Lissajous information.

Unimanual performance. The analysis of harmonicity (Figure 4D) detected a main effect group, $F(2, 21) = 5.16$, $p < .05$, $\eta_p^2 = .35$. Duncan's new multiple range test indicated more harmonic motion for the covered limb-Lissajous group than for the uncovered limb-Lissajous and covered limb-no Lissajous groups. The main effect of limb was also significant, $F(1, 21) = 35.35$, $p < .01$, $\eta_p^2 = .65$, with right-limb motion more harmonic than the left-limb. The Group \times Limb interaction was also significant, $F(2, 21) = 4.82$, $p < .01$, $\eta_p^2 = .34$. Simple main effects analysis failed to indicate a difference between the H values for the left and right limbs in the covered limb-Lissajous but did detect a difference

between left and right limbs for the uncovered limb-Lissajous and covered limb-no Lissajous groups with harmonicity for the left limb substantially lower than for the right limb.

As expected, the analysis of the mean cycle duration data (Figure 4E) indicated a main effect of limb, $F(1, 21) = 45.53$, $p < .01$, $\eta_p^2 = .71$, with the right limb having shorter cycle durations than the left limb in all groups. The main effect of group and the Group \times Limb interaction were not significant. In terms of the standard deviation of cycle duration (Figure 4F), the main effect of group, $F(2, 21) = 4.35$, $p < .01$, $\eta_p^2 = .32$, was significant. Duncan's multiple range test indicated cycle duration variability was lower in the covered limb-Lissajous group than in the uncovered limb-Lissajous and covered limb-no Lissajous groups. The

main effect of limb and the Group \times Limb interaction were not significant.

Discussion

The bimanual measures indicate that the uncovered limb-Lissajous and covered limb-no Lissajous groups did not produce the 2:1 ratio as effectively as the covered limb-Lissajous group after 4.5 minutes of practice. The level of bimanual performance attained by the covered limb-Lissajous group in the current experiment was remarkable, especially when compared to other research wherein performers required several days of practice (e.g., 5 days/80 trials per day) to achieve similar levels of performance on a 2:1 ratio (e.g., Swinnen, Dounskaia, et al., 1997). In the uncovered limb-Lissajous group, the motion of the slower moving left arm was less harmonic, and cycle duration variability for both limbs were larger than that in the covered limb-Lissajous group. This indicates that vision of the limbs disrupted left-arm performance, which in-turn produced a decrement in bimanual performance. A comparison of the covered limb-Lissajous and covered limb-no Lissajous groups' performance demonstrates that, while both groups produced similar unimanual characteristics, bimanual performance was greatly enhanced by providing the Lissajous feedback. Apparently, providing vision of the limbs when Lissajous feedback is provided increases the likelihood that participants will direct their attention to the conscious control of their left, slower moving limb to the detriment of producing the desired 2:1 ratio. This suggests that at least part of the success demonstrated by participants in the Mechsner et al. (2001) work (Experiment 3) was due to the fact that vision of their limbs was occluded and not solely due to the perceptual character of the gears/flags arrangement. Thus, these findings demonstrate quite clearly that covering of the limbs in combination with visual information in the form of Lissajous plots allowed participants to efficiently detect and correct coordination errors and precisely tune in the desired 2:1 movement pattern.

Experiment 2: Ratio of 3:2

The purpose of Experiment 2 was to determine if the same pattern of results found for a 2:1 ratio would be replicated when participants are required to produce a 3:2 ratio that is typically considered a more difficult bimanual coordination pattern (deGuzman & Kelso, 1991; Deutsch, 1983; Povel, 1981). From a descriptive standpoint, a 2:1 ratio has one movement frequency that is an integer multiple of the other. With regard to moving limbs, this temporal relationship is characterized by well defined position markers that can be used as feedback by the participant to assess and adjust the relative motion of the two limbs. For example, in Experiment 1, each return of the slower moving left-arm to flexion coincided with every other return of the faster moving right-arm to flexion. Indeed, the alternate returns of the faster moving right-arm coincided with peak extension of the slower moving left-arm. Alternatively, a 3:2 ratio involves producing one cycle of motion in the faster limb for each 2/3 cycle of motion in the slower limb. Markers are also available for the bimanual 3:2 ratio, but they occur less frequently, e.g., often when performed correctly the limbs come together at a flexion position once every three cycles for the faster moving limb, which coincides with every two cycles for the slower moving limb.

We are not aware of an experiment using a 3:2 ratio requiring continuous movement of the limbs without the aid of either a torque motor to drive the movement of one limb or pendulums to aid the movement of one or both limbs. Presumably, the lack of experiments is related to the difficulty of producing this coordination pattern. A number of researchers have used 3:2 ratios in discrete tapping tasks (e.g., Klapp et al., 1998) and often with trained musicians as participants (e.g., Bogacz, 2005; Collier & Wright, 1995). De Guzman and Kelso (1991) did use a continuous finger task, but the movement of the left finger was driven by a torque motor. The participant's task in the deGuzman and Kelso experiments was to maintain either a 1.5 or 2.0 Hz movement with the right finger while the apparatus moved the left finger at a preset frequency to achieve the desired polyrhythm. In addition, Treffner and Turvey (1993) asked participants to produce various polyrhythms including a 3:2 while holding pendulums in one or both hands. The pendulums had different length/weight combinations that assisted the production of the desired coordination pattern.

We proposed, based on the work by Mechsner et al. (2001) and our findings from Experiment 1, that participants will be able to produce a continuous 3:2 bimanual polyrhythm with relatively little practice. As in Experiment 1, we predicted that an uncovered limb-Lissajous condition will result in decreased harmonicity in the left limb and increased cycle to cycle variability, which will result in less effective bimanual coordination compared to the covered limb-Lissajous condition. Further, we predict that the covered limb-Lissajous condition will result in more effective bimanual coordination as indicated by reduced relative phase variability and RMSE of relative phase than the covered limb-no Lissajous and uncovered limb-Lissajous conditions. To test these predictions, we use the same paradigm and measures as used in Experiment 1 but simply changed the verbal description provided to all participants and the goal Lissajous plot provided to the covered and uncovered limbs Lissajous conditions to that appropriate for a 3:2 polyrhythm. Only 4.5 minutes of practice will be provided because we propose that given the appropriate perceptual information that participants can essentially tune-in the required motor responses to achieve the goal coordination pattern.

Methods

Participants. Self declared right-handed undergraduate students ($N = 24$; 8 per group) volunteered to participate in the experiment after reading and signing a consent form approved by the IRB for the ethical treatment of experimental participants. None of the participants was an active musician, had significant musical training, or had participated in a previous bimanual coordination experiment. Each participant received class credit.

Apparatus. The apparatus was the same as used in Experiment 1.

Procedure. The practice conditions (groups) and procedures were identical to those used in Experiment 1 with the exception that participants in the two Lissajous conditions were provided instructions to make continuous movements of the left and right limbs such that the right limb made three complete cycles for every two of the left limb. They were told that a complete cycle involved extension and flexion of the limbs of about 60 degrees. After these instructions, the experimenter demonstrated 60 degrees of extension and flexion but informed them that the maintaining the

cycling relationship was more important than maintaining the precise amplitude of movement. In addition, the goal Lissajous pattern representing a 3:2 ratio was provided. The Lissajous plot for a 3:2 ratio and waveforms used to generate the plot are illustrated in Figure 5. As in Experiment 1, all participants completed 10 trials (30 sec each). They were informed that Trials 1–9 were practice trials and Trial 10 was a test trial. After completing the nine practice trials, participants were provided a short break followed by the test trial. The test trial was conducted under the same conditions as experienced during the nine practice trials.

Measures and data reduction. Data reduction was performed as described in Experiment 1, with the exception of computing the continuous phase difference between limbs. In Experiment 2, the continuous phase difference between the right and left arm was computed for each epoch comprising three complete cycles of the right (fast moving) arm as the reference. The line in Figure 5C represents the continuously changing continuous relative phase associated with a perfect 3:2 polyrhythmic ratio between two oscillators.

Results

Practice trials. Mean relative phase variability and RMSE of relative phase were analyzed in 3 Group (covered limb-Lissajous, uncovered limb-Lissajous, covered limb-no Lissajous) \times Trial (1–9) ANOVAs with repeated measures on trial. The analysis of relative phase variability (Figure 6A) indicated a main effect of trial, $F(8, 168) = 10.05$, $p < .05$, $\eta_p^2 = .35$. In addition, the Group \times Trial interaction, $F(16, 168) = 3.23$, $p < .05$, $\eta_p^2 = .25$, was significant. Simple main effects analysis failed to detect a decrease in relative phase variability across trials for the covered

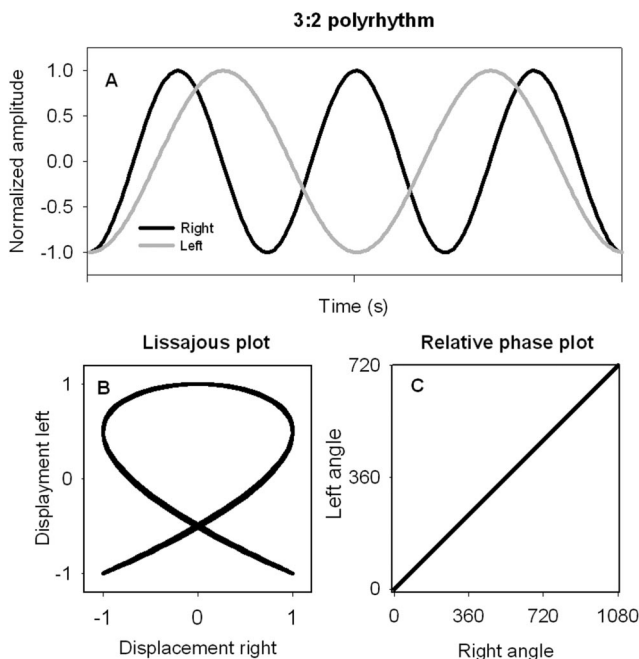


Figure 5. Displacements (A), Lissajous (B), and relative phase (C) plots for simulated left and right limb movements that result in a perfect 3:2 polyrhythm.

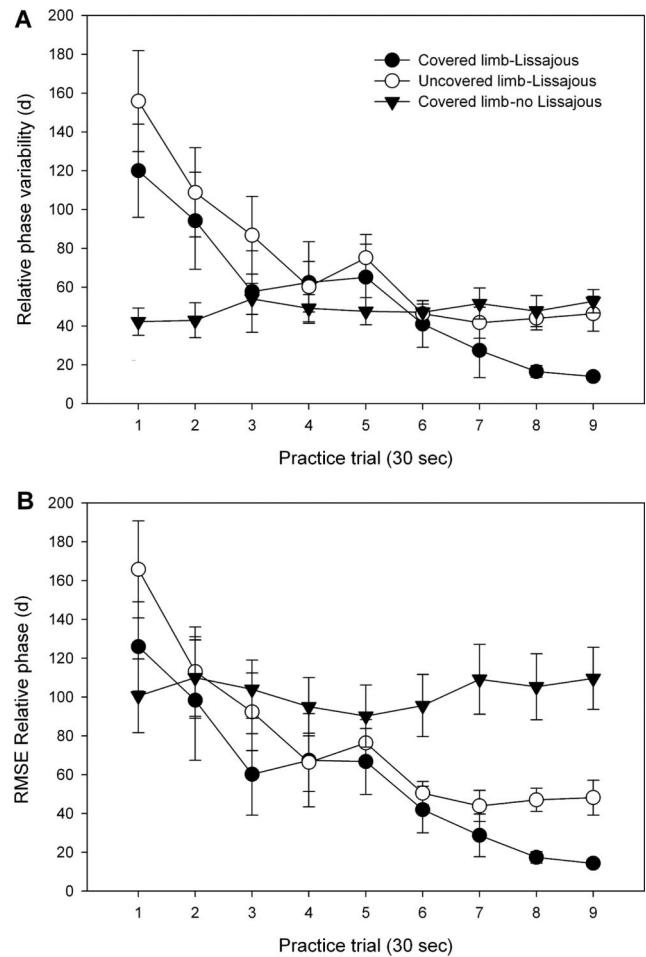


Figure 6. Mean relative phase variability (A) and RMSE (B) relative phase for practice trials 1–9 in Experiment 2. Error bars represent \pm standard errors.

limb-no Lissajous group but did detect decreases across trials for the covered limb-Lissajous and uncovered limb-Lissajous groups. Simple main effects analysis also detected reduced relative phase variability for the covered limb-no Lissajous group relative to the covered and uncovered limb Lissajous groups on Trials 1–2, but smaller relative phase variability was found for the covered limb-Lissajous group on Trials 8–9, relative to the uncovered limb-Lissajous and covered limb-no Lissajous groups.

The analysis of RMSE of relative phase (Figure 6B) indicated a main effect of trial, $F(8, 168) = 11.13$, $p < .05$, $\eta_p^2 = .37$. In addition, the Group \times Trial interaction, $F(16, 168) = 3.17$, $p < .05$, $\eta_p^2 = .25$, was significant. Simple main effects analysis failed to detect a decrease in RMSE of relative phase across trials for the covered limb-no Lissajous group but did detect decreases in the covered limb-Lissajous and uncovered limb-Lissajous groups. Simple main effects analysis also detected reduced relative phase RMSE for the covered limb-Lissajous and uncovered limb-Lissajous groups relative to the covered limb-no Lissajous group on Trials 6–9. On Trials 8–9, the covered limb-Lissajous group resulted in smaller RMSE of relative phase than the other two groups.

Test trial. Examples of displacement, Lissajous plots, and continuous relative phase plots on the test trial for two participants from each group are provided in Figure 7. The time series and associated Lissajous plots illustrate clearly enhanced performance for the covered limb-Lissajous group relative to the uncovered limb-Lissajous and covered limb-no Lissajous groups. Overall, the covered limb-Lissajous group produced more sinusoidal limb trajectories and produced more consistently the goal Lissajous plot compared to the uncovered limb-Lissajous and covered limb-no Lissajous groups. Both the right and left-arm trajectories for the uncovered limb participants appear to have significant slowing at the reversal points, something not evident in the covered limb participants. The distortion in the Lissajous plots in the uncovered limb-Lissajous and covered limb-no Lissajous groups also emerge in the relative angle plots.

Mean cycle frequency ratio, relative phase variability, and RMSE of relative phase were analyzed in 3 group (covered limb-Lissajous, uncovered limb-Lissajous, covered limb-no Lissajous) ANOVAs and these results are presented in the bimanual performance section. Mean harmonicity, cycle duration, and standard deviation of cycle duration data were analyzed in 3 Group (covered limb-Lissajous, uncovered limb-Lissajous, covered limb-no Lissajous) \times 2 Limb (left, right) ANOVAs with repeated measures on limb and these results are presented in the unimanual performance section. Duncan's new multiple range test and simple main effects post-hoc tests were performed when appropriate ($\alpha = .05$).

Bimanual performance. The cycle frequency ratio (Figure 8A) analysis detected a significant main effect of group, $F(2, 21) = 4.13, p < .05, \eta_p^2 = .27$. The multiple range test detected differences between the covered limb-Lissajous and covered limb-no Lissajous groups with the covered limb-Lissajous group more closely matching the required ratio. The uncovered limb-Lissajous was not different from the other two groups.

The analysis of variability in relative phase (Figure 8B) found a main effect of group, $F(2, 21) = 12.35, p < .01, \eta_p^2 = .57$. The multiple range test found the covered limb-Lissajous group more stable than the uncovered limb-Lissajous and covered limb-no Lissajous groups. The analysis of the RMSE data (Figure 8C) from the relative angle plots revealed a significant main effect of group, $F(2, 21) = 20.14, p < .01, \eta_p^2 = .68$. The multiple range test found all groups different from each other. Indeed, RMSE of relative phase for the uncovered limb-Lissajous group was approximately 5 times larger than the values for the covered limb-Lissajous group. The covered limb-no Lissajous group produced in even higher RMSE values.

Unimanual performance. The analysis of harmonicity (Figure 8D) detected a main effect of group, $F(2, 21) = 7.36, p < .05, \eta_p^2 = .44$. Duncan's multiple range test indicated harmonicity values were higher (more harmonic) in the covered limb-Lissajous and covered limb-no Lissajous groups compared to the uncovered limb-Lissajous group. The main effect of limb, $F(1, 21) = 43.21, p < .01, \eta_p^2 = .69$, was also significant with right-arm motion in general more harmonic than left-arm motion. The Group \times Limb interaction was also significant, $F(2, 21) = 4.67, p < .05, \eta_p^2 = .32$. Simple main effects analysis indicated a difference between the H values for the left and right limbs in each group. Further, H values for the left limb in the uncovered limb-Lissajous group were lower than for the respective left limbs in the covered limb-Lissajous and covered limb-no Lissajous group.

The analysis of cycle duration (Figure 8E) found a main effect of limb, $F(1, 21) = 85.66, p < .01, \eta_p^2 = .81$. As expected shorter cycle durations were found for the right limb than the left limb in all groups. The main effect of group and the Group \times Limb interaction were not significant. The analysis of the standard deviation of cycle duration (Figure 8F) indicated main effects of group, $F(2, 21) = 15.87, p < .01, \eta_p^2 = .44$, and limb, $F(1, 21) = 9.96, p < .05, \eta_p^2 = .50$. The multiple range test on the group main effect indicated cycle duration was less variable in the covered limb-Lissajous and covered limb-no Lissajous groups than in the uncovered limb-Lissajous group. Cycle duration variability for the left-arm¹ was more variable than in the right-arm. The Group \times Limb interaction was not significant.

Discussion

The uncovered limb-Lissajous group was not able to produce the continuous 3:2 polyrhythm with as low relative phase variability and RMSE as the covered limb-Lissajous group. Even more remarkable was the precise and consistent performance of the covered limb-Lissajous group after only 4.5 minutes of practice. A continuous 3:2 bimanual polyrhythm has been deemed almost impossible to produce effectively by Summers et al. (2002). However, as the harmonicity data illustrates, the motion of both limbs was more harmonic and cyclical in nature in the covered limb-Lissajous group compared to the uncovered limb-Lissajous group. Bimanual performance of the covered limb-no Lissajous group was quite poor demonstrating the power of the Lissajous feedback. These findings demonstrate quite clearly that a salient visual feedback display provided via the cursor and Lissajous plots was sufficient to allow the performer to tune in precisely the desired 3:2 movement pattern with vision of the limbs disrupting this process.

General Discussion

In two experiments, participants that were not permitted to view their limbs but who were provided vision of the cursor and goal template presented in the form of a Lissajous plot (covered limb-Lissajous groups) were able to perform a 2:1 and a 3:2 bimanual coordination patterns with remarkably low relative phase variability and RMSE with less than 5 minutes of practice. Both multi-frequency patterns were maintained not only at discrete check points (e.g., beginning and ending of the rhythm cycle), consistent with discrete tapping work (e.g., Bogacz, 2005; Collier & Wright, 1995; Peper et al., 1995a, 1997b), but also continuously throughout the movement. When producing the simple 2:1 ratio and the more complex 3:2 ratio, both the left and right limb motions were harmonic. However, when vision of the limbs was permitted and Lissajous information was provided (uncovered limb-Lissajous groups), the production of the desired continuous relative phase coordination pattern and the harmonic nature of the left-arm's

¹ Comparisons of the standard deviation of the cycle duration means between the limbs should be viewed with caution because the left limb in both experiments was moving slower than the right limb to achieve the desired frequencies. Thus, if the variability results were expressed in relation to cycle duration (coefficient of variation), the differences could disappear or even reverse.

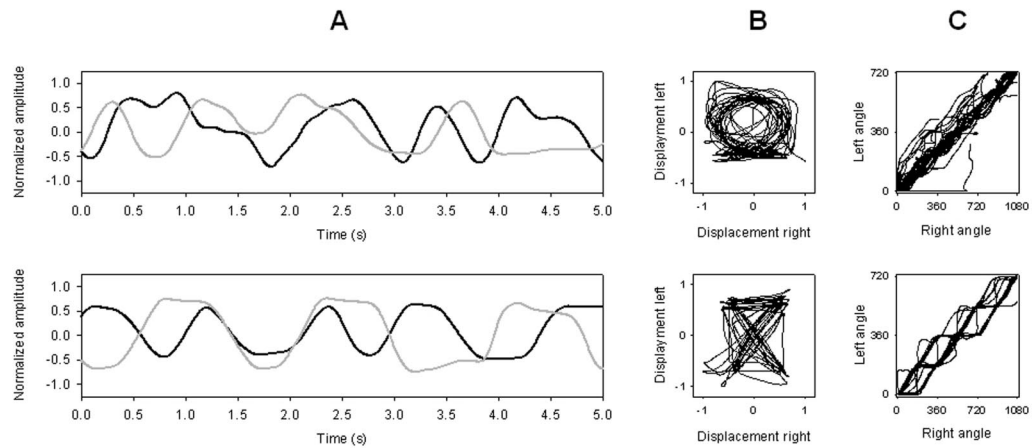
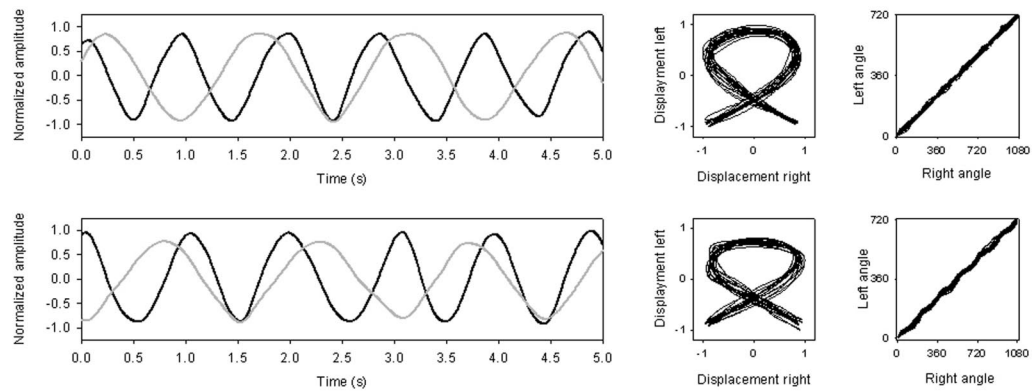
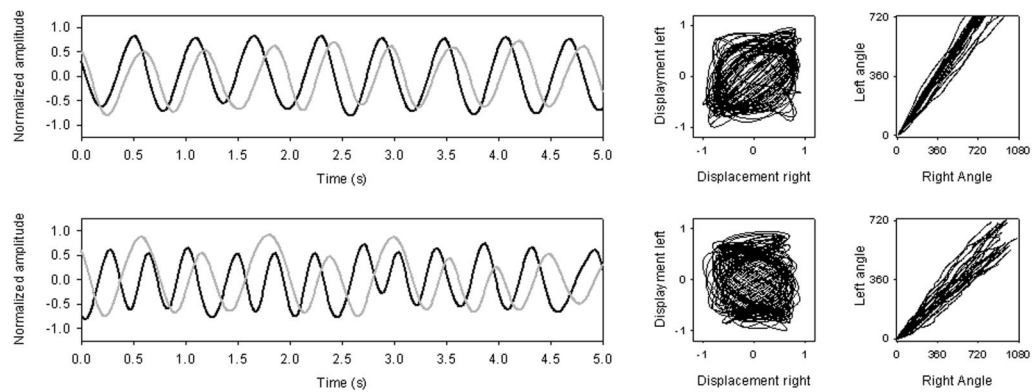
Uncovered limb/Lissajous**Covered limbs/Lissajous****Covered limbs/No Lissajous**

Figure 7. Examples of the time series for two participants in the uncovered limb-Lissajous (top), covered limb-Lissajous (middle), and covered limb-no Lissajous (bottom) conditions in Experiment 2. Normalized left and right limb displacements (A), Lissajous plot (B), and relative angle plots (C) from the test trial are provided.

motion were both reduced with both disruptions larger in the 3:2 ratio task than in the 2:1 ratio task. Overall, relative phase RMSE was 2.5 times larger in the uncovered limb-Lissajous group compared to the covered limb-Lissajous group for the 2:1 ratio pattern

in Experiment 1, with the same comparison being nearly 5 times larger in the 3:2 ratio in Experiment 2. Apparently, covering the limbs was necessary for the system to fully utilize the visual information in the Lissajous plot in order to produce the goal

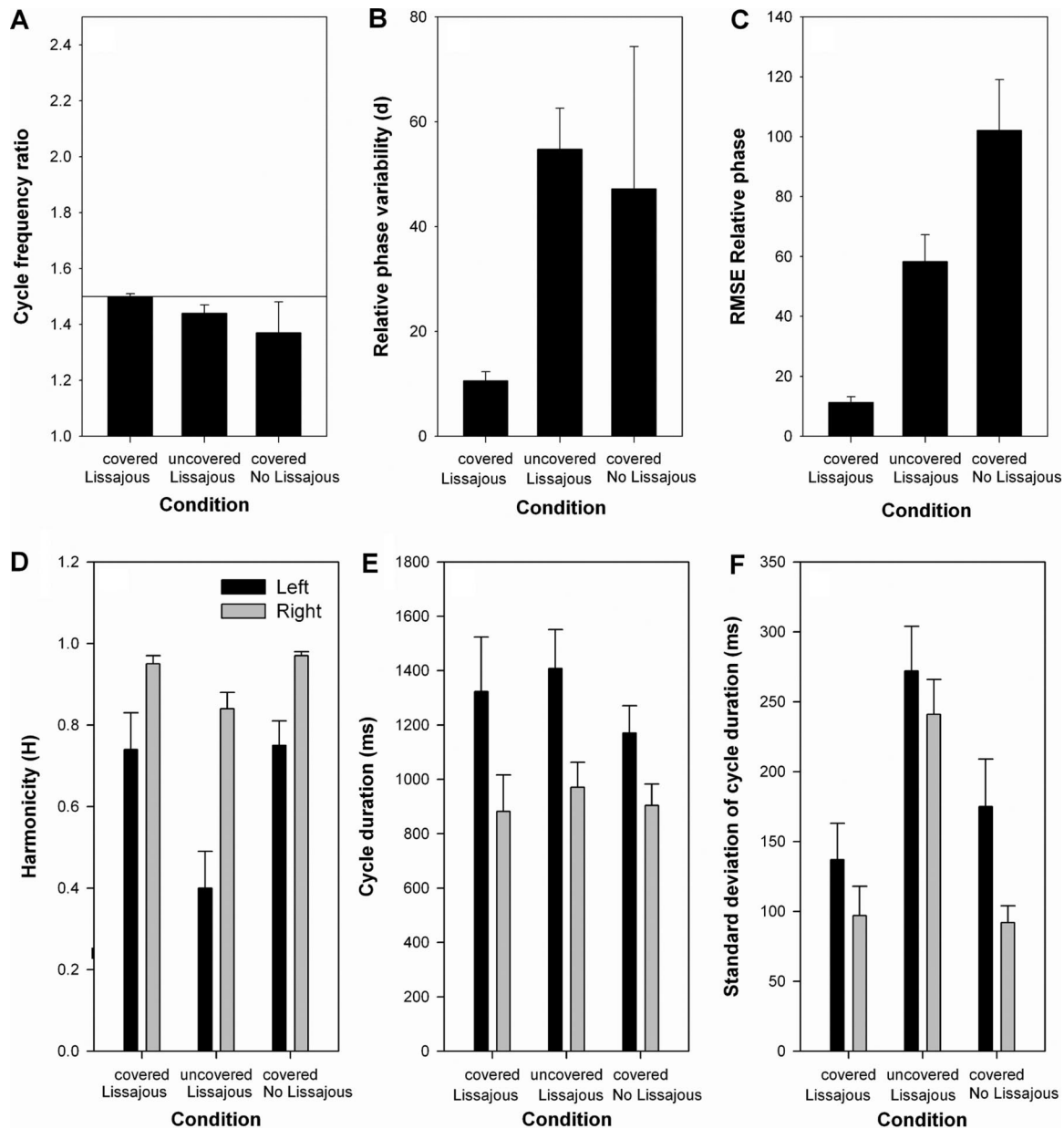


Figure 8. Mean cycle frequency ratio (A), relative phase variability (B), relative phase RMSE (C), harmonicity (D), cycle duration (E), and cycle duration variability (F) in Experiment 2. Error bars represent \pm standard errors.

patterns. When the limbs were covered but no Lissajous information was provided, bimanual performance (RMSE) was quite poor although limb harmonicity and cycle duration variability were similar to that of the covered limb-Lissajous groups and variability in relative phase was actually lower early in practice compared to the covered limb-Lissajous groups. Indeed, variability in relative phase for the covered limb-no Lissajous groups in both experiments was lower relative to the groups that received Lissajous feedback early in practice and did not appreciably change over the course of practice. This finding is consistent with the notion that without Lissajous feedback participants are relatively ineffective in detecting and subsequently correcting errors in achieving the goal relative phase.

The difficulty in producing multi-frequency coordination patterns has been attributed to attraction of the more complex ratios to 1:1 in-phase and anti-phase coordination patterns as well as decreased widths of the resonance regions whereby higher order ratios are associated with narrower resonance channels. These narrower resonance channels are associated with decreased coupling strength in that coordination pattern stability is inversely related to the width of the channel and, thus, the pattern can be more easily disrupted by smaller perturbations as the width and/or depth of the channel decreases (e.g., de Guzman & Kelso, 1991; Haken, Peper, Beek, & Daffertshofer, 1996; Kelso & de Guzman, 1988; Peper et al., 1995a, 1995c; Treffner & Turvey, 1993). However, through extensive practice, the coupling strength for a

given pattern is thought to increase and attractor landscapes altered resulting in increasingly stable performance for initially unstable relative phase relationships (Zanone & Kelso, 1992) or higher order frequency ratios. Swinnen, Dounskaia, et al. (1997), for example, found after 5 days of practice with a continuous arm movement task (80 trials of 15 s per day) that participants could produce relatively stable 2:1 ratios (i.e., discrete relative phase variability of approximately 12 degrees). In the covered limb-Lissajous conditions in the present experiments, participants' performance of the 2:1 and the 3:2 ratio patterns of bimanual coordination were remarkably stable after only 4.5 minutes of practice. We argue that this was possible because salient, unified extrinsic visual information was provided in the form of the cursor and Lissajous plots. This visual display together with the reduced attentional demands allowed the participant to "tune-in" the required behavior. It appears that these conditions resulted in an increase in coupling strength and/or an alteration in the attractor landscape as evidenced by increased stability of bimanual performance. Consequently, it is possible that the visual display altered the inherent resonance constraints (Treffner & Turvey, 1993) of the component oscillators allowing remarkably stable performance within the altered resonance region. In other words, the resonance regions associated with the structural stability of a given frequency ratio appeared to be changed. Indeed, it is plausible to argue that changes in the resonance regions occurred a perceptual level. Vision of the limbs in the uncovered limb-Lissajous group, however, appeared to functionally reduce coupling strength between the limbs, at least compared with the covered limb-Lissajous group. The result was more variable bimanual performance when the limbs were uncovered.

When the limbs were visible, increased cycle duration variability and reduced harmonicity were observed for the left but not for the right limb. This pattern of results may indicate that attention was preferentially directed to one of the limbs (Amazeen et al., 1997; de Poel et al., 2008). In the present experiments, attentional focus was not manipulated *per se* by experimenter instruction, but rather participants were free to direct their focus to what seemed to be the more meaningful source(s) of feedback. Laterally focused attention may have occurred in the uncovered limb conditions. Attention to one or the other limb has been shown to alter coordination dynamics not only at the collective level but also influence the asymmetry at the level of individual components (Amazeen et al., 1997; de Poel et al., 2008). The pattern of unimanual measures in the present experiments seem to be in agreement with other studies using mono-frequency coordination patterns, whereby directing attention of right-handed participants toward their non-dominant left limb disrupted coordinated behavior and altered the asymmetric coupling relationship (Amazeen et al., 1997; de Poel et al., 2008). Thus, it appears that covering the limbs when Lissajous feedback was provided not only increased coupling strength but also altered the asymmetry in coupling as evidenced by reduced cycle duration variability and increased harmonicity of the limb movement. Asymmetric coupling has also been shown in multi-frequency coordination tasks. Byblow et al. (1998), for example, have demonstrated that the faster moving limb influences to a greater extent the slower moving limb than vice versa. Note that in the present experiments increased cycle duration variability and reduced harmonicity was found in the slower moving left limb for the uncovered limb conditions. Vision

of the limbs may also have allowed phase attraction linked to in-phase and anti-phase to become more prominent since those points in the cycle wherein the limbs come together may have received the most attention. What needs to be further explored is whether or not the rapid tuning afforded by the experimental conditions in the present experiments is directly linked to increased coupling strength between limbs or reduced phase attraction linked to the system's intrinsic dynamics. We propose that the altered asymmetric coupling and reduced harmonicity of the left limb was due to preferential focus of attention toward this limb when vision of the limbs was permitted, and that the manipulation of attentional focus must be undertaken to determine how the coupling between limbs was altered so rapidly.

In the present experiments, the information provided through the Lissajous display permitted participants not distracted by vision of their limbs to quickly and effectively (low relative phase RMSE and variability) tune-in the required frequency ratios. We feel this was accomplished, in part, because the Lissajous template and cursor allowed participants to easily determine when they deviated from the desired coordination pattern and presumably were then able to accurately re-tune their actions. This finding is important because it clearly demonstrates that the perceptual-motor system is fully capable of producing these coordination patterns when provided salient visual information. It should be noted, however, that while performance was greatly enhanced by the visual information provided the present set of experiments do not assess the degree to which the coordination patterns were learned. In a recent experiment, Kovacs et al. (2009a) provided a Lissajous template and feedback to participants attempting to produce a 1:1 bimanual coordination pattern with a 90° relative phase offset between the limbs both with and without a metronome. While provided the Lissajous feedback without the metronome, participants were able to quickly (5 minutes) tune-in the desired phase relationship. Participants provided the Lissajous feedback with the metronome performed substantially poorer than the no metronome group. However, when the Lissajous feedback for the no metronome group was withdrawn, participants tended to drift from the required 90° relative phase, but the cycle duration variability in the two limbs remained stable and limb motion remained stable. This finding suggests that participants, at least with relatively little practice, are dependent on the Lissajous feedback to maintain performance at high levels but have not developed an internal representation capable of sustaining performance. That is, the attractor landscape of the bistable system did not change in the long-term when practicing with Lissajous feedback as evidenced by poor performance when Lissajous feedback was withdrawn (Kovacs et al., 2009a) but was somehow temporarily altered by the presentation of the Lissajous information.

The Status of Perception in Perception-Action Dynamics

The development of abstract models based on non-linear coupled oscillators has been at the forefront of the coordination dynamics approach to identifying the laws that govern the formation of stable coordination patterns between limbs and joints (Haken et al., 1985, 1996; Kelso, 1995; Schöner et al., 1986). A primary characteristic of such modeling approaches has been that the coupling among the component oscillators was represented in

abstract mathematical terms with the functional aspects of the coupling not linked to any specific neuromuscular and/or cognitive-perceptual process. Although specific links to underlying neural areas or processes are not necessary to develop these formal models that have successfully captured many of the phenomenon linked to 1:1 and multi-frequency ratio performance, the bimanual literature is replete with attempts to reveal neural areas and cognitive-perceptual principles to support such functional coupling. An issue that surrounds the nature of this coupling is whether or not motoric, perceptual, and cognitive constraints should be treated as independent and exclusive factors or as contributing and interacting factors supporting an integrated perception-action cycle (Carson & Kelso, 2004; Mechsner et al., 2001). For example, the concept of neural crosstalk has been used to explain the findings of stability differences, phase transitions, and difficulty in producing simple and complex ratio bimanual patterns based on interactions in forward command streams in the highly interconnected and redundant organization of the nervous system (for review, see Swinnen, 2002). Emphasis may also be placed on identifying neural structures that support forward command streams (SMA, M1, S1, PM, cingulate motor cortex) and identifying different levels of interference (uncrossed corticofugal fibers, branched bilateral corticomotoroneuronal projections, segmental networks) that can occur across the many levels through which these command signals travel (for review, see Carson & Kelso, 2004). Moreover, some research has shown that somatosensory feedback is not necessary to establish and maintain stable symmetric and asymmetric bimanual circle tracing patterns (Spencer, Ivry, Cattaert, & Semjen, 2005). Thus, one contribution to the coupling and stability characteristics of bimanual coordination clearly resides in forward commands and the interactions that arise from those commands as the result of shared neural pathways (Ridderikhoff, Peper, & Beek, 2005).

Research has also shown that cognitive processes, such as intention (Scholz & Kelso, 1990) and strategy selection (Kelso, DelColle, & Schöner, 1990), can influence the stability of bimanual and unimanual coordination patterns. Recent theorizing has attempted to link neural areas like the anterior cingulate cortex to cognitive constraints that may impact the "functional representations" of muscles underlying sensorimotor coordination in general (Carson & Kelso, 2004). Other research has demonstrated that bimanual coordination is also constrained by egocentric and allocentric reference frames and that abstract directional codes through practice become part of the memory representation for bimanual movements and can constrain transfer more so than muscle pairs (e.g., Salesse, Oullier, & Temprado, 2005; Salesse, Temprado, & Swinnen, 2005; Temprado & Swinnen, 2005). Clearly, cognitive and memory factors interact with and can override the motoric aspect of the coupling that drives the phase attraction towards in-phase and anti-phase coordination (Swinnen & Wenderoth, 2004).

What role does perceptual information contribute to the production and stabilization of bimanual coordination patterns? Research has revealed a role for proprioception (Baldissera et al., 1991; Ridderikhoff et al., 2005; Ridderikhoff, Peper, & Beek, 2007) and tactile input (Aschersleben & Prinz, 1995; Buchanan & Ryu, 2005; Kelso, Fink, DeLaplain, & Carson, 2001) in stabilizing in-phase and anti-phase coordination. Bingham and colleagues (e.g., Bingham, Schmidt, & Zaal, 1999; Bingham, 2004a, 2004b; Wilson,

Collins, & Bingham 2005a, 2005b) have argued that bimanual coordination can be limited by the performer's ability to visually detect a given relative phase pattern. That is, they propose that if a participant rates a given pattern of behavior as uncoordinated and cannot distinguish the amount of variability in the pattern based on visual input, then it is likely that they will not be able to produce the pattern. Using this logic, the reason for poor performance in some bimanual tasks is that participants are unable to detect their errors and, thus, are unable to initiate effective corrections. The tacit assumption of this argument is that if perceptual information is provided that facilitates pattern detection then error detection (and correction) will follow allowing stable performance to be effectively tuned-in. The work of Bingham and colleagues establishes a potential link between visual perception and the stability of symmetric and asymmetric coordination patterns, but they have not directly tested the role that such perceptual processes actually play or can play in the tuning of bimanual coordination patterns. Work by Mechsner et al. (2001) demonstrated that a highly complex 4:3 polyrhythm could be performed relatively well with little practice when available visual information provided salient performance and error information. In the task used by Mechsner et al. (2001), participants had no vision of their arms while turning cranks geared at different ratios for each arm but were instructed to turn the cranks such that two flags driven by the cranks were either in an in-phase or anti-phase relationship. What the Mechsner et al. (2001) finding reveals is that perceptual constraints based on in-phase and anti-phase coordination can actually allow the system to tune-in quite rapidly a more difficult pattern with out extensive training. Thus, an intrinsic constraint arising from the motor system facilitated performance when presented in a relevant perception-action framework.

In the current experiments, the visual information provided via the cursor and Lissajous plot presumably facilitated error detection and correction processes and these conditions allowed for a very rapid tuning of difficult 2:1 and 3:2 bimanual coordination patterns. When vision of the limbs was provided, performance deteriorated suggesting that attention was directed away from the extrinsic information contained within the Lissajous to monitoring and controlling the limbs. Recent work has shown that both vision of the limbs and visual metronomes can result in less stable performance of a variety of 1:1 relative phase patterns between 0° and 180° (Amazeen et al., 2008; Kovacs et al., 2009b). The current findings imply that a salient visual reference frame, when attention splitting features of a task are removed, can free the motor system from constraints that typically limit it to a bi-stable regime without extensive practice. The rapidity with which the current perceptually defined patterns were mapped onto the motor system indicates that the motor system's capabilities are extensive when visual information is provided that allows effective error detection and correction. What future research needs to identify is how the current visual display afforded the motor system an opportunity to override intrinsic constraints that tend to pull the system towards in-phase and anti-phase coordination. In other words, the perceptual display did not eliminate neural crosstalk or proprioception nor did the visual display eliminate the perceptual attraction to in-phase or anti-phase coordination, but the display clearly decreased the influence of these factors and probably others (e.g., asymmetric coupling, phase attraction). That is, the visual display appeared to allow the motor system to initiate effective forward

based motor commands that were not overly constrained by motoric, cognitive, and/or perceptual factors. The current findings suggest that a key component in revealing the cooperative process that couple motor output with perceptual feedback must involve the manipulation of attentional demands on the moving limbs. These results emphasize that a true understanding of the “design of the brain” can only be forthcoming when the roles of both the motor side (e.g., Kelso & deGuzman, 1988) and the perceptual side (e.g., Mechsner et al., 2001) are integrated in a true perception-action dynamics perspective (see Atchy-Dalama, Peper, Zanone, & Beek, 2005; Bingham 2004a; Bingham et al., 1999; Carson & Kelso, 2004; Swinnen & Wenderoth, 2004; Zaal, Bingham, & Schmidt, 2000).

Focus of Attention

A relatively recent but growing literature on attentional focus, spearheaded by the work of Wulf (see Wulf, 2007, for recent review), has demonstrated that participants instructed to focus on the movements of their limbs (internal focus) while learning or performing a motor skill perform and learn more poorly than participants instructed to focus on the outcome (external focus) of their movement. This appears to hold regardless of the skill level of the performer (e.g., Wulf, McConnel, Gärtner, & Schwarz, 2002; Wulf & Su, 2007) and has been demonstrated for a large variety of tasks ranging from balancing on a stabilometer (e.g., McNevin et al., 2003) to hitting a golf ball (e.g., Wulf, Lauterbach, & Toole, 1999; Wulf & Su, 2007). The benefit of external vs. internal focus of attention is thought to result because participants instructed to focus on the movement of their limbs attempt to actively intervene in the ongoing control processes required to produce the movement. In this regard, McNevin et al. (2003) proposed the constrained action hypothesis. This hypothesis was based on two main findings: First, when participants attempted to maintain balance on a stabilometer under internal focus of attention instructions, the frequency characteristics (MPF – mean power frequency) of the platform’s motion decreased and the average deviation from horizontal (RMSE) increased. Second, when instructions that focused attention externally were provided, the frequency characteristics of the platform’s motion increased and deviations from horizontal decreased. The slowing down of the corrective actions under internal focus was thought to result from active intervention of the participants in the control processes with this type of control inhibiting more natural, reflective control processes typically responsible for balance control.

In the present experiment, attentional focus instructions were not provided to the participants. However, participants provided vision of their limbs may have directed some of their attentional resources to their limbs and away from the Lissajous plots. This could result in a shift from an external to internal focus of attention. Participants not permitted vision of their limbs would certainly be less likely to adopt an internal focus of attention. Indeed, a number of participants indicated at the end of the experiment that they were not aware that horizontal movement of the cursor resulted from movement of the right limb and vertical movement of the cursor resulted from left hand movement. Indeed, some participants not provided vision of their limbs indicated that when they attempted to monitor what their arms were doing, performance was negatively impacted so they tried to keep their attention

on the display. When vision of the limbs was permitted in the uncovered limb-Lissajous condition, multi-frequency performance deteriorated, particularly because of left limb motion. Harmonicity decreased substantially, cycle durations were longer and more variable, the required ratios were not achieved, and continuous relative phase errors increased. This seems quite remarkable given that both groups were provided the same instructions and the same extrinsic feedback (Lissajous plot and cursor representing limb position) with only vision of the limbs manipulated. This suggests that vision of the limbs, even though other salient information is provided, introduces a strong inducement to adopt an internal focus of attention and actively intervene in the control of the limbs to the detriment of coordinated performance.

Emerging Picture

The present findings are consistent with recent bimanual coordination research (Kovacs & Shea, 2010; Kovacs et al., 2009a, 2009b, 2010; Mechsner et al., 2001), visuo-motor tracking research (Ryu & Buchanan, 2009; Wilson et al., 2005a, 2005b), and even rapid aiming research constrained by Fitts’ Law (Kovacs, Buchanan, & Shea, 2008), which report that salient perceptual information can override some aspects of the system’s intrinsic dynamics typically linked to motor output control. The strong tendencies toward mirror symmetry found in numerous previous bimanual movement studies and the difficulties in producing simple and complex ratios may actually represent detrimental effects attributable to the perceptual information available in the environment and the attentional focus participants adopt. Given an external focus of attention and integrated salient visual information participants can essentially tune-in complex multi-frequency bimanual coordination patterns with little practice (also see Kovacs et al., in press). Indeed, when attentional distractions were reduced and Lissajous feedback was provided relative phase variability ($\sim 10^\circ$) and RMSE ($\sim 10^\circ$) were similar for both the 2:1 and 3:2 coordination patterns after less than 5 min of practice. This notion is in stark contrast to earlier claims that the system’s intrinsic dynamics constrain certain patterns of limb motion and that 2:1 coordination patterns are difficult and 2:3 coordination patterns are substantially more difficult to produce in continuous tasks (e.g., Summers et al., 2002). This finding also suggests that more complex ratios (e.g., 5:3, 4:3) could also be effectively produced with relatively little practice when Lissajous feedback appropriate for the specific ratio is provided and attentional distractions are reduced.

References

- Amazeen, E. L., Amazeen, P. G., Treffner, P. J., & Turvey, M. T. (1997). Attention and handedness in bimanual coordination dynamics. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1552–1560.
- Amazeen, E. L., DaSilva, F., & Amazeen, P. G. (2008). Visual-spatial and anatomical constraints interact in a bimanual coordination task with transformed visual feedback. *Experimental Brain Research*, 191, 12–24.
- Arnold, V. I. (1983). Geometrical methods in the theory of ordinary differential equations. New York, NY: Springer-Verlag.
- Aschersleben, G., & Prinz, W. (1995). Synchronizing actions with events: The role of sensory information. *Perception and Psychophysics*, 57(3), 305–317.

- Atchy-Dalama, P., Peper, C. E., Zanone, P. G., & Beek, P. J. (2005). Movement-related sensory feedback mediates the learning of a new bimanual relative phase pattern. *Journal of Motor Behavior*, 37, 186–196.
- Baldissera, F., Cavallari, P., & Civaschi, P. (1982). Preferential coupling between voluntary movements of ipsilateral limbs. *Neuroscience Letters*, 34, 95–100.
- Baldissera, F., Cavallari, P., Marini, G., & Tassone, G. (1991). Differential control of in-phase and anti-phase coupling of rhythmic movements of ipsilateral hand and foot. *Experimental Brain Research*, 83, 375–380.
- Bingham, G. P. (2004a). A perceptually driven dynamical model of bimanual rhythmic movement (and phase perception). *Ecological Psychology*, 16, 45–53.
- Bingham, G. P. (2004b). Another timing variable composed of state variables: Phase perception and phase driven oscillators. In H. Hecht & G. I. P. Savelsbergh (Eds.), *Advances in Psychology: Time to Contact*. Amsterdam, The Netherlands: Elsevier.
- Bingham, G. P., Schmidt, R. C., & Zaal, F. T. J. M. (1999). Visual perception of relative phasing in human limb movements. *Perception and Psychophysics*, 61, 246–258.
- Bogacz, S. (2005). Understanding how speed affects performance of polyrhythms: Transferring control as speed increases. *Journal of Motor Behavior*, 37, 21–34.
- Boonstra, T. W., Daffertshofer, A., Breakspear, M., & Beek, P. J. (2007). Multivariate time-frequency analysis of electromagnetic brain activity during motor learning. *Neuroimage*, 36, 370–377.
- Buchanan, J. J., & Kelso, J. A. S. (1993). Posturally induced transitions in rhythmic multijoint limb movements. *Experimental Brain Research*, 94, 131–142.
- Buchanan, J. J., & Ryu, Y. U. (2005). The interaction of tactile information and movement amplitude in a multijoint bimanual circle-tracing task: Phase transitions and loss of stability. *Quarterly Journal of Experimental Psychology*, 58A, 769–787.
- Buchanan, J. J., & Ryu, Y. U. (2006). One to one and polyrhythmic temporal coordination in bimanual circle tracing. *Journal of Motor Behavior*, 38, 163–184.
- Byblow, W. D., Bysouth-Young, D., Summers, J. J., & Carson (1998). Performance asymmetries and coupling dynamics in the acquisition of multifrequency bimanual coordination. *Psychological Research-Psychologische Forschung*, 61, 56–70.
- Byblow, W. D., & Goodman, D. (1994). Performance asymmetries in multifrequency coordination. *Human Movement Science*, 13, 147–174.
- Carson, R. G., & Kelso, J. A. S. (2004). Governing coordination: Behavioural principles and neural correlates. *Experimental Brain Research*, 154(3), 267–274.
- Collier, G. L., & Wright, C. E. (1995). Temporal rescaling of simple and complex ratios in rhythmic tapping. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 602–627.
- Debaere, F., Swinnen, S. P., Beatse, E., Sunaert, S., Van Hecke, P., & Duysens, J. (2001). Brain areas involved in interlimb coordination: A distributed network. *Neuroimage*, 14, 947–958.
- Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., & Swinnen, S. P. (2003). Internal vs external generation of movements: Differential neural pathways involved in bimanual coordination performed in the presence or absence of augmented visual feedback. *Neuroimage*, 19, 764–776.
- deGuzman, G. C., & Kelso, J. A. S. (1991). Multifrequency behavioral patterns and the phase attractive circle map. *Biological Cybernetics*, 64, 485–495.
- de Poel, H. J., Peper, C. E., & Beek, P. J. (2008). Laterally focused attention modulates asymmetric coupling in rhythmic interlimb coordination. *Psychological Research-Psychologische Forschung*, 72(2), 123–137.
- Deutsch, D. (1983). The generation of two isochronous sequences in parallel. *Perception and Psychophysics*, 34, 331–337.
- Fraisse, P. (1946). Contribution a etude du rythme en tant que forme temporelle. *Journal de Psychologie Normale et Pathologique*, 39, 283–304.
- Guiard, Y. (1993). On Fitts's and Hooke's laws: Simple harmonic movement in upper-limb cyclical aiming. *Acta Psychologica*, 82, 139–159.
- Haken, H., Kelso, J. A. S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics*, 51, 347–356.
- Haken, H., Peper, C. E., Beek, P. J., & Daffertshofer, A. (1996). A model for phase transitions in human hand movements during multifrequency tapping. *Physica D: Nonlinear Phenomena*, 90, 179–196.
- Hiraga, C. Y., Summers, J. J., & Temprado, J. J. (2004). Attentional costs of coordinating homologous and non-homologous limbs. *Human Movement Science*, 23, 415–430.
- Hurley, S. R., & Lee, T. D. (2006). The influence of augmented feedback and prior learning on the acquisition of a new bimanual coordination pattern. *Human Movement Science*, 25, 339–348.
- Kagerer, F. A., Summers, J. J., & Semjen, A. (2003). Instabilities during antiphase bimanual movements: Are ipsilateral pathways involved? *Experimental Brain Research*, 151, 489–500.
- Kelso, J. A. S. (1981). On the oscillatory nature of movement. *Bulletin of the Psychonomics Society*, 18, 63.
- Kelso, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology: Regulatory, Integrative, and Comparative Physiology*, 15, 1000–1004.
- Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, Mass.: The MIT Press.
- Kelso, J. A. S., Buchanan, J. J., & Wallace, S. A. (1991). Order parameters for the neural organization of single, multijoint limb movement patterns. *Experimental Brain Research*, 85, 432–444.
- Kelso, J. A. S., & deGuzman, G. C. (1988). Order in time: How cooperation between the hands informs the design of the brain. In H. Haken (Ed.), *Neural and synergetic computers* (pp. 180–196). Berlin, Germany: Springer-Verlag.
- Kelso, J. A. S., DelColle, J. D., & Schöner, G. (1990). Action-perception as a pattern formation process. In M. Jeanrod (Ed.), *Attention and performance XIII* (pp. 139–170). Hillsdale, NJ: Erlbaum.
- Kelso, J. A. S., Fink, P. W., DeLaplaine, C. R., & Carson, R. G. (2001). Haptic information stabilizes and destabilizes coordination dynamics. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 268, 1207–1213.
- Kelso, J. A. S., Scholz, J. P., & Schöner, G. (1986). Nonequilibrium phase transitions in coordinated biological motion: Critical fluctuations. *Physics Letters A*, 118, 279–284.
- Kennerley, S. W., Diedrichsen, J., Hazeltine, E., Semjen, A., & Ivry, R. B. (2002). Callosotomy patients exhibit temporal uncoupling during continuous bimanual movements. *Nature Neuroscience*, 5, 376–381.
- Keogh, J., Morrison, S., & Barrett, R. (2004). Augmented visual feedback increases finger tremor during postural pointing. *Experimental Brain Research*, 159, 467–477.
- Kinsbourne, M. (1970). The cerebral basis of lateral asymmetries in attention. *Acta Psychologica*, 33, 193–201.
- Klapp, S. T., Nelson, J. M., & Jagacinski, R. J. (1998). Can people tap concurrent bimanual rhythms independently. *Journal of Motor Behavior*, 30, 301–322.
- Kovacs, A. J., & Shea, C. H. (2010). Amplitude differences, spatial assimilation, and integrated feedback in bimanual coordination. *Experimental Brain Research*, 202, 519–525.
- Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2008). Perceptual influences on Fitt's law. *Experimental Brain Research*, 190, 99–103.
- Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2009a). Bimanual 1:1 with 90° continuous phase: Difficult or easy? *Experimental Brain Research*, 193, 129–136.
- Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2009b). Using scanning trials

- to assess intrinsic coordination dynamics. *Neuroscience Letters*, 455, 162–167.
- Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2010). Impossible is nothing: 5:3 and 4:3 multi-frequency bimanual coordination. *Experimental Brain Research*, 201, 249–259.
- Kurtz, S., & Lee, T. D. (2003). Part and whole perceptual-motor practice of a polyrhythm. *Neuroscience Letters*, 338, 205–208.
- Lee, T. D., Swinnen, S. P., & Verschueren, S. (1995). Relative phase alterations during bimanual skill acquisition. *Journal of Motor Behavior*, 27(3), 263–274.
- McNevin, N. H., Shea, C. H., & Wulf, G. (2003). Increasing the distance of an external focus of attention enhances learning. *Psychological Research*, 67, 22–29.
- Mechner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature*, 414, 69–73.
- Meesen, R. L. J., Wenderoth, N., Temprado, J. J., Summers, J. J., & Swinnen, S. P. (2006). The coalition of constraints during coordination of ipsilateral and heterolateral limbs. *Experimental Brain Research*, 174, 367–375.
- Peper, C. E., Beek, P. J., & van Wieringen, P. C. W. (1995a). Coupling strength in tapping a 2:3 polyrhythm. *Human Movement Science*, 14, 217–245.
- Peper, C. E., Beek, P. J., & van Wieringen, P. C. W. (1995b). Multifrequency coordination in bimanual tapping: Asymmetrical coupling and signs of supercriticality. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 1117–1138.
- Peper, C. E., Beek, P. J., & van Wieringen, P. C. W. (1995c). Frequency-induced phase-transitions in bimanual tapping. *Biological Cybernetics*, 73, 301–309.
- Peper, C. E., de Boer, B. J., de Poel, H. J., & Beek, P. J. (2008). Interlimb coupling strength scales with movement amplitude. *Neuroscience Letters*, 437, 10–14.
- Peters, M. (1989). Do feedback processing, output variability, and spatial complexity account for manual asymmetries. *Journal of Motor Behavior*, 21, 151–155.
- Peters, M., & Schwartz, S. (1989). Coordination of the two hands and effects of attentional manipulation in the production of bimanual 2:3 polyrhythm. *Australian Journal of Psychology*, 41, 215–224.
- Povel, D.-J. (1981). Internal representation of simple temporal patterns. *Journal of Experimental Psychology: Human Perception and Performance*, 7, 3–18.
- Puttemans, V., Wenderoth, N., & Swinnen, S. P. (2005). Changes in brain activation during the acquisition of a multifrequency bimanual coordination task: From the cognitive stage to advanced levels of automaticity. *The Journal of Neuroscience*, 25, 4270–4278.
- Ridderikhoff, A., Peper, C. E., & Beek, P. J. (2005). Unraveling interlimb interactions underlying bimanual coordination. *Journal of Neurophysiology*, 94, 3112–3125.
- Ridderikhoff, A., Peper, C. E., & Beek, P. J. (2007). Error correction in bimanual coordination benefits from bilateral muscle activity: Evidence from kinesthetic tracking. *Experimental Brain Research*, 181, 31–48.
- Riek, S., Carson, R. G., & Byblow, W. D. (1992). Spatial and muscular dependencies in bimanual coordination. *Journal of Human Movement Sciences*, 23, 251–265.
- Riek, S., & Woolley, D. (2005). Hierarchical organization of neuroanatomical constraints in interlimb coordination. *Human Movement Science*, 24, 798–814.
- Ryu, Y., & Buchanan, J. J. (2009). Learning an environment-actor skill: Visuomotor transformation and coherency of perceptual structure. *Experimental Brain Research*, 196, 279–293.
- Salesse, R., Oullier, O., & Temprado, J. J. (2005). Plane of motion mediates the coalition of constraints in rhythmic bimanual coordination. *Journal of Motor Behavior*, 37, 454–464.
- Salesse, R., Temprado, J. J., & Swinnen, S. P. (2005). Interaction of neuromuscular, spatial and visual constraints on hand-foot coordination dynamics. *Human Movement Science*, 24, 66–80.
- Scholz, J. P., & Kelso, J. A. S. (1990). Intentional switching between patterns of bimanual coordination depends on the intrinsic dynamics of the patterns. *Journal of Motor Behavior*, 22(1), 98–124.
- Schöner, G., Haken, H., & Kelso, J. A. S. (1986). A stochastic theory of phase transitions in human hand movement. *Biological Cybernetics*, 53, 247–257.
- Schöner, G., & Kelso, J. A. S. (1988). Dynamic pattern generation in behavioral and neural systems. *Science*, 239, 1513–1520.
- Spencer, R. M. C., Ivry, R. B., Cattaert, D., & Semjen, A. (2005). Bimanual coordination during rhythmic movements in the absence of somatosensory feedback. *Journal of Neurophysiology*, 94, 2901–2910.
- Sternad, D., Turvey, M. T., & Saltzman, E. L. (1999a). Dynamics of 1:2 coordination: Generalizing relative phase to n:m rhythms. *Journal of Motor Behavior*, 31, 207–223.
- Sternad, D., Turvey, M. T., & Saltzman, E. L. (1999b). Dynamics of 1:2 coordination: Sources of symmetry breaking. *Journal of Motor Behavior*, 31, 224–235.
- Summers, J. J., Davis, A. S., & Byblow, W. D. (2002). The acquisition of bimanual coordination is mediated by anisotropic coupling between the hands. *Human Movement Science*, 21, 699–721.
- Summers, J. J., Maeder, S., Hiraga, C. Y., & Alexander, J. R. M. (2008). Coordination dynamics and attentional cost of continuous and discontinuous bimanual circle drawing movements. *Human Movement Science*, 27, 823–837.
- Summers, J. J., Todd, J. A., & Kim, Y. H. (1993). The influence of perceptual and motor factors on bimanual coordination in polyrhythmic tapping task. *Psychological Research*, 55, 107–125.
- Swinnen, S. P. (2002). Intermanual coordination: From behavioral principles to neural-network interactions. *Nature*, 3, 350–361.
- Swinnen, S. P., Dounskaia, N., Verschueren, S., Serrien, D. J., & Daelman, A. (1995). Relative phase destabilization during interlimb coordination: The disruptive role of kinesthetic afferences induced by passive movements. *Experimental Brain Research*, 3, 439–454.
- Swinnen, S. P., Dounskaia, N., Walter, C. B., & Serrien, D. J. (1997). Preferred and induced coordination modes during the acquisition of bimanual movements with a 2:1 frequency ratio. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1087–1110.
- Swinnen, S. P., Lee, T. D., Verschueren, S., Serrien, D. J., & Bogaerts, D. J. (1997). Interlimb coordination: Learning and transfer under different feedback conditions. *Human Movement Science*, 16, 749–785.
- Swinnen, S. P., Verschueren, M. P., Bogaerts, H., Dounskaia, N., Lee, T. D., Stelmach, G. E., & Serrien, D. J. (1998). Age related deficits in motor learning and differences in feedback processing during the production of a bimanual coordination pattern. *Cognitive Neuropsychology*, 15, 439–466.
- Swinnen, S. P., & Wenderoth, N. (2004). Two hands, one brain: Cognitive neuroscience of bimanual skill. *Trends in Cognitive Sciences*, 8, 18–25.
- Temprado, J. J., & Swinnen, S. P. (2005). Dynamics of learning and transfer of muscular and spatial relative phase in bimanual coordination: Evidence for abstract directional codes. *Experimental Brain Research*, 160, 180–188.
- Temprado, J. J., Zanone, P. G., Monno, A., & Laurent, M. (1999). Attentional load associated with performing and stabilizing preferred bimanual patterns. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 1579–1594.
- Treffner, P. J., & Turvey, M. T. (1993). Resonance constraints on rhythmic movement. *Journal of Experimental Psychology: Human Perception and Performance*, 19, 339–363.
- Treffner, P. J., & Turvey, M. T. (1995). Handedness and the asymmetric dynamics of bimanual rhythmic coordination. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 318–333.
- Treffner, P. J., & Turvey, M. T. (1996). Symmetry, broken symmetry and

- handedness in bimanual coordination dynamics. *Experimental Brain Research*, 107, 463–478.
- Tuller, B., & Kelso, J. A. S. (1989). Environmentally-specific patterns of movement coordination in normal and split brain subjects. *Experimental Brain Research*, 75, 306–316.
- Walter, C. B., Corcos, D. M., & Swinnen, S. P. (1998). Component variability during bimanual rhythmic movements: Not all harmonic timing ratios are alike. *Research Quarterly for Exercise and Sport*, 69, 75–81.
- Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005a). Perceptual coupling in rhythmic movement coordination: Stable perception leads to stable action. *Experimental Brain Research*, 164, 517–528.
- Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005b). Human movement coordination implicates relative direction as the information for relative phase. *Experimental Brain Research*, 165, 351–361.
- Wulf, G. (2007). *Attention and motor skill learning*. Champaign, IL: Human Kinetics.
- Wulf, G., Lauterbach, B., & Toole, T. (1999). Learning advantages of an external focus of attention in golf. *Research Quarterly for Exercise and Sport*, 70, 120–126.
- Wulf, G., McConnel, N., Gärtner, M., & Schwarz, A. (2002). Feedback and attentional focus: Enhancing the learning of sport skills through external-focus feedback. *Journal of Motor Behavior*, 34, 171–182.
- Wulf, G., & Su, J. (2007). An external focus of attention enhances golf shot accuracy in beginners and experts. *Research Quarterly for Exercise and Sport*, 78, 384–389.
- Yamanishi, J., Kawato, M., & Suzuki, R. (1980). Two coupled oscillators as a model for the coordinated finger tapping by both hands. *Biological Cybernetics*, 37, 219–225.
- Zaal, F. T. J. M., Bingham, G. P., & Schmidt, R. C. (2000). Visual perception of mean relative phase and phase variability. *Journal of Experimental Psychology: Human Performance and Perception*, 26, 1209–1220.
- Zanone, P. G., & Kelso, J. A. S. (1992). Evolution of behavioral attractors with learning: Nonequilibrium phase-transitions. *Journal of Experimental Psychology: Human Performance and Perception*, 18, 403–421.

Received August 25, 2008

Revision received December 9, 2009

Accepted December 14, 2009 ■